Modelling Seal Energetics.

Alasdair Hind

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Degree of Doctor of Philosophy,
Department of Statistics and Modelling Science,
University of Strathclyde.

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to Sandra.

Forest guffawed, the first time he had laughed since Hobson walked into the office. It was a sight and sound more sinister than his mumbling and snarling.

“Now, Hobson, you think you’ve got me there. You think I don’t know what a thesis is. Well I do. I’ve got a daughter at polytechnic and she’s doing one. Great fat bundle of words about sod all. What’s yours about?”

From The Beiderbecke Affair by Alan Plater.

Publications

Hind, A.T. and Gurney, W.S.C. (1997). The Metabolic cost of swimming in marine homeotherms. *Journal of Experimental Biology, 200*, 531-542.

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Abstract

Fisheries management requires information on the impact of predators such as seals. Estimation of the energy requirements of seal populations remains the best approach. Such estimates are based on the bioenergetics of individuals and it is in this area that this thesis seeks to make a contribution.

The keystone of this work is the development of a model of the metabolic cost of swimming. This combines the hydrodynamic aspects of locomotory cost with the thermal balance of the seal. The resultant model represents a powerful predictive tool for considering the bioenergetics of seals. A second physiological model is developed to predict the thermal balance of a seal in air. The model predicts that a common seal (*Phoca vitulina*) hauled-out in Scotland incurs an energetic cost due to thermoregulation. I provide circumstantial evidence to support this, by considering the thermal constraints on the timing of pupping.

The common seal population of the Moray Firth, Scotland is an ideal case study for a bioenergetic study. Using the detailed physiological models I estimate the seasonal energy requirements of individual seals. The cost of foraging varies little with season and, since foraging is the dominant cost, the daily energy requirements also vary little. The predicted energy requirements are significantly higher than previous predictions for common seals, a direct result of the improved estimate of the foraging cost. The actual intake of the seals varies more with season, but the estimates are robust to assumptions about the structure and condition of the population. Estimates of the consumption of fish species by common seals suggest that they have a significant impact on stocks in the Moray Firth. Improving on the synoptic picture of prey consumption requires a predictive model and I describe a model of the individual foraging behaviour of a common seal.

Contents

Part I

Introduction

Chapter 1

Seals: a modeller's view

Marine mammals have evolved from land based animals to marine ones, spending much of their lives hidden beneath the waves. This has always given them an air of mystery and stimulated our interest and curiosity. The steady increase in the knowledge we have of these creatures adds to our interest as we are given an insight into the adaptations involved in their exploitation of the marine environments. The cetaceans are fully aquatic and, apart from beachings, never return to the land. Seals, sea lions and walrus on the other hand straddle the two environments, moving between land and sea throughout their lives. Some species are tied only to the land as a site for breeding and moulting, while others leave the water on a much more regular basis. Clearly, seals are a fascinating group of organisms and, for many, this is reason enough to try and understand their biology. True seals (family Phocidae), are distinguished from sea lions, fur seals and walrus by the absence of an external ear. Their inability to raise themselves on their fore flippers is another distinguishing feature, leading to an inability to run and their characteristically ungainly movement on land. Ridgway and Harrison's Handbook of Marine Mammals provides a good overview of all aspects of the biology of phocid seals. They ascribe eight genera to the family and these are found in both hemispheres, between the poles and tropics.

Seals occupy a position near the top of the marine food chain and this has provided another motivation for studying their ecology. Man has long exploited the oceans as a food source and there has been an inevitable clash between the interests of two top predators, man and seals. Although man has exploited seals directly as a resource (sealing has declined somewhat in the latter part of this century) it is the competition for diminishing fish stocks that has provided a political motivation for advancing our knowledge of seals. As a very visible predator, seals are perceived by fishermen to consume significant quantities of the fish stocks that are commercially important. Some recent examples of conflict between seal populations and modern commercial fisheries will serve to illustrate some of the issues involved.

Between 1978 and 1988 large migrations of harp seals (*Phoca groenlandica*) southwards into the coastal waters of Finnmark, North Norway, occurred. It has been suggested that the change was a result of the collapse of capelin stocks in the Barents Sea (Haug and Nilssen 1995), the harp seal's traditional winter food source. There was considerable direct interference with the coastal fisheries in the form of net damage and partial consumption of large fish held in nets. There was also an apparent change in the availability of commercial species such as large cod and herring.

Both harp seals and cod feature in the second example; the cod fishery in Eastern Canada. The conflict between the Canadian fishing industry and the harp and grey seal (*Halichoerus grypus*) populations is long standing. A brief summary of the conflict up to 1991 is given by Lavigne (Anon. 1991). He concluded that there was a lack of scientific evidence to support the idea that seal culls would resolve the conflict and suggests that many of the problems are the result of an excessive growth of the commercial fishery. In recent years this region has witnessed a dramatic collapse in the cod fishery, leading to its closure, and the consumption of fish by seals has re-surfaced in the political arena. The collapse of the cod stocks has been paralleled by the continuing increase in the grey seal population, as it recovers from exploitation earlier in the century (Hammill et al. 1995). Fishermen have been quick to lay the blame for the collapse of the fishery on the harp and grey seals and the resultant political pressure led to an increase in the annual seal hunt in Newfoundland. As is always the case the real causes for the dramatic ecological shift are less clear and Hammill et al. (1995) point to the need to consider the impact of other predators such as seabirds.

Conflict between marine mammals and commercial fisheries is not exclusive to phocid seal populations in the northern hemisphere. Wickens (1994) describes the interaction between South African fur seals (*Arctocephalus pusillus pusillus*) and the purse-seine fishery in South Africa. Direct observations made by scientific observers on the fishing vessels were used to categorise the interactions and estimate their frequency. Seals were observed to enter the drawn purse-seine in pursuit of fish. This can result in the escape of significant amounts of fish, interference with the fish pump or the entanglement and landing of the seal. Attempting to place a cost on the interference of seals with commercial fisheries is difficult, but the author suggests that seal interference may result in a loss in the region of 1.6% to 4% of the landed value of the fishery.

Fisheries management is increasingly adopting a multi-species approach with the development of mathematical models representing the biological interactions between fish species (Magnusson 1995). An example of such a model is MSVPA (Multi-Species Virtual Population Analysis), a multi-species model developed for the North Sea under the umbrella of ICES (the International Council for the Exploration of the Sea). It is not appropriate to enter into a detailed discussion of this field and I would refer the interested reader to Stokes (1992) for a useful overview. The relevance to this study lies in recent developments to MSVPA carried out by the Multi-species Assessment Working Group (Anon. 1992). Traditionally the model has focused on five fish species but this has now been extended. At the same time the predation mortality on the fish species by top predators was explicitly included for the first time. Three classes were considered; seabirds, grey seals and other predators. The estimates of the size of the grey seal population of the North Sea and the consumption of fish by individual seals were provided by the Sea Mammal Research Unit (SMRU, St Andrews University, Scotland). The 'other predators' category was considered to comprise mostly cetacean species. The successful incorporation of estimates of predation mortality (inflicted on fish species by predators such as seals) into multi-species fisheries models will clearly depend on the quality of those estimates. In the light of this development of MSVPA a detailed and comprehensive study of seal energetics appears to be most timely.

A desire to assess the impact of seals on fisheries leads to a need for detailed information on their foraging patterns and diet. The difficulty of directly measuring these things in animals that spend much of their time at sea has forced people to adopt indirect methods to produce quantitative estimates of their role in the ecosystem. Mathematical models have provided a means of synthesising the state of knowledge of seal biology and extrapolating it to predictions of their impact on prey species. Review and discussion of these studies is deferred to Chapter 5. The approach requires an understanding of the energetic constraints and requirements of wild seals. It is in this area that this thesis seeks to increase our understanding of these marine predators. It is critical to make a comprehensive evaluation of the energetic cost to the seal of its activities and this lies at the heart of the work described in this thesis.

Detailed physiological models of the energetics of individual seals provide a bridge between fine-scale experimental observation and the broader focus of assessing their role within the ecosystem. In order to illustrate the wealth of experimental information on seals that can be drawn on I review some of the key studies (with respect to energetics) in Chapter 2. These are arranged into six sections based on the different aspects of a seal's energetic requirements; maintenance, thermoregulation, locomotion, growth, reproduction and digestion.

For an organism which is principally aquatic the energetic cost of swimming is an obvious place to start. There have been a number of studies of both the hydrodynamics and metabolic consequences of swimming, but, in Chapter 3, I highlight some previously unexplained features of the observed relationship between metabolic rate and swim speed. Where previously only the hydrodynamic aspects of seal locomotion had been considered, I describe a mechanistic model which tackles both these and the consequences for the seal's thermal biology. This dual approach proves critical in explaining the particular form of the relationship between metabolic rate and swimming speed in seals and other homeothermic marine species.

Having detailed the influence of a seal's aquatic environment on its thermal balance it seemed a natural progression to shift my attention to the thermal balance of a seal in air. Although the metabolic consequences of locomotion no longer apply, a number of new features must be considered. In addition to the convective heat exchange experienced by a seal in water, a seal on land experiences radiative and conductive heat exchange (with the air and ground respectively). Furthermore, if the seal is wet then evaporative cooling will also take place. In Chapter 4 I describe a model of the thermal balance of a seal on land, based on the same underlying principles as the model described in the previous chapter. Unfortunately, experimental data against which to test this model are more limited and only a partial validation is possible. If seals do experience thermoregulatory cost whilst 'hauled-out' on land then some influence of adverse weather on the hauling-out behaviour could be expected. For the common seal (which hauls out regularly throughout the year) the evidence for this influence remains inconclusive. What is apparent is the increased amount of time that female common seals spend hauled out whilst suckling pups (Grellier et al. 1996). Since the mother must meet both her own metabolic costs and those of her pup I suggest that pupping would be timed to coincide with favourable weather conditions and so minimise the energetic cost to the mother. Using the model to predict the combined metabolic cost for a common seal mother and pup (hauled out in Northeast Scotland) I show that the timing of pupping does indeed coincide with the most favourable weather conditions. Within the specific aims of this thesis, the significance of this is in lending support to the model's prediction that common seals in temperate regions experience an energetic cost associated with thermoregulation during haul-out periods.

The models described in Chapters 3 and 4 are applicable to any phocid seal species and indeed (with the appropriate modification) to sea lions, fur seals and walrus. In order to progress from looking at the metabolic processes of seals to a consideration of individual and population energetics I must narrow my focus somewhat. To this end the second half of the thesis relates to the common seal population in an inshore region of the North Sea, the Moray Firth. The common seal is one of two species found in Scottish waters, the other being the larger grey seal. Common seals are widely distributed, occurring along the coasts of both the North Atlantic and North Pacific, and is known by a number of names. In this thesis I shall use the British name of common seal, although in the literature it is more often referred to as the harbour seal. There are a number of reasons for the selection of both the seal species and the particular population. The first attraction of the common seal to a modeller is the extent of knowledge about the species, it has been extensively studied both in the wild and, more particularly, in captivity (see Chapter 2).

Within Scotland a considerable amount is known about the common seal, much of it the result of an extended study (by the University of Aberdeen) of the semi-isolated population in the Moray Firth. In the work described in the second half of the thesis I have made extensive use of the products of this long-term study and the collaboration of the principal scientists has been most beneficial. The other reason for selecting this seal population relates back to the issue of the conflict between seals and fisheries.

The Moray Firth region of the North Sea is one area that sees potential conflict between man and seals. The region is home to a resident, breeding population of common seals. The region also supports an economically important salmon (*Salmo salar*) sport fishery and a coastal net salmon fishery. Rae (1973) found salmon to be much less prevalent in the diet of the common seal (5%) than grey seals (27%), based on the stomach content of seals. This early work is now considered to be severely biased (Pierce et al. 1991) since many of the animals were shot in or near salmon nets. More recent studies of the diet of common seals in the Moray Firth (e.g. Tollit 1996) suggests that salmonids, as a group, represent only 2% of the summer diet (percentage by energy). Even such a low occurrence may represent a significant impact on a fishery in which individual fish are highly valued. In addition to the salmon fishery, the Moray Firth has also been identified as an important overwintering area for sprat and herring (Thompson et al. 1996). Although there is no longer a local fishery, these fish are thought to be part of the wider North Sea stocks. In some years these two species make up tthe entire winter diet of common seals in the Moray Firth (Pierce et al. 1991).

Having formulated and tested models of the metabolic processes of seals in water and in air I am in a position to predict the energy requirements of individual seals under different conditions, the subject of Chapter 6. Radio tracking of common seals in the Moray Firth has given us a picture of the division of time between haul-out periods and offshore foraging trips (e.g. Thompson and Miller 1990). At a finer scale, records of the depth and swim speed of diving common seal males have been obtained by telemetry (Bjørge et al. 1995) and fall into three classes; travelling, foraging and display dives. Combining these with the predictions from the swimming cost model, I am able to estimate the cost of foraging. Using meteorological data for Northeast Scotland I have also estimated the seasonal variation in the cost during haul-out periods, by using the model described in Chapter 4. The next step is to incorporate time budgets for the seals, maintenance costs and details of the reproductive costs, to estimate the seasonal change in the energy requirements of common seals.

From the estimates of the energy requirements of individual seals it is an easy progression to estimating the consumption of prey species described in Chapter 7. Some adjustment is required to allow for the periods of fasting that adult seals undergo in association with breeding. The other requirement is information on the prevalence of different prey species within the diet of the seals. In this, I am particularly fortunate in being able to make use of the wealth of information in Tollit (1996). Tollit has identified seasonal difference in the diet of common seals in the Moray Firth and I am able to turn these into seasonal estimates of the consumption of individual species, having first taken account of seasonal changes in the energy intake of the seal population.

In some winters large numbers of sprat and herring are found in the vicinity of Inverness and coincident with this seals are observed to congregate in this area (Thompson et al. 1996). A change in the diet of the seals is also seen and it becomes dominated by these two fish species, as opposed to a more varied diet in which sandeels are the main species (Tollit and Thompson 1996). The type of energy budget described in Chapter 7 provides a useful estimate of the consumption of prey species. A more predictive model of prey consumption, allowing such prey switching to be represented, requires an understanding of the foraging strategies used by seals. Although there has been a great deal of modelling effort directed at foraging behaviour, there has been no investigation of the foraging strategies of seals. Chapter 8 describes a model of the foraging of an individual common seal. The behaviour of the model is investigated using a simplified version that uses a square arena. The model is then applied to the more complex environment of the Moray Firth.

Finally, Chapter 9 provides an overview of the thesis. The key findings are discussed in their broader context and some suggestions are made for avenues of further investigation.

Chapter 2

The energetics of individuals

In this chapter I will briefly review current knowledge of the energetics of seals. The work is discussed under six sections, representing the energetic costs of an individual seal; maintenance, thermoregulation, locomotion, growth, reproduction and digestive costs. Although the studies described are predominantly experimental, some previous modelling studies are included. I shall defer discussion of past studies of the energetics of seal populations to a later chapter (Chapter 5).

2.1 Maintenance

Basal metabolism is the metabolic cost of staying alive for a mammal. It is measured as the metabolic rate of a quiescent, post-absorptive animal in thermoneutral conditions. Animals which are gestating or growing will have a resting metabolism higher than basal. A relationship between basal metabolism and size (body weight) for mammals was found by Kleiber (1947), sometimes referred to as the 'mouse to elephant curve' ($BMR(\mathrm{W}) = 3.39W^{0.75}$). This has become the standard yardstick in discussions of basal metabolism in mammals.

Early studies of seals concluded that they had an elevated basal metabolism (Iverson and Krog 1973; Miller and Irving 1975; Miller et al. 1976), up to 2.6 times 'Kleiber'. These measurements were not made under conditions that met Kleiber's criteria, in particular juvenile animals were used. More recent studies have confirmed that adult seals have basal metabolic rates conforming to Kleiber's relationship (Gallivan and Ronald 1979; Lavigne et al. 1986; Folkow and Blix 1987). Consistent with the additional energy cost of growth (over and above basal costs) the resting metabolic rate of juveniles seals is between 1.5 and 2.6 times 'Kleiber' (Boily and Lavigne 1996; Hansen et al. 1995; Øritsland and Ronald 1978; Nordøy et al. 1990; Worthy 1987).

2.2 Thermoregulation

Over a range of temperatures a homeothermic animal's resting metabolism will produce sufficient heat to balance the loss of heat to the environment, without causing overheating. This temperature range is referred to as the animal's thermoneutral zone, within which its resting metabolic rate is independent of environmental temperature. The bounds of the thermoneutral zone are known as the lower and upper critical temperatures (T_{XL} and T_{XU}, respectively).

At temperatures below T_{XL} the animal must raise its metabolic rate in order to balance heat loss and maintain its core temperature, there is a limit to which mammals can do this. Alternatively it can alter its behaviour in order to alter its thermal environment, such as moving between water and air. Above T_{XU} an inactive animal is gaining heat from internal generation and external heating faster than it can be lost, this leads to an increase in metabolic rate and core temperature. Sleep may lower heat production by depressing the metabolic rate, but beyond this limited physiological response the animal must alter its circumstances or suffer potentially fatal hyperthermia.

Seals occupy two very different thermal environments; water and air. Water is highly conductive and with a high specific heat capacity makes a good heat sink. Air is much less conductive and has the additional complexities of radiative heat exchange, evaporative heat-loss and wind-cooling. Whilst hauled-out, seals are in contact with a third thermal environment, sand, rock or ice.

The balance of heat between a seal's heat generating core and the surrounding medium is affected by its anatomy and physiology. Phocid seals deposit fat (blubber) in a subcutaneous layer which acts as insulation. This layer is by-passed by blood vessels over which the seal can exert control to vary heat flow. This is a key adaptation to life in cold conditions (Davydov and Makarova 1964), where the seal is able to restrict peripheral blood flow to maximise its insulation. In warmer conditions increasing peripheral blood flow increases the transport of heat to the seal's skin. The skin is covered by hairs which, although not as dense as the fur of other mammals, will affect heat exchange. An important physiological aspect of thermoregulation is the inability of seals to sweat (Matsuura and Whittow 1974) and thereby increase evaporative cooling. Evaporative cooling does however occur through the respiratory tract. Most aspects of seal thermoregulation have been subject to empirical study, studies pre 1986 were reviewed by Whittow (1987).

The thermoneutral range of phocids in water has been measured for common and harp seals. The lower critical temperature has been found to vary greatly between individuals and species, and seasonally (Hart and Irving 1959). A number of studies of juvenile common seals measured T_{XL}, recording values in the range 10-20 C (Miller and Irving 1975; Miller et al. 1976; Iverson and Krog 1973; Irving and Hart 1957; Hart and Irving 1959). For juvenile harp seals Iverson and Krog (1973) recorded a T_{XL} of 7 C, in contrast to an earlier study which failed to identify T_{XL} within the range 0-20 C (Irving and Hart 1957). It should be noted that the animals studied by Iverson and Krog (1973) were undergoing starvation which affects the metabolic rate (Markussen et al. 1992). Gallivan and Ronald (1979) observed the metabolic rate of freely diving adult harp seals and recorded no systematic variation with water temperature down to 1.8 C. The upper critical temperature is much less studied. For juvenile common seals there are two measurements of 25 and 31 C (Miller et al. 1976). Gallivan and Ronald (1979) did not observe an upper critical temperature for adult harp seals in water up to 28.2 C.

Studies of the thermoneutral range of phocids in air have been conducted on juvenile common and grey seals. Irving and Hart (1957) recorded no significant change in metabolic rate for a juvenile common seal at temperatures down to -10 C and estimated T_{XL} at -30 C, however in a subsequent study (Hart and Irving 1959) they found T_{XL} to be 2 C. Miller and Irving (1975) found newborn common seals to have a T_{XL} of 3 C, dropping to -5 C in juvenile animals. They found no increase in metabolic rate at high air temperatures, but core temperatures did increase when the air temperature exceeded 25 C. Øritsland and Ronald (1978) found no change in the metabolic rate of harp seal pups exposed to variable natural weather conditions. They did record an increase in body temperature at elevated air temperatures and high solar irradiences. A recent study (Hansen et al. 1995) of the metabolism of juvenile common seals in air found them to be thermoneutral in the range -2.3 C to 25.1 C (T_{XL} and T_{XU}, respectively). The animals metabolic rates increased with changing temperature (excess cooling and excess heating) outside this thermoneutral zone. They found that the core temperatures increased from a mean of 38.2 C, at 27.5 C, to 40.2 C, at an air temperature of 32.5 C. A comparable study on juvenile grey seals (Boily and Lavigne 1996) found no significant change in metabolic rate over a range of air temperature, -18 to 35 C, for two animals. A third seal showed an increased metabolic rate at -18 C. All three showed signs of elevated core temperatures above 30 C. On average the resting metabolic rate of the seals was 1.6 times that predicted by Kleiber's relationship. In contrast Folkow and Blix (1987) report a T_{XL} value for juvenile grey seals of -11 C, the difference between the studies may be due to lower resting metabolic rates (1.1 times the Kleiber value) in the second study. Both the flippers and the trunk were found to be involved with temperature regulation.

A number of seals give birth on ice which has led to an interest in the thermal biology of seals on ice, in particular pups. Harp seal pups are born with a thick coat of white fur which acts as an insulating layer against convective heat loss. Øritsland et al. (1978) found the radiative temperatures of adult harp seals (short hairs) to be more sensitive to changes in wind speed than those of "whitecoat" pups. The colour of fur also plays a roll in thermoregulation, the high reflectivity of the white hairs enhances the heat trapping ability of the fur (Øritsland 1971; Øritsland and Ronald 1973).

Since phocid seals lack sweat glands (Tarasoff and Fisher 1970) they are only able to loose heat by evaporation through their respiratory system, once their pelage has dried. Folkow and Blix (1987) measured nasal heat loss in young grey seals and found it to account for between 6% and 13% of metabolic heat production, they attribute these low values to a low respiratory minute volume. Gallivan and Ronald (1979) calculated evaporative heat loss in freely diving adult harp seals and found it to account for 1.8% of metabolic production, on average. Even in the California sea lion (*Zalophus californianus*), which is able to sweat on the bare skin of its flippers, heat loss by evaporation is estimated to account for only 20% of heat production (Matsuura and Whittow 1974).

Heat loss by conduction to dry and wet sand has been measured for a common seal in air at 30 C (Ohata and Whittow 1974). The heat loss to dry sand was estimated as 18% of production and to wet sand as 26%. This implies that under conditions of heat stress there is some benefit to lying on wet sand. Measurement of the rate of heat loss to sand in elephant seal pups (McGinnis 1975) indicate it to be highest when the rest of the body is experiencing a net heat gain and negligable when the converse is true. This may indicate the reduction of peripheral blood flow in an animal experiencing body cooling.

Behavioural responses of seals to heat stress have also been studied, in particular the hauling out patterns of common seals in relation to heat stress in temperate latitudes (Watts 1992). The environmental conditions were recorded during observation of the number of seals hauled out and incorporated into a model of the net heat flux experienced by the seals. For positives fluxes (seal gaining heat), a negative correlation was found between flux and the number hauled-out . Haul-out numbers remained constant for negative flux values. This implies that even in temperate latitudes common seals are subject to heat stress in air and avoid hauling-out under these conditions, or endeavour to maintain a wet pelage (the number of dry seals decreased and wet increased during conditions of positive flux). Whittow (1987) also suggests that hauled-out common seals return to the water if they become heat stressed. The benefit of “sand flipping” to enhance cooling has been demonstrated in an elephant seal (McGinnis 1975). This behaviour is not reported in other phocid seals, although there is anecdotal evidence that common seals may use mud rolling to achieve a similar result (McGinnis 1975).

In addition to empirical studies of thermoregulation there has also been interest in constructing mechanistic models of seal thermoregulation; either as an aid to interpreting empirical data, or as a means of examining the thermoregulatory constraints on seals.

Work falling into the first category includes the use of flux values by Watts (1992), described above. The flux included radiative heat gain from shortwave solar energy, longwave atmospheric energy and the loss of heat by longwave emittance. Also included was convective heat loss as a function of wind speed. Whole animal heat balance was not modelled and the skin temperature was taken from an empirical relationship. Also neglected were loss by evaporation and conduction to the substrate.

Gallivan and Ronald (1979) used a model of whole animal heat balance in their interpretation of data for freely diving harp seals. Heat generation by metabolism and loss by respiratory evaporation and convective exchange with the water were included. The expression used for convective heat loss was for free convection, despite the animals being able to move, and the authors did not calculate any tests to support this assumption.

A model complementary to an empirical study of thermal balance in whitecoat harp seal pups was described by Øritsland and Ronald (1978). The model splits the seal into two linked components, the trunk and flippers. The heat transfer properties of the fur were taken to be a function of the wind speed squared. The expression used for the effect of solar radiation was not given. The core temperature was calculated from the body heat content, assuming a specific heat capacity of 3100 $\mathrm{Jkg^{-1}C^{-1}}$. The model predicted that a 'lean' pup with metabolic rate equal to that predicted by Kleiber's relationship has a T_{XL} value of -1 C. For a pup with a 10 cm blubber layer and a metabolism elevated by a factor of 1.5 the predicted T_{XL} was -59 C.

A model of the thermal balance of California sea lions, in air and water, was described by Leucke et al. (1975). The animal was divided into four components; the head, trunk, fore flippers and hind flippers. Each component was treated as a cylinder consisting of four layers; the core, muscle, blubber and skin, the sea lion's hair was not included. The model had a separate, variable core temperature for each body component. The circulatory system was explicitly included and control of this provided the mechanism by which thermoregulation was achieved. The model predicted a lower critical temperature (T_{XL}) in air between 5 and 10 C and an upper critical temperature (T_{XU}) between 20 and 25 C. For a sea lion swimming at 2.6 $\mathrm{ms^{-1}}$ T_{XL} was predicted to be between 5 and 10 C, this decreased to less than 0 C if the animal swims at 3.2 $\mathrm{ms^{-1}}$. At this faster speed the sea lion was predicted to have a T_{XU} in water of 20 C. The authors assumed that vaso-constriction occurs as part of the animals dive response, severely reducing its ability to loose heat and potentially leading to elevated core temperatures.

A general model of thermoregulation for marine mammals, principally whales, was described by Hokkanen (1990). The steady-state heat transfer across the blubber layer was modelled, with heat generated in the muscle and lost from the skin. The body and flippers were treated separately, the body as a cylinder and the flippers as flat plates. The animals blood flow was explicitly included and blood flow rates were calculated. The minimum metabolic rate of all animals was assumed to be 1.5 times that predicted by Kleiber (1947). The fitting parameters for the model were blubber thickness and blood flow rate, the skin temperature was assumed to approximate water temperature at all times.

Four different heat-flow models, for an animal immersed in water, were evaluated by Watts et al. (1993) in an attempt to determine the most appropriate. The models being; a flat plate model, a cylindrical model, a modified cylinder model and an equivalent thickness model (the latter two were originally presented by Ryg et al. 1988). The authors applied the models to data for whales and common seals. For the common seals, basal metabolism was calculated from Kleiber's relationship and the metabolic rate of immersed animals elevated by a factor of 2.5. The models were all sensitive to changes in the seals blubber thickness and metabolic rate. The lower critical temperatures predicted by the models were compared with observed values for a juvenile common seal (T_{XL} ranged from 7-11, Hansen, S. unpublished data). The cylinder model gave slightly closer predictions than the flat plate model, but consistently underestimated T_{XL}. In contrast, the flat plate model consistently overestimated T_{XL}. The other two models performed poorly by comparison, both consistently over-estimating T_{XL}.

In order to meet the thermal requirements of the skin during moult, marine mammals must maintain skin temperatures above 17 C (Feltz and Fay 1966). To estimate the thermal constraints this entails for animals in water, Boily (1995) constructed a model of surface heat flux, based on a flat plate geometry. The conceptual advantages of a flat plate versus a cylinder model were discussed. The model differentiated between free and forced convection, with the skin temperature as an unknown variable. Assuming that heat production is twice the basal level, the rate of heat production per unit area was taken to be 180 Wm^{-2} for all animals. The author justified this on the premis that surface area and metabolic rate increase at a similar rate with body size. The model predicted that both a common seal and southern elephant seal (*Mirounga leonina*) are capable of tolerating the heat flux associated with moulting only in water of a warmth they are unlikely to encounter in the wild. Even in such warm water the energetic cost of maintaining an elevated skin temperature would be high. The model also indicated an energetic advantage to moulting beluga whales (*Delphinapterus leucas*) of moving to warmer estuarine waters.

2.3 Locomotion

The primary means of locomotion in seals is swimming, for which they have become highly adapted. Their limbs have evolved into flippers and their body has become 'torpedo' shaped. Observing a seal swimming, one cannot fail to be impressed by its grace and apparent ease. Propulsion is provided by the hind flippers, which perform alternate strokes. The fore flippers are used in steering or are flattened to the side of the body. In contrast seals moving on land are almost comical, being obliged to 'hump' along like over-animated caterpillars. Given that seals spend the majority of their time in water and remain close to the water when hauled-out I will not dwell on terrestrial movement, concentrating on aquatic locomotion.

The hydrodynamics and swimming abilities of seals have received considerable empirical attention. Williams and Kooyman (1985) studied the performance and hydrodynamics of common seals. They determined the maximum swimming speed from film of seals swimming prior to jumping at a target. For an adult seal the maximum velocity attained was 4.9 ms^{-1}. The drag of seals was measured by towing the animals around a circular tank at different speeds and also from film of gliding seals. They found the drag coefficient of towed seals to be greater than that calculated from glide observations. The authors attributed this to the body configuration the seals were obliged to take during tow experiments, in order to follow the circular path. A marked increase in drag was observed in tows made at the surface, as opposed to a depth of 1 m. Observation of bioluminescence around a swimming seal indicated that boundary layer flow was turbulent. Fish et al. (1988) filmed harp and ringed seals (*Phoca hispida*) swimming in a flume. They found that the frequency of flipper stroke increased linearly with swimming velocity. Consideration of the kinematics of flipper motion led them to conclude that seal swimming most closely resembles that of thunniform swimmers, which include scombrid fish and cetaceans. Calculations of thrust characteristics, based on unsteady wing theory, yielded propeller efficiency estimates between 0.8 and 0.88 and there was no correlation with swimming speed. Calculated thrust power increased curvilinearly with swimming speed.

There have been a number of experimental studies of the energetic cost of locomotion in seals. These have made direct measurements of metabolism made on seals swimming in either flumes (Davis et al. 1985; Feldkamp 1987; Thompson et al. 1993; Fedak 1986) or circular tanks (Craig and Påsche 1980; Markussen et al. 1992).

Davis et al. (1985) used indirect calorimetry to measure the metabolic rates of an adult and a juvenile common seal swimming (separately) in a flume. They found that metabolic rate increased over the range 0.5 to 1.4 ms^{-1}. They also recorded the resting metabolic rate of both animals. Using a similar approach Williams et al. (1991) measured the metabolic rate of juvenile common seals in a flume. In order to extend the range of speed beyond the flumes maximum (1.4 ms^{-1}), drag cups were attached to the animals. Experiments were done to measure the drag of the animals with and without drag cups, by towing them round a tank at a known speed. The relationships for drag with and without cups were used to calculate the effective swimming speed of animals with cups swimming in the flume. Pooling their data they observed an exponential increase over the range 0.5 to 3.5 ms^{-1}. Indirect calorimetry has also been used to measure the metabolic rates of grey seals swimming in a flume (Fedak 1986) and data are presented by Thompson et al. (1993). For both animals (a 270 kg male and a 81 kg female) the metabolic rate increased exponentially over the range 0 to 1.6 ms^{-1}.

The cost of swimming for a sea lion was investigated by Feldkamp (1987). The metabolic rate of California sea lions swimming in a flume was measured using indirect calorimetry. Following the same approach as Williams et al. (1991) drag cups were attached to the animals to simulate speeds greater than the flumes maximum (1.3 ms^{-1}). Oxygen consumption was found to rise exponentially with swimming speed.

Both Craig and Påsche (1980) and Markussen et al. (1992) measured the metabolic rate of common seals free swimming in circular tanks. Based on the observed number of laps and the circumference of the tanks they estimated the swimming speed of the seals. Both studies found an increase in oxygen consumption with increasing swimming speed.

2.4 Growth

The resting metabolism of common seals has been found to be greater for juveniles than for adults (1.5 to 2.6 times that predicted by Kleiber's relationship), see section 2.1. Lavigne et al. (1986) found that twice 'Kleiber' was a good predictor of the resting metabolic rate of juveniles. The elevation of resting metabolic rate is consistent with the cost of growth experienced by juvenile animals.

The actual growth rate of seals has been studied in animals in captivity. Worthy (1987) monitored the growth rate and metabolism of young harp and grey seals for the period after the onset of feeding (which is preceded by the postweening fast). He recorded daily growth rates in the range 0.03 to 0.32 kg d^{-1}, but noted preferential growth of the body core. The animals metabolic rates were observed to increase (to levels consistent with other studies) concurrent with the onset of feeding and growth. The author concludes that the elevation of metabolic rate was associated with the cost of growth.

The growth rate of seals in the wild have been estimated from data for length and mass as a function of age (e.g. Innes et al. 1981). McLaren (1993) provides an extensive review of such datasets for most pinniped species. Included are common seal populations in British Columbia, Alaska, Nova Scotia, Norway and Denmark. For the common seal population in the Moray Firth, Scotland, Corpe (1996) found the adults to be smaller than the other common seal populations. Growth in the first year was linear, followed by a reduction in growth rate with age. The size/age relationship was fitted with both von Bertalanfy and Gompertz growth models.

2.5 Reproduction

During foetal development and the post-natal lactation period a seal pup acquires its energy exclusively from its mother, common seal pups often show a decrease in mass after weaning (Markussen et al. 1989). It has therefore been the practice in assessing energetic costs to credit the pups cost to the mother during this period. Information is clearly necessary on various aspects, such as neonate size, pup growth rate, size at weening, rate of milk production, energy density of milk and length of lactation. The first three factors have been considered to be a function of maternal size, W_{mt} (kg), (Kovacs and Lavigne 1992). Based on data from the literature they present the following regression relationships for phocids as a group; litter mass (kg) $= 0.123W_{mt}$, pup growth (kg.d^{-1}) $= 3.46 \times 10^{-3}{W_{mt}}^{1.18}$ and weaning mass (kg) $= 0.437{W_{mt}}^{0.91}$. Iverson et al. (1993) also found a positive, but linear, relationship for grey seal pup growth (kg.d^{-1}) as a function of initial maternal mass. Stewart (1986) reports no significant relationship between harp seal neonate mass and maternal age (of which maternal mass may be a function) and concludes that maternal investment is constant with maternal age.

Bowen et al. (1992) give estimates of the maternal energy investment over 80% of lactation for a number of phocids (expressed as a function of metabolic mass, $W^{0.75}$, at parturition). For harp, grey and common seals the values are very similar and are equivalent to a maternal cost of lactation of 32.4, 31.5 and 30.3 MJ.kg$^{-0.75}$ respectively. The maternal cost of lactation for hooded seals (*Cystophora cristata*) is much lower, 17 MJ.kg$^{-0.75}$, possibly due to their extremely short lactation period. Härkönen and Heide-Jørgensen (1991) report a value of 544,000 KJ for the cost during lactation for a common seal female, based on mass loss. Bowen et al. (1992) report the energy content of the common seal foetus to be 93,000 KJ and the energy loss by mothers during lactation to be 714,000 KJ, combining these gives a cost over the 18 day lactation period of 807,000 KJ for common seal females. It should be noted that both estimates of the cost to the female are based on mass loss and therefore include the mothers maintenance costs.

2.6 Digestion and excretion

A significant proportion of energy ingested in a seals food is lost in the animals faeces and urine. Keiver et al. (1984) measured the faecal and urinary losses of grey seals and report a mean of 17% of the energy content of the food. This implies a digestive efficiency of 83% . The digestive efficiency of juvenile harp seals has also been measured (Ronald et al. 1984) and was found to range between 86% and 89%.

Of the remaining ingested energy in the food a further proportion is liberated as the heat increment of feeding (or specific dynamic action, SDA). There has been little effort directed at measuring this in seals, but Gallivan and Ronald (1981) have recorded a value of 17% for harp seals.

Part II

Metabolic Processes

Chapter 3

Metabolic cost of swimming.

3.1 Introduction

For an aquatic animal such as a seal the metabolic processes involved in swimming are an obvious starting point for an investigation of their energetics. The past ten years have seen considerable efforts to measure the energetic cost of locomotion in pinnipeds (a collective term for seals, sea lions, fur seals and walrus). There have been direct measurements of metabolism made on seals and sea lions swimming in flumes (Davis et al. 1985; Feldkamp 1987; Thompson et al. 1993; Fedak 1986) and in tanks of known circumference (Craig and Påsche 1980; Markussen et al. 1992).

The starting point for any mechanistic model of locomotion cost is a description of the hydrodynamic drag which the animal experiences. The drag force acting on an object moving in a fluid scales with velocity (V) squared (Hoerner 1957). The rate at which work must be done to overcome this drag force, must therefore scale with velocity to the power 3. The metabolic cost of swimming (M_L) is the mechanical power required to propel the animal divided by the aerobic efficiency. Assuming that the aerobic efficiency is independent of velocity implies;

$$M_L(V) \propto V^3 \tag{3.1}$$

Previous workers (Davis et al. 1985) have noted that measurements of the velocity dependence of total metabolic rate in common seals do not conform to this expected pattern. It has been hypothesised that this stems from velocity dependence of either the drag coefficient or the animals propulsive efficiency (Feldkamp 1987).

Later in this chapter I analyse several sets of direct drag-force measurements for common seals and sea lions (Williams and Kooyman 1985; Feldkamp 1987) and show that these measurements are consistent with the view that drag scales with V^2. Under the assumption that mechanical propulsion is the only velocity dependent metabolic cost, the slower than expected rise in overall metabolic rate with speed would imply that propulsive efficiency rises with workload.

As I discuss in detail below, careful examination of data for the total metabolic rates of several swimming pinnipeds reveals a further interesting anomaly. If one fits all the data except that obtained at zero velocity and then compares the intercept of this fitted curve with the actual value observed at rest, a significant discrepancy is often observed, figure 3.1.

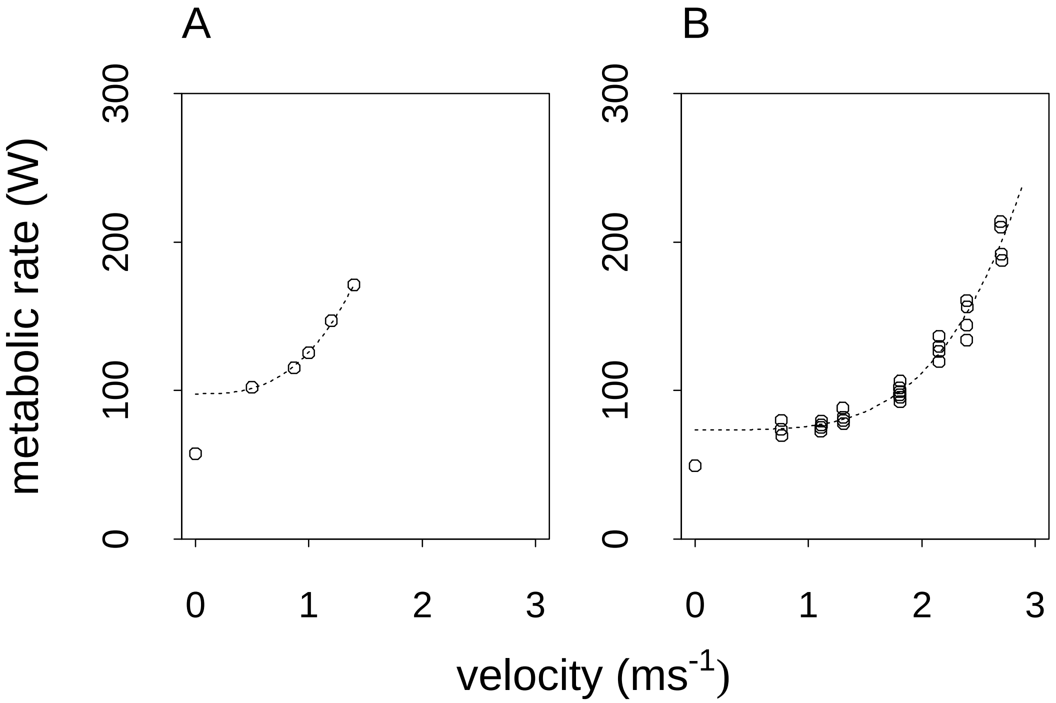

Figure 3.1: Observed metabolic rates of swimming pinnipeds from a variety of sources. A: mean values, ± S.D., for a 33 kg common seal (Davis *et al.* , 1985). B: measured values for a 23 kg California sea lion (Feldkamp, 1987). The broken lines represent best fit curves for data recorded at velocities greater than zero, extrapolated to zero.

In general, the observed value is lower than that extrapolated from the remaining data. Since the mechanical cost of locomotion at very low velocity is small compared to the basal metabolic rate, such an anomaly is clearly not explicable on the basis of a velocity dependent propulsive efficiency.

In this chapter I construct an integrated model of locomotion and thermoregulation which provides an explanation for both key features of the observed velocity dependence of total metabolic rate. Free convection is the dominant mechanism by which heat is transferred across the skin/water boundary when the animal is at rest. For a moving animal, even one swimming relatively slowly, the dominant boundary layer heat transfer mechanism is forced convection, implying that the heat transfer rate across the skin/water boundary will increase with velocity. When the animal increases its swimming velocity two countervailing effects take place; the increased flow of waste heat from muscular activity heats the body core, while the increased 'wind-chill' effect cools it. If the rise in waste heat generation is greater than the rise in cooling then the animal must arrange to dump the waste heat, but if the reverse is true then it must expend extra energy (and hence raise its overall metabolic rate) to maintain its core temperature.

I argue that a mechanistic model of locomotion costs must take explicit account of the thermoregulatory status of the animal. Hence, if M_T is the metabolic cost of maintaining a constant body core temperature, and M_B is the metabolic cost of all other activities then the total metabolic rate (M) is given by

$$M = M_B + M_T(V) + M_L(V). \tag{3.2}$$

In the rest of this chapter, I show that this model is able to account for the apparent anomalies in a group of total metabolic rate measurements for seals and sea lions. I then demonstrate that it is also consistent with total metabolic rate data for both penguins and whales. In order to evaluate the potential of the model as a predictor of metabolic costs, I also determine the quality of fit to a test data set, using parameters wholly derived from literature sources.

3.2 The metabolic cost of propulsion

In order to maintain a constant swimming speed an animal must exert a propulsive force which exactly balances the drag force resulting from its movement. The magnitude of this drag force depends on the animal's size, its shape, the physical properties of the water, and the swimming speed. The drag force (D) acting on a passive body of length L and surface area S, moving at speed V through a medium of density ρ can be written

$$D = \frac{1}{2}\rho S C_D V^2. \tag{3.3}$$

The drag coefficient, C_D, is a function of the object's size, shape and the flow characteristics. If the boundary layer flow is laminar, C_D depends significantly on velocity, while if it is turbulent this dependence is much weaker (Hoerner 1957). The Reynolds number ($Re \equiv LV/\nu$) for a seal swimming faster than 0.5 ms^{-1} is greater than 5×10^5, which suggests a turbulent boundary layer. Visualisation experiments on swimming common seals support this (Williams and Kooyman 1985). The drag acting on seals and sea lions passively towed in water has been measured by Williams and Kooyman (1985) and Feldkamp (1987). Fitting these data with a general allometric relationship produces a best-fit exponent of velocity of 2, for three out of the four individuals examined. I, therefore, make the simplifying assumption that C_D is constant over the range of speeds with which we are concerned. The drag data are shown in Figure 3.2 along with re-fitted regression relationships (having an exponent of velocity of 2).

I now assume that the drag force acting on an actively swimming animal scales with velocity in the same way as that for one being passively towed, so that the

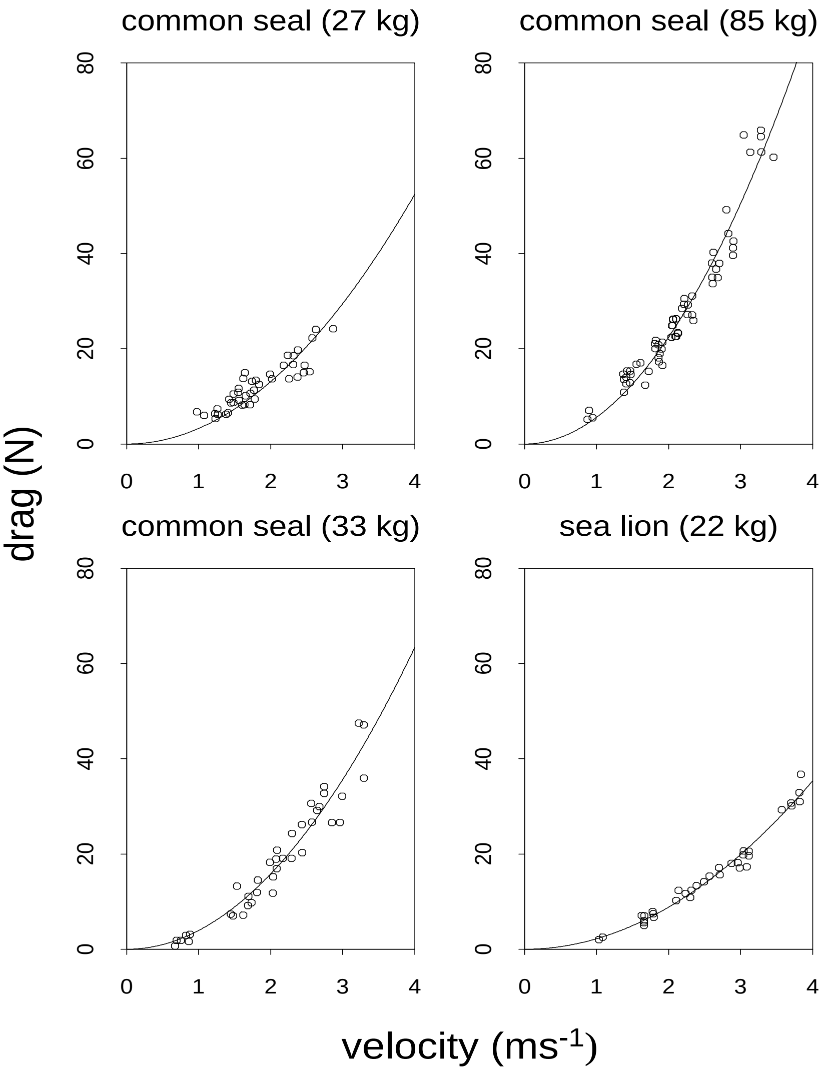

Figure 3.2: Drag data and fitted relationships for three common seals (Williams and Kooyman 1985) and a sea lion (Feldkamp 1987). The weight of the seals is given as an indicator of size.

rate of delivery of mechanical work by a swimming animal is

$$W = \frac{\lambda}{2}\rho S C_D V^3 \tag{3.4}$$

where the constant λ is the ratio of the drag of an active swimmer to that of a passive object moving at the same speed.

The cost to the seal of generating this mechanical work depends both on the efficiency with which muscular movements are translated into forward thrust (the propeller efficiency, ε_P) and the efficiency with which chemical energy is transformed into muscular work (the aerobic efficiency, ε_A). Thrust calculations for swimming seals show no systematic variation of ε_P with velocity (Fish et al. 1988) and I therefore take it to be constant. Experimental work on isolated mammalian muscle tissue suggests that the aerobic efficiency varies with work rate (Gibbs and Gibson 1972). The metabolic cost of the mechanical effort required to propel an animal at speed V is thus

$$M_L = \frac{\lambda}{\varepsilon_A(V)\varepsilon_P}\frac{\rho S C_D V^3}{2}. \tag{3.5}$$

3.3 The metabolic cost of thermoregulation

I regard a seal as consisting of a core at temperature T_C, surrounded by a (relatively) thin layer of blubber. All energy expended on processes internal to the animal will ultimately be realised as body heat. I assume that this heat generation occurs in the animal's core. The proportion of the energy expenditure on locomotion (M_L) which does work external to the animal is ε_A and so the fraction $(1 - \varepsilon_A)$ is realised as internal heat. If the metabolic expenditure on thermoregulation is M_T, then the total rate of internal heat generation for an animal swimming at speed V is,

$$Q_C = Q_{CM}(V) + M_T. \tag{3.6}$$

The composite quantity

$$Q_{CM} \equiv M_B + (1 - \varepsilon_A)M_L, \tag{3.7}$$

represents the minimum heat generation rate for such an animal.

I now assume that the animal is in a state of thermal equilibrium with its environment, so that the rate of internal heat generation is exactly matched by the rate at which heat is lost across the boundary layer separating the skin (i.e the outer surface of the blubber) and the main body of water. The details of the thermal conductivity of this boundary layer are highly complex and will be discussed in detail below. For the present I recognise that the rate of heat loss per unit area (q_S) must be a function of the skin temperature (T_S), the water temperature (T_W) and the swimming velocity V. Hence, for an animal of surface area S, I can write

$$q_S(T_S, T_W, V) = \frac{Q_C}{S}. \tag{3.8}$$

For a fixed value of Q_C, this equation determines the skin temperature needed to ensure an appropriate rate of heat loss across the boundary layer. For future convenience I write the solution of equation 3.8 as $T_{SE}(T_W, V)$.

Heat generated in the core of the animal reaches the skin surface by being transported through the blubber layer. As an approximation, I ignore the inhomogeneous distribution of blood-vessels over the animal's surface, and simply regard the blubber as a homogeneous layer with heat transfer coefficient h_C. If the core and skin temperatures are T_C and T_S respectively, then (at equilibrium) I know that

$$Q_C = Sh_C(T_C - T_S). \tag{3.9}$$

I regard the purpose of the thermoregulatory system as being to maintain the animal in thermal equilibrium with a fixed core temperature. In the first instance the animal will try to do this without incurring additional metabolic cost (i.e. with $M_T = 0$), by adjusting the heat transfer coefficient of its blubber to

$$h_C = h_{CE} \equiv \frac{Q_{CM}}{S\,(T_C - T_{SE})}. \tag{3.10}$$

In order to change the "effective" heat transfer coefficient of the blubber layer, the animal must alter the blood flow to the skin and extremities. This places both an upper and a lower limit (h_{CU} and h_{CL} respectively) on the range of possible values. If the value defined by equation 3.10 is above h_{CU}, then thermal equilibrium is not achievable, the core temperature rises and (unless some behavioural modification intervenes) heat stroke must ensue. If h_{CE} is in the practicable range, then thermal equilibrium is achievable without added expenditure.

Where $h_{CE} < h_{CL}$, thermal equilibrium can only be maintained by additional metabolic expenditure. If I assume that, in this regime, the animal sets the heat transfer coefficient of its blubber to its lowest practicable value (h_{CL}), then the skin temperature (T_{SL}) is the solution of

$$h_{CL}(T_C - T_{SL}) = q_S \tag{3.11}$$

and the total metabolic expenditure needed to maintain thermal equilibrium is

$$Q_{CR} = Sh_{CL}(T_C - T_{SL}) \equiv S\frac{k_B}{d_B}(T_C - T_{SL}) \tag{3.12}$$

where d_B represents the physical thickness of the blubber layer, and k_B represents the thermal conductivity of blood-free blubber.

The final statement of my thermoregulation sub-model is

$$M_T(T_W, V) = \begin{cases} 0 & h_{CE} > h_{CL} \\ \\ Q_{CR} - M_B - (1 - \varepsilon_A)M_L(V) & \text{otherwise.} \end{cases} \tag{3.13}$$

3.4 Surface heat loss

I now consider the transfer of heat across the boundary layer between the skin and the surrounding water. The relatively complex geometry of the external surface of the animal is the source of great potential complexity in the calculation of the boundary layer heat flux q_S. Previous workers (e.g. Boily 1995) have made successful calculations of heat loss from marine mammals under the assumption that local heat transfer rates are equal to those for a flat plate. I shall follow the same strategy.

A second source of potential complexity, which is less easy to avoid, is the fact that the skin surface of pinnipeds is covered, albeit relatively sparsely, with hair. While this covering provides little direct insulation for an animal immersed in water, it may be expected to disrupt the formation of convection currents and so reduce the rate of free convective heat loss from an animal which is stationary, or moving very slowly.

There are two processes by which heat can be transferred from a solid object to the surrounding fluid. Free convection depends on the formation of local circulation driven by the temperature difference across the boundary layer and is thus easily disrupted by advective flows along the solid surface. By contrast, forced convection is driven by the advective flow parallel to the heated surface. It is, therefore, reasonable to expect that free convection will be the dominant heat transfer mechanism when the animal is stationary, while a rapidly moving animal will lose heat predominantly by forced convection. The detail of the transition between these two regimes is controversial and not well understood. Because the data sets against which I shall test the model have few if any points at very low velocities, I can safely assume that heat transfer takes place by free convection at zero velocity and by forced convection whenever the velocity is finite.

Free convection from a hairy surface has been considered by Lage and Bejan (1991) and Bejan (1990) who applied a model developed by Cheng and Minkowyz (1977) describing free convection across a solid/fluid boundary occupied by a homogeneous porous medium. They found that the heat flux into a body of fluid at temperature T_W, generated by free convection from a hair-covered surface at temperature T_S is given by

$$q_S = \theta(T_S - T_W)^{3/2}. \tag{3.14}$$

The scaling coefficient (θ) depends inversely on the length of the seal (L) and also on the effective height of the seal (L_H). The latter is calculated as the short side of a rectangular surface that corresponds to half the animal's surface area (S);

$$L_H = \frac{S}{2L}. \tag{3.15}$$

The coefficient θ also depends on the physical properties of water and the properties and configuration of the hair layer;

$$\theta = 0.888 \frac{k}{L_h^{1/2}} \left[\frac{Kg\beta}{\alpha\nu}\right]^{1/2} \frac{1}{L}. \tag{3.16}$$

The coefficient of thermal expansion of the water (β) and the kinematic viscosity of the water (ν) are functions of water temperature. The acceleration due to gravity (g) was taken as 9.812 ms^{-1}. The terms k, K and α are the conductivity, permeability and thermal diffusivity of the porous boundary layer, respectively. The thermal diffusivity is dependant on the thermal conductivity (k), the density (ρ) and the specific heat capacity (c_p);

$$\alpha = \frac{k}{\rho c_p}. \tag{3.17}$$

An expression for the permeability of a hair covered surface was taken from Lage and Bejan (1991);

$$K = \frac{\phi^3 d_h^2}{180(1-\phi)^2} \tag{3.18}$$

where ϕ is the porosity and d_h the diameter of the hair strands. The porosity depends on the cross sectional area of each hair strand and the number (n). Assuming that the hairs are cylindrical gives the area as a function of the diameter and hence

$$\phi = 1 - n\left(\frac{\pi d_h^2}{4}\right). \tag{3.19}$$

Scheffer (1964) describes the hair patterns for seals and taking values for a common seal the porosity is of the order 0.95. This implies that the boundary layer is almost entirely water and so k and α were taken to be the conductivity and thermal diffusivity, respectively, of the surrounding water. Both k_W and α_W depend on water temperature.

Since pinnipeds lack arrector pili muscles (Ling 1970) the hair of a moving animal flattens onto the skin. In this condition, I can consider the skin to be covered by a thin, solid mat of hair of thermal conductivity k_H and thickness d_H. Heat is lost from the outer surface of this mat (at temperature T_H) by forced convection. Taking relationships from Kreith and Bohn (1986) for forced convection heat flux from a flat surface (at temperature T_H) with a turbulent boundary layer separating it from water (at temperature T_W) gives

$$q_S = h_{Sf}(T_H - T_W). \tag{3.20}$$

The forced convection heat transfer coefficient, h_{Sf}, is

$$h_{Sf} = 0.036\frac{k_W}{L^{1/5}\nu^{4/5}}Pr^{1/3}V^{4/5} \tag{3.21}$$

where k_W, Pr and ν are all temperature dependant properties of the water. The terms L and V are the length of the animal and its swimming velocity, respectively.

Provided that the boundary layer and the skin mat are both in thermal equilibrium, they must be carrying equal heat fluxes and I can, therefore, calculate a relationship between T_H, T_W and T_S. Back substituting this relationship into equation 3.20 and simplifying yields the boundary layer heat flux, under conditions of forced convection,

$$q_S = \left[\frac{h_{Sf}}{1 + (d_H h_{Sf}/k_H)}\right](T_S - T_W). \tag{3.22}$$

3.5 Testing the model

3.5.1 Model parameters

The model parameters fall into two categories; species specific (Table 3.1) and individual specific (table 3.2).

Species	common seal	grey seal	California sea lion	Adelie penguin	minke whale
Drag coeff. C_D	9.44×10^{-3}	9.44×10^{-3}	7.32×10^{-3}	4.46×10^{-3}	3.40×10^{-3}
Prop. eff. ε_T (%)	85	85	85	85	85
Aerobic eff. ε_A (%)	$0.0679 + 0.441(\frac{V}{5})^3 - 0.422(\frac{V}{5})^6$				
Core temp. T_C (C)	37	37	37	37	34.7
Blubber cond. $k_B(\mathrm{Wm^{-1}C^{-1}})$	0.2	0.2	0.2	0.2	0.2
Hair cond. $k_H(\mathrm{Wm^{-1}C^{-1}})$	0.37	0.37	0.37	0.37	-
Hair mat depth d_H (mm)	1	1	1	1	-
Interface permeability K (m ^{2})	1×10^{-8}	1×10^{-8}	1×10^{-8}	1×10^{-8}	-

Table 3.1: Species specific parameters.

The drag constants for passively towed seals and sea lions were obtained by fitting the drag measurements reported by Williams and Kooyman (1985) and Feldkamp (1987) under the assumption that drag-force is proportional to V^2, Figure 3.2. The data sets for common seals give similar values of C_D (0.00976, 0.01032 and 0.00778) for seals of 27, 33 and 85 kg, respectively. Since there was no systematic variation with the weight or size of the animals I have used the mean value (0.00944). The California sea lion data set gives a best fit C_D value of 0.00732 which (unsurprisingly) indicates that the drag constant is species specific. The value for penguins was derived in a similar way from experimental data obtained on a model Adelie penguin torso (Bannasch et al. 1994). Since I could find no experimental measurements of drag forces on whales I used a value of 0.0034 reported for a dolphin (Lang and Daybell 1963). No value was available for grey seals so the value derived for the common seals was used

The core temperatures of all the animals was assumed to be 37 C, except in the case of whales where, to be consistent with the work of Blix and Folkow (1995) I used a value of 34.7 C. The conductivity of blood-free blubber was taken as 0.2 $Wm^{-1}C^{-1}$ (Ryg et al. 1988) and for hair a value of 0.37 $Wm^{-1}C^{-1}$ (Lage and Bejan 1991) was used.

Based on a kinematic study of ringed seals, Fish et al. (1988) present a velocity independent propeller efficiency (ε_P) of 85%. In the absence of estimates for sea lions, penguins and whales obtained by this method I have used this value for all animals. The best estimate of the aerobic efficiency (ε_A) is the energy conversion efficiency of isolated muscles. No measurements are available for the muscles of marine mammals. Gibbs and Gibson (1972) found that for rat muscle the efficiency varied with work rate, between 9% and 19%, with the peak occuring at intermediate work rates. In the absence of more precise information I have used a fitted relationship for these values, rescaled such that the maximum work rate corresponds to that for a common seal swimming at its maximum speed, 5 ms^{-1} (Williams and Kooyman 1985).

For animals with a hair layer on the skin surface I calculated the permeability of the porous skin/water interface (K) using data for the hair characteristics of common seals and California sea lions (Scheffer 1964). I was unable to obtain any quantitative data for the thickness of the hair layer when flattened by motion, and used anecdotal evidence relating to the Moray Firth common seal population (D. Tollit, personal communication).

The values used for the individual specific parameters are presented in table 3.2.

Animal	Weight (kg)	Length, L (m)	Surface area, S (m^2)	Basal metab. M_B (W)
common seal 1	33	1.10	0.751	57.7
common seal 2	63	1.36	1.16	97.1
grey seal 1	81	1.47	1.37	122
grey seal 2	270	2.16	3.05	291
Calif. sea lion 1	18	1.23	0.501	59.3
Calif. sea lion 2	23	1.31	0.590	49.4
penguin	4	0.70	0.184	33.6
whale	4000	7.00	18.4	2040

Table 3.2: Indiviual specific parameter values.

Where a measurement of length was available it was used directly. Otherwise, length was inferred from individual weight using an allometric relationship (Innes et al. 1990). In all cases, surface area was estimated from weight using a relationship from Innes et al. (1990). On the assumption that individuals have no thermoregulatory cost at rest, I took basal metabolic rates as equal to the measured resting metabolic rates; with the means being used when multiple values were available. No measurement of resting metabolic rate was given for the juvenile sea lion so I used a value twice that predicted by Kleiber's relationship

(Kleiber 1947), to allow for the elevated metabolism of juveniles (Lavigne et al. 1986).

3.5.2 Data sets

Metabolic rate data deduced from oxygen consumption measurements made on animals swimming in a flume are available for two phocid species. Davis et al. (1985) present data for an adult common seal (*Phoca vitulina*) and a juvenile of the same species swimming (separately) in a flume. Mean metabolic rates are given, with standard deviations, over the velocity range 0-1.4 ms^{-1}. The experiments were carried out at water temperatures between 15 C and 18 C, but it is not specified whether the water was fresh or saline. For this analysis the water is taken to be saltwater at 16.5 C, the mid-range value. Thompson et al. (1993) report similar flume experiments using grey seals (*Halichoerus grypus*). Metabolic rates are presented for a male (weighing 270 kg) and a female (weighing 81 kg) swimming at speeds in the range 0-1.7 ms^{-1}. Freshwater was used for the experiments (Thompson D, personal communication) and I have used a representative temperature of 16 C.

Feldkamp (1987) measured the metabolic rate of a number of California sea lions (*Zalophus californianus*) swimming in a flume. While it is not explicitly specified whether the water in the flume was fresh or saline, the resting metabolism of the larger sea lions is stated to have been made in saltwater of the same temperature. I therefore assume in what follows that the flume water was saline. In order to simulate speeds higher than the 1.4 ms^{-1} maximum of the flume, drag cups were attached to the animals. Experiments were done to measure the drag of the animals with and without drag cups, by towing them round a tank at a known speed. The relationships for drag with and without cups were used to calculate the effective swimming speed of animals with cups swimming in the flume. In fitting the model to this data I have calculated the drag using the effective velocity but have used the actual water velocity in calculating heat loss.

Since the principles upon which the model for pinnipeds is based are common to any homeotherm swimming in water I have extended the work to include data for two non-pinniped species. The metabolic rate of Adelie penguins (*Pygocelis adeliae*) swimming in a water channel has been measured by Culik et al. (1994). The penguins, of mean mass 4 kg, swam at a range of speeds in saltwater at 4 C. The metabolic rate of a free ranging minke whale (*Balaenoptera acutorostrata*), estimated mass 4000 kg, has been inferred from observed breathing patterns (Blix and Folkow 1995). A mean water temperature of 4.2 C is given for the coastal waters where the observations were made (Folkow and Blix 1992). Since whales are smooth skinned I used a revised expression for the boundary layer heat flux under natural convection conditions. Taking an appropriate relationship from the literature (Welty 1978) for free convection from a smooth, vertical plate I get

$$q_S = \theta(T_S - T_W)^{5/4}. \tag{3.23}$$

The scaling coefficient (θ) is calculated from

$$\theta = 0.555\frac{k_W}{L_h^{1/4}}\left[\frac{g\beta Pr}{\nu^2}\right]^{1/4} \tag{3.24}$$

where Pr is the Prandtl number, a temperature dependant, dimensionless group of water properties.

3.5.3 Methodology

In Tables 1 and 2 I give independently determined values for all but two of the model parameters. Before I can examine the quality of fit to the data discussed above I need values for λ, the ratio of active to passive drag, and h_{CL}, the lower bound for the heat transfer coefficient across the blubber layer. Although approximate values are available for h_{CL} (see below) they are insufficiently accurate to provide a good structural test of the model. I therefore treat λ and h_{CL} as free fitting parameters and use the literature estimates to evaluate the plausibility of the optimal fit values.

Because of the complex and highly non-linear nature of the model it is not practical to use automatic optimisation to find the best fit values of the free parameters. Instead I note that equations 3.6 and 3.7 imply that the rate of heat generation is related to the total metabolic rate M and the velocity V, by

$$Q_C = M - \frac{\lambda}{\varepsilon_P}\frac{\rho S C_D V^3}{2}. \tag{3.25}$$

For a known value of λ, this enables me to calculate the rate of heat dissipation which must be implied by a measured value of total metabolic rate. If the animal is in thermal equilibrium this rate of heat generation must be matched by the rate of heat loss across the blubber layer and into the surrounding water. To enable this to happen the animal must set the heat transfer coefficient across the blubber layer to a value, h_{Cest}, given by the analogue of equation 3.10;

$$h_{Cest} = \frac{Q_C}{S\left[T_C - T_{SE}\right]}. \tag{3.26}$$

If h_{Cest} is plotted against velocity (e.g. figure 3.3) we see that the values for $V > 0$ tend asymptotically to a lower bound as $V \to 0$. I take this asymptote as our estimate of h_{CL}. Given a value for λ, the procedure outlined above enables me to identify the appropriate value of h_{CL}. I did this for each animal over a range of values of λ and, in each case, found a linear relationship. Determining the linear regression of h_{CL} on λ reduced the optimisation problem to a single dimension.

Although most of the fits and parameter values reported in the next section were derived by the above procedure, the sparseness of some of the data sets

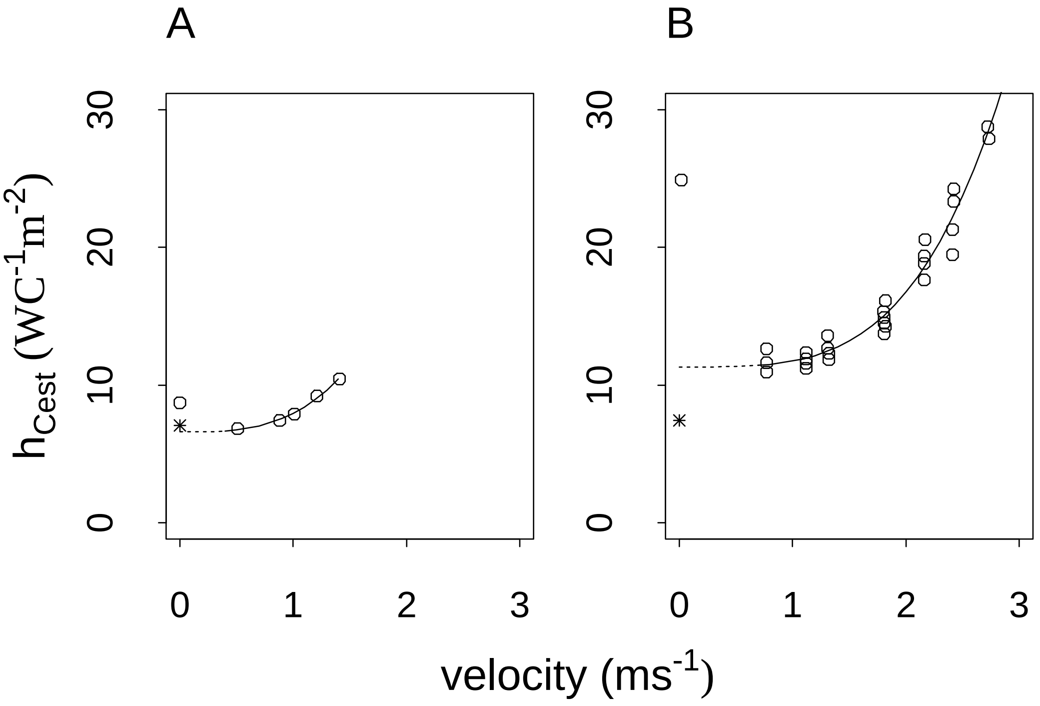

Figure 3.3: Calculated values of the heat transfer coefficient away from the core (h_C) for two swimming homeotherms A: common seal 1 B: sea lion 2. The points marked $*$ are the minimum value of h_C calculated using the blubber thickness relationship given by Ryg *et al.* (1993). The lines are best fit curves for the values at velocities greater than zero (solid line) extrapolated to zero (broken line).

necessitated some minor modifications. I could not make a reliable determination of the asymptotic value of h_{Cest} from the data set for the larger common seal and so took h_{CL} as equal to the lowest observed value of h_{Cest}. The value of h_{Cest} calculated from the resting metabolic rate of the minke whale was slightly lower than that inferred from the data for non-zero velocities and I used the resting value of h_{Cest} as my estimator of h_{CL}. For the grey seals, the non-zero velocity data could not be used to make a reliable inference of a lower asymptotic value of h_{Cest}. I therefore used the allometric relationship of Ryg et al. (1993) to calculate the blubber thickness and used the ratio of the known thermal conductivity of blood-free blubber (Ryg et al. 1988) to the blubber thickness to make a first estimate of h_{CL}. Where this first estimate was lower than the lowest observed value of h_{Cest} I used it in subsequent calculations, otherwise I used the lowest observed value of h_{Cest} as the estimator of h_{CL}.

3.5.4 Results

Metabolic rate versus velocity curves generated from the model using the optimal values of the active to passive drag ratio, λ, are shown in figure 3.4, together with the test data. The predictions of the model are in good agreement with the experimental data, including the ‘anomalous’ step between resting metabolic rates and those measured at low velocities. Where the data show no such step (e.g. the cetacean) the model behaves appropriately. The data set for which the model performs least well is the juvenile sea lion (sea lion 1).

Table 3.3 shows the optimal values of λ together with the accompanying values of h_{CL} and an estimate of effective blubber thickness derived from the h_{CL} values using the thermal conductivity of blood-free blubber (Ryg et al. 1988).

The optimal values of the active to passive drag ratio (λ) are less than one for all the animals. The values for the phocid seals are generally higher than the other animals. The optimal value of λ for the two sea lions and the penguin are similar to each other, whereas that for the minke whale is somewhat lower again.

Animal	Active/passive drag ratio λ	Blubber heat transfer coeff. h_{CL} ($\mathrm{Wm^{-1}C^{-1}}$)	Blubber thickness d_B (mm)	
			effective	allometric
common seal 1	0.829	6.51	30.7	28.7
common seal 2	0.508	5.26	38.0	31.5
grey seal 1	0.876	5.37	37.2	32.7
grey seal 2	0.980	5.14	39.0	39.0
Calif. sea lion 1	0.446	12.9	15.5	26.2
Calif. sea lion 2	0.335	11.7	17.1	27.2
penguin	0.576	8.80	22.7	21.1
whale	0.200	3.64	54.9	57.7

Table 3.3: Predicted values of key parameters.

The values of effective blubber thickness derived from our estimates of h_{CL} (table 3.3 column 3) may be compared with the allometric estimates of blubber thickness (Table 3.3 column 4) based on the work of Ryg et al. (1993). It should be noted that the quantity estimated from h_{CL} represents a whole-body average and thus includes an unquantifiable allowance for regions where blood-flow cannot be eliminated. None the less, the two estimates should be similar and Table 3.3 shows that this is broadly true; the worst discrepancy being a factor of almost 2 for the sea lions. However, Ryg *et al.*'s relationship was obtained using data for phocid seals and cetaceans and so might be expected to be less accurate for otariids.

In order to illustrate the operation of the model, figure 3.5 shows the predicted relationships between model variables and swimming speed for an individual with

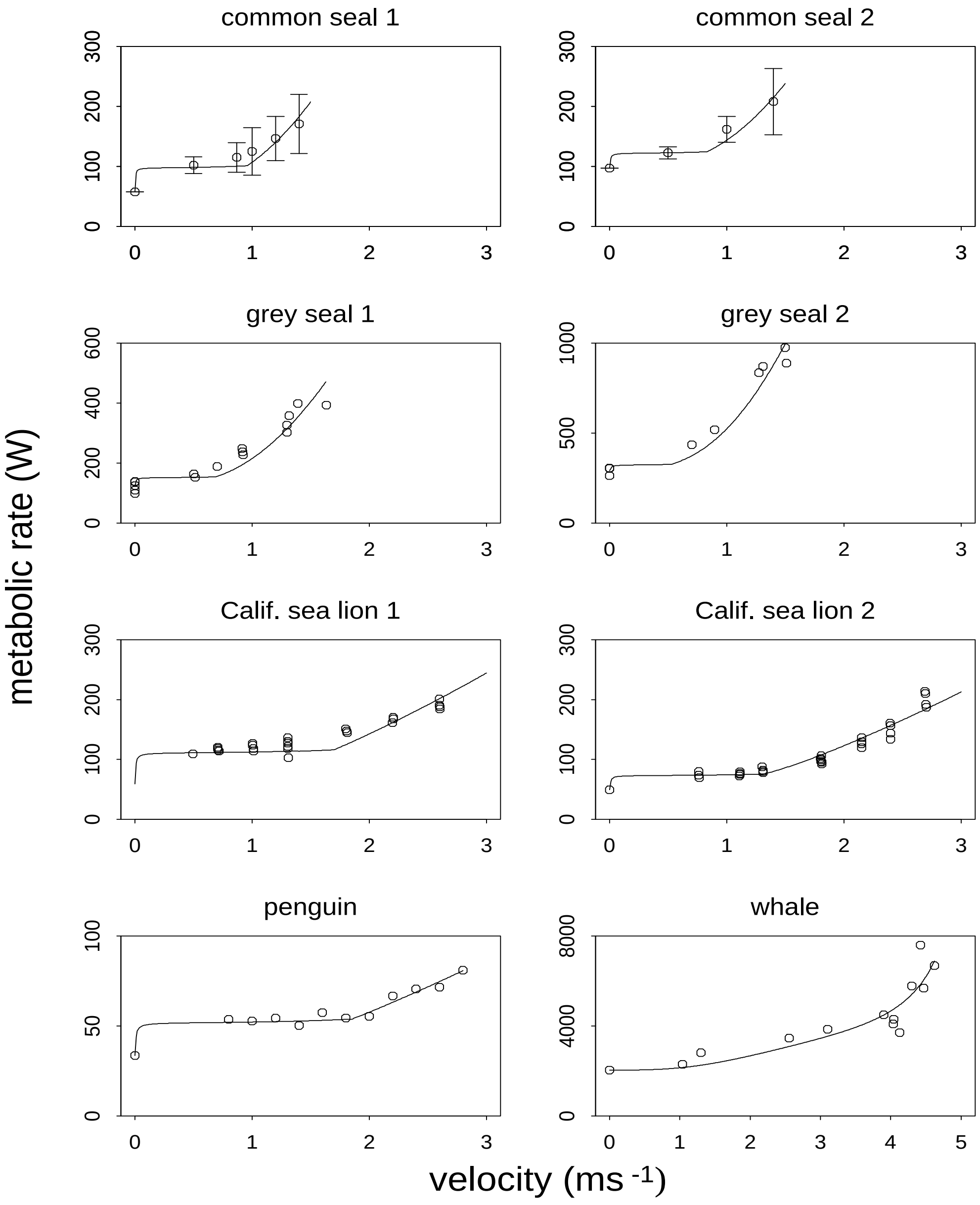

Figure 3.4: Observed and predicted metabolic rates for swimming homeotherms, see text. The curves are the relationships predicted by an integrated model of the cost of locomotion and thermoregulation for a pinniped in water.

characteristics identical to sea lion 2. At rest, total metabolic rate (M) is greater than the minimum surface heat loss so the heat transfer coefficient of the blubber (h_C) is raised to enable the excess heat to be dissipated. This is reflected in a raised skin temperature (T_S). When the animal begins to move the heat transfer

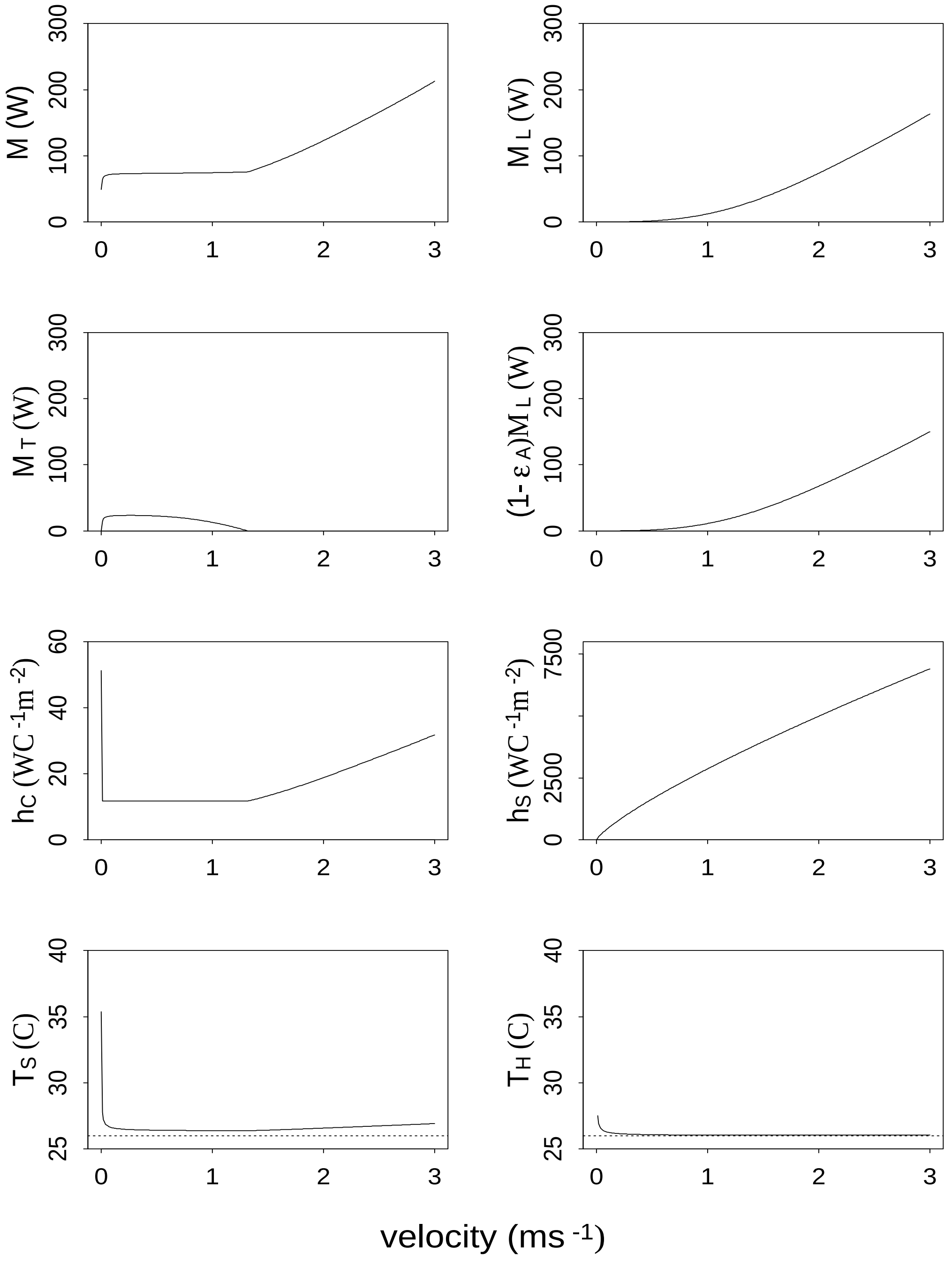

Figure 3.5: The predicted relationships for model parameters; metabolic rate (M), cost of locomotion (M_L), cost of thermoregulation (M_T), the heat transfer coefficients (h_C and h_S), the waste heat from locomotion ($(1-\varepsilon_A)M_L$) and the skin and pelt temperature (T_S and T_H). The relationships are based on data for sea lion 2, a 23 kg California sea lion (Feldkamp, 1987).

coefficient describing loss from the skin surface (h_S) increases rapidly. In order to conserve heat the animal reduces the blubber heat transfer coefficient (h_C)

which rapidly reaches its minimum value h_{CL}. The increased surface cooling and decreased effective blubber conductivity are reflected in a reduction in skin temperature. The compressed hair mat has little insulative value and so the temperature at its surface (T_H) is little different to the skin temperature. At low velocities the heat generated as a by-product of locomotion is small and there is a discrepancy between the minimum heat loss and the heat generated from basal metabolism and the action of swimming. In order to maintain a constant core temperature the seal must increase its metabolism. The cost of thermoregulation (M_T) decreases as the seal swims faster and the waste heat from locomotion offsets the heat loss. When the heat generated from basal metabolism and locomotion exceeds the minimum heat loss, total metabolic rate increases exactly in proportion to the mechanical costs of locomotion. The seal must now act to lose heat and h_C is increased, resulting in an increase in T_S.

3.6 Discussion

Data collected in flume- and tank-based experiments and in the field all show clearly that the metabolic rate of swimming animals increases with velocity. It has long been understood that the main factor underlying this rise is the rapid increase in hydrodynamic drag with increasing speed. However, many of the available data sets show unexpected features which have awaited a satisfactory explanation. The first of these is that, taken overall, many data sets show metabolic rate rising slower with increasing velocity than would be expected on the basis of the known velocity dependence of the hydrodynamic drag. It has previously been argued (Feldkamp 1987) that this effect could be explained on the basis of a velocity or work rate dependent overall propulsive efficiency (c.f. equation 3.5). The kinematic study of Fish et al. (1988) of ringed seals found the propulsive efficiency to be constant over a range of swimming speeds. This explanation, therefore, requires aerobic efficiency to increase with velocity over the full range of work loads measured, whereas work on isolated mammalian muscle tissue implies that it should, if anything, decrease at high work loads (Gibbs and Gibson 1972). The second anomaly, clearly visible in the metabolic rate data for a number of hairy or feathered marine homeotherms, can either be seen as an anomalously low value of resting metabolism, or an anomalously rapid rise in metabolic rate at very low velocities. This feature cannot be explained by a velocity dependant aerobic efficiency, since the effect is seen at velocities for which the metabolic cost of locomotion is insignificant.

In this chapter I have constructed a model of the energetics of a swimming pinniped which combines mechanical and thermal considerations. This model postulates that the initial anomalous rise in metabolic rate occurs because forced convection causes a rapid rise in body surface cooling with increasing velocity. This forces the animal to thermoregulate and implies a velocity range over which metabolic rate is virtually independent of velocity, as waste heat from mechanical propulsion is substituted for expenditure on thermoregulation. At higher velocities the waste heat from propulsion exceeds that needed for thermoregulation and the excess is dumped by increasing blood flow across the blubber. In this regime the metabolic rate rises in exactly the manner one would expect from hydrodynamic considerations.

The model has proved capable of reproducing the features of a varied data set comprising data from both seals and sea lions. I have successfully extended it to mimic the metabolic behaviour of a penguin and a whale. It is interesting to note that the form of the metabolic relationship differs markedly between the pinnipeds and the whale. The absence of hair in the whale means that the rate of heat loss at rest is much closer to the rate of heat loss when it is swimming and the increase is offset by heat produced from locomotion. The model clearly demonstrates the need to take account of the thermoregulatory status of the animals, when investigating the metabolic cost of swimming in marine mammals.

The species-specificity of the best-fit values of the active to passive drag ratio (λ) appears to divide along lines of swimming mode. The highest values are for the phocid seals which use their hind flippers. The sea lions and penguin, which use forelimb 'flying', have similar values. The lowest value is for the minke whale, which uses a fluke for propulsion. The optimal values of the active to passive drag (λ) imply that the drag of an actively swimming animal is less than for a passive animal. Although recent work on oscillating foils (Triantafyllou et al. 1993) lends support to this idea there are a number of complications that make it difficult to reach a firm conclusion. The drag coefficients for the seals and sea lions were calculated from measurements of the drag of animals towed around a circular tank and constraining the animals to follow a circular path may have led to over-estimates. Furthermore the value of the propellor efficiency (ε_P) used for all species is based on data for ringed seals, a higher actual value for any species would result in a higher λ value. The λ value for the whale implies that the drag of a swimming whale is only 20% of that during gliding. The data for the whale were obtained by calculation from observations of breathing pattern and may be subject to error, I therefore tested the sensitivity of the predicted λ to change in the metabolic data. Assuming a systematic underestimate of 20% in the metabolic data results in a 70% increase in λ.

3.6.1 Use of the model for predictions

Using optimally chosen parameters, the model I have described is clearly capable of mimicking the main features of observed metabolic rate in a number of swimming homeotherms. When making (for example) demand estimates for an arbitrarily chosen species it is unlikely that data will be available for the parameter optimisation methods used here. In this section I aim to evaluate the likely accuracy of prediction made using the model structure set out here with parameters taken entirely from the literature. To do this I parameterise the model with reference to the literature for a common seal of 33 kg. The length, surface area and blubber thickness are taken from allometric relationships (Innes et al. 1990;

Ryg et al. 1993). The basal metabolic rate was taken from Kleiber's relationship (Kleiber 1947). The drag coefficient is taken as 0.00944, the drag ratio as 1 and the propeller efficiency as 85%. The predicted relationship using these parameter values gives an acceptable fit to the data, (figure 3.6) with a maximum inaccuracy of about 15%.

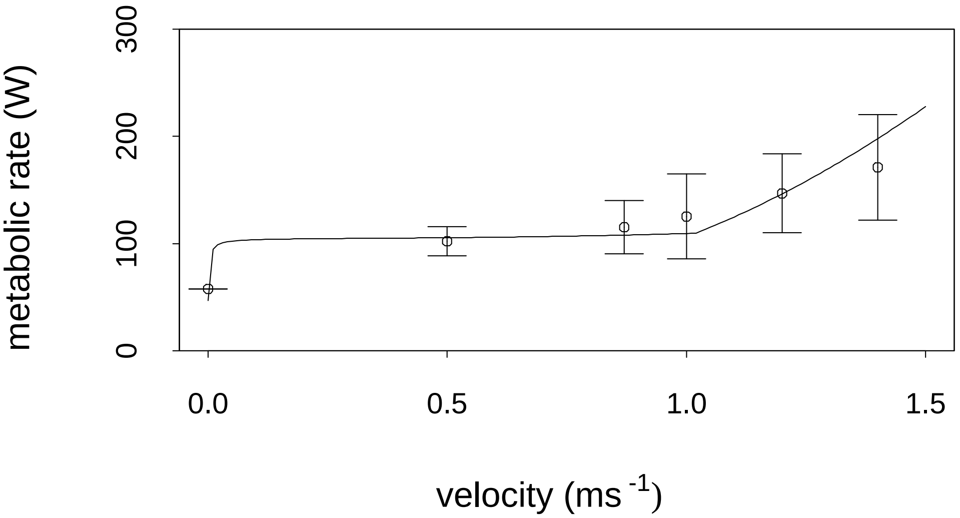

Figure 3.6: The relationship between metabolic rate and swimming speed predicted by the model. The model was parameterised for a 33 kg common seal, see text, and is plotted with mean observations, ± S.D., for a common seal of that size (Davis *et al.* , 1985).

3.6.2 Broader implications

To interpret the ecological significance of work on the metabolic cost of swimming I now examine the cost of transport ($COT \equiv M/V$), that is, the amount of energy required to move one metre. The argument is that all other things being equal, an animal might be expected to swim at the speed (V_{opt}) which minimises the costs of travelling any given distance. Since it is possible to measure the average swimming speed of non-foraging animals in the wild, predictions on this basis can readily be compared with observation. The model I have developed in this paper links the cost of locomotion and the cost of thermoregulation. It is therefore unsurprising to find that the minimum cost of transport (COT_M) and the optimal swimming speed (V_{opt}) are a function of water temperature, as well as varying between animals. Figure 3.7 shows values calculated for both these quantities as a function of water temperature, for the four phocid seals investigated in earlier sections of this chapter.

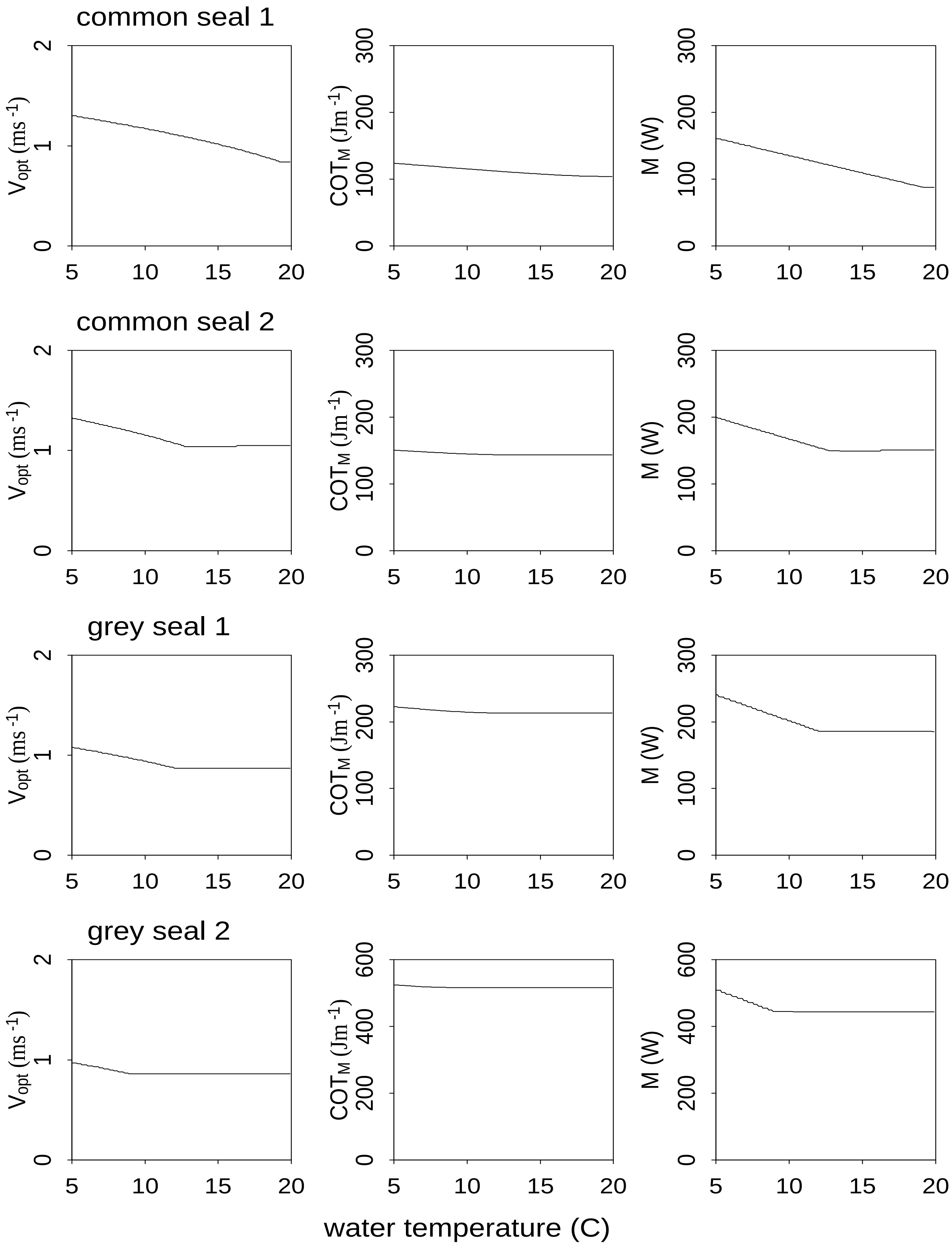

Figure 3.7: The temperature dependency of the models predictions of optimal travelling speed (V_{opt}) minimum cost of transport (COT_M) and the corresponding metabolic rate (M). The relationships are based on output from the model using parameters for the four phocid seals.

Whilst there are many differences between the conditions under which the experimental animals were swimming and those encountered in the wild, I would expect reasonable correspondence between the optimal swimming speeds predicted by the model and the cruising speeds of free ranging animals. For free ranging common and grey seals average cruising speeds of about 1.5 ms^{-1} have been recorded (Thompson D. personal communication), somewhat higher than those predicted by the model for appropriate temperatures. There are no data in the literature for California sea lions but Ponganis et al. (1993) recorded modal swim speeds in the range 1.2-1.9 ms^{-1} for Galapagos fur seals (*Arctocephalus galapagoensis*). The two sea lions dealt with here have predicted V_{opt} values of 1.70 and 1.38 ms^{-1}. The model predicts a favoured swimming speed of 2.36 ms^{-1} for the penguin, comparable to the mean cruising speed of 2.2 ms^{-1} for wild Adelie penguins recorded by Culik et al. (1994). Blix and Folkow (1995) suggest 3.25 ms^{-1} as an upper value for the cruising speed of minke whales. Our model predicts an optimum speed of 3.49 ms^{-1} for the minke whale. There is clearly broad agreement between the V_{opt} values predicted by the model and the observed cruising speeds of wild animals.

Chapter 4

Thermoregulation during haul-out periods.

4.1 Introduction

In Chapter 3 I described a detailed model of the energy demand that swimming places on seals of different sizes. Unlike the fully aquatic cetaceans, seals return to land and in this chapter I turn my attention to the energetic consequences of moving between environments. In some species the need to haul-out (come onto land) is reduced to two brief periods associated with breeding and moulting (e.g. Boyd and Arnbom 1991). Common seals, the focus species for this thesis, haul-out on a very regular basis throughout the year (e.g. Thompson 1993). Since this small phocid is generally confined to more temperate latitudes it has often been assumed that they do not face any thermoregulatory energy demand whilst hauled-out (e.g. Olesiuk 1993). There is some evidence that this assumption is open to challenge.

If the weather conditions experienced by a hauled-out seal result in excess cooling it may seek to avoid the energetic cost of thermoregulation by altering its behaviour. In these circumstances a reduction in the time spent ashore would be expected. A number of studies have looked at the correlation between local weather conditions and the haul-out behaviour of seals, both in polar (e.g. Smith 1965) environments and at lower latitudes (e.g. Pauli and Terhune 1987). Although relationships have been found between some meteorological parameters and haul-out numbers (Pauli and Terhune 1987; Stewart 1987; Kovacs et al. 1990; Godsell 1988) no clear picture of the effect of weather conditions has emerged.

In this chapter I describe a detailed, mechanistic model of heat balance in a seal at rest in air. I follow the principles used in the previous chapter to successfully model the thermal balance of a seal in water, with appropriate modifications. I test the model against data from a laboratory study of thermoregulation in juvenile common seals. Finally I take the timing of pupping in common seals in Scotland as a possible indication that thermoregulation does influence the behaviour of seals. Using the model in combination with meteorological data for north-east Scotland I predict the cost of hauling out for a female adult common seal and her pup, throughout the year. The premise being that pupping is timed to coincide with the most favourable weather conditions, suckling a pup entails increased periods of haul-out.

4.2 A model of thermal balance

Before beginning to construct the model I shall first consider which of the thermal characteristics of the seal must be incorporated.

The seal can be thought of as consisting of a core, containing the major organs, which must be maintained within a narrow temperature range. It is also in this region that the seal generates heat as a by-product of metabolism. At its outer extreme the seal continually exchanges heat with the environment through its skin. Although phocid seals lack fur, most species do have a pelt of coarse hairs which can have a limited but significant insulative effect (see Chapter 3). In addition seals loose heat directly from the body-core to the air during exhalation from the respiratory tract.

Between the core and the skin lies a thick layer of fat which acts as both an energy store and an insulative layer. Seals have a high degree of control over the amount of blood crossing the blubber layer and reaching the skin. By constricting blood flow the seal is able to minimise heat transfer away from the core, allowing the skin temperature to drop to near the ambient temperature and thus reducing heat loss from the skin. As external conditions improve, the temperature difference between the skin and the surroundings must be maintained so that the heat loss remains in balance with production. The requisite increase in skin temperature is achieved by relaxing the arteries and increasing blood flow to the skin. There is a limit to the seals ability to increase blood flow to the skin and further increase in air temperature will result in a net heat gain by the seal. At this point the seal is no longer able to regulate its core temperature and must alter its circumstances to avoid hyperthermia.

A hauled out seal is simultaneously in contact with two different surfaces, air and the substrate (sand, rock or ice). The seal constantly exchanges heat with both media via a number of pathways. For the region in contact with the substrate heat exchange is limited to conduction through the pelt. Heat exchange with the surrounding air is, however, more complicated and involves; convection, radiative transfer and evaporation. Since phocid seals lack sweat glands (Tarasoff and Fisher 1970), evaporative cooling occurs only after emergence from the water, as the pelt dries. The exchange of heat with the atmosphere would also be expected to vary with changing weather conditions such as, air temperature, insolation and wind speed. A mechanistic model of thermoregulation in air must take account of all these factors.

I shall begin by noting that the purpose of thermoregulation is to maintain the core temperature (T_C) within a narrow range through the generation of heat as the end product of metabolism. Given the narrow range for T_C, I can make the simplifying assumption that it remains constant. Seals are generally inactive whilst hauled out and only two metabolic processes need to be considered: basal metabolism (M_B) and thermoregulation (M_T). Since seals loose heat directly from the core during respiration this must be removed from the heat production terms of my model of heat balance. Respiratory loss depends on the rate of respiration and is thus proportional to the metabolic rate, allowing me to represent it as a fraction (γ) of metabolic heat. The proportion of heat lost has been found to depend on the thermoregulatory status of the seal (Folkow and Blix 1987). For the present I need only note that the net rate of heat liberation in the animals core is the sum of the metabolic costs less the fraction lost through the respiratory tract.

The seal's core and skin are separated by a layer of blubber and connected by the blood system. Within the model the circulatory system is subsumed within the blubber giving it variable thermal properties. Ignoring the heterogeneous nature of the blubber and blood system and assuming that the physiological controls act universally across the body enables me to use a single term for the heat transfer coefficient (h_C) of blubber. Whilst seals are hauled out they are in contact with the air and also the substrate on which they rest. Since these have very different thermal properties I divide the seals surface area (S) into two regions with independent skin temperatures, T_{SA} and T_{SR} (for the areas in contact with the air and substrate respectively). Taking ψ as the fraction of the seal in contact with the air I can write an equation for the internal thermal balance of the seal

$$(M_B + M_T)(1-\gamma) = \psi S h_C (T_C - T_{SA}) + (1-\psi) S h_C (T_C - T_{SR}). \qquad (4.1)$$

Heat is exchanged between the skin and the surroundings through the seal's pelt and as a simplification I treat this as a flat slab (with heat transfer coefficient h_P). The rate of heat loss to the surroundings depends on the temperature of the pelt surface (T_{PA} or T_{PR}) and on h_P, a function of the pelt's conductivity and depth. Since these are likely to differ between the regions in contact with the air and rock I define separate coefficients (h_{PA} and h_{PR} respectively). If the seal is in thermal equilibrium then for each region the rate of heat transfer across the pelt must equal the rate of transfer across the blubber and also the rate of heat loss to the surroundings (q_A and q_R for transfer to the air and rock). For the region in contact with the air I have;

$$h_C(T_C - T_{SA}) = h_{PA}(T_{SA} - T_{PA}) = q_A \qquad (4.2)$$

The situation for the region in contact with the substrate is analogous;

$$h_C(T_C - T_{SR}) = h_{PR}(T_{SR} - T_{PR}) = q_R. \qquad (4.3)$$

The heat transfer rates q_A and q_R depend on both; the temperatures at the surface of the pelt and the external conditions. Since they encompass a number of complex heat transfer relationships I shall postpone discussion of the details, but note that for a given set of external conditions they reduce to functions of the pelt temperatures. Although I have now defined the heat balance of the seal we must make some additional assumptions in order to reduce the number of unknown terms and be able to solve for those remaining. The heat transfer coefficient for the pelt can be determined for a set of conditions (e.g. wet or dry) and so for a given situation becomes constant (see section 4.4.1).

Finally I turn my attention to the heat transfer coefficient for the blubber. This represents both the insulative properties of the blubber layer and the variability of the peripheral blood flow. Clearly h_C has a fixed range, limited at either end by details of the anatomy and physiology of the seal. The simplest to estimate is the lower limit (h_{CL}). This corresponds to minimal blood flow and can be taken as the conductivity of blubber (k_B) divided by the thickness of the blubber layer (d_B). The upper limit (h_{CU}) occurs at maximal peripheral blood flow and depends on the flow rate and the heat capacity of the blood.

Although h_C is variable I can progress by making an initial assumption that it is at its lower limit, h_{CL}. Solving equations 4.2 and 4.3 as pairs of simultaneous equations yields the skin temperatures; T_{SA} and T_{PA}. Rearranging equation 4.1 gives the metabolic cost of thermoregulation,

$$M_T = \left[\frac{Sh_C}{(1-\gamma)}\right][T_C - \psi T_{SA} - (1-\psi)T_{SR}] - M_B. \tag{4.4}$$

Substituting the skin temperatures into equation 4.4 yields the thermoregulatory cost for the seal when peripheral blood flow is minimised. A positive value of M_T indicates that the seal is forced to elevate its metabolic rate above resting levels in order to maintain its core temperature. If M_T is negative the seal's resting metabolic rate is generating more heat than the minimum loss to its surroundings and it must increase peripheral blood flow (increase h_C above h_{CL}) in order to dump the excess heat. In this case I know there is no thermoregulation cost ($M_T = 0$) and since M_T is now a constant, I can reverse the process to obtain new solutions for the boundary temperatures (T_{SA}, T_{PA}, T_{SR} and T_{PR}) and thus calculate a value for h_C.

Earlier, I noted that the proportion of metabolic heat lost through the respiratory tract (γ) varied with the seal's conditions. If the seal is actively thermoregulating then γ will be at its minimum (γ_L), increasing to its maximum (γ_U) when the seal is under heat stress. This variation can be readily incorporated by making γ a linear function of the heat transfer coefficient across the blubber layer (h_C);

$$\gamma = \begin{cases} \gamma_L & h_C = h_{CL} \\ \gamma_L + \left(\frac{\gamma_U - \gamma_L}{h_{CU} - h_{CL}}\right) h_C & h_{CL} < h_C < h_{CU}. \\ \gamma_U & h_C = h_{CU} \end{cases} \tag{4.5}$$

4.3 Surface heat exchange

A number of processes facilitate the exchange of heat between a seal and its environment during haul out. Heat loss during respiration has been accounted for in the previous section. The rate of heat loss to the surrounding air, q_A is the sum of the heat transfer by radiation, convection and evaporation. The rate of heat loss to the substrate, q_R, is more easily determined since only conduction is involved and I shall address this first.

A fraction $(1-\psi)$ of the seals surface area (at temperature T_{PR}) is in contact with either rock, sand or ice. In order to avoid the considerable complexity of modelling the internal temperature distribution of a solid body (the substrate) in contact with a seal I make a number of simplifying assumptions. Since the conductivity of the substrate is high (for all three types) and the volume very large I assume that heat is dissipated away from the area in contact with the seal. The temperature of the substrate surface (T_R) is therefore taken to be constant. For rock and sand I further assume that the substrate temperature is equal to that of the air.

Given that the seal is in thermal equilibrium and that the hair is compressed against the seals body, I take the temperature at the pelt surface (T_{PR}) to equal T_R. The description for the heat flux from the pelt is now the same as that for the flux from the skin, i.e.

$$q_R = h_{PR}(T_{SR} - T_{PR}) \qquad \text{where} \quad T_{PR} = T_R. \tag{4.6}$$

Solving for T_{SR} (for a given value of h_C) becomes a simple matter of rearranging equation 4.3,

$$T_{SR} = \frac{h_{CL}T_C + h_{PR}T_R}{h_{CL} + h_{PR}}. \tag{4.7}$$

Next I turn my attention to the more complicated case of heat exchange with the air. Three different heat exchange mechanisms are involved; radiative transfer, evaporative cooling and convection. The heat flux from the seal to the air is the sum of these different fluxes,

$$q_A = q_{rad} + q_{conv} + q_{evap}. \tag{4.8}$$

An object in air emits heat from its surface as longwave radiation and given that its surroundings also emit radiation the object must be subject to incident longwave radiation. In addition to the balance of longwave emittance and absorption a seal in air is also exposed to direct insolation from the sun, in the form of shortwave energy. Of the radiation incident on the seal's pelt a fraction is reflected and the rest is absorbed, this fraction depends on the type of radiation and I define a_{sw} and a_{lw} as the absorptivity of the pelt to longwave and shortwave radiation respectively. Under an irradience I the net radiative flux is given by,

$$q_{rad} = \epsilon_P\sigma(T_{PA} + 273)^4 - a_{sw}I - a_{lw}\epsilon_A\sigma(T_A + 273)^4. \tag{4.9}$$

where the temperatures T_{PA} and T_A are in degrees centigrade. The terms ϵ_P and ϵ_A are the emissivity of the seal's pelt and the air respectively and σ is the Stefan Boltzman constant (5.673×10^{-8} Wm^{-2} K^{-4}).

The emissivity of the atmosphere (ϵ_a) depends on both the temperature and vapour density, but treating it as a function of T_A alone gives a reasonable estimate (Campbell 1977);

$$\epsilon_a = 0.72 + 0.005 * T_A. \tag{4.10}$$

The heat flux for convective loss depends on the temperature difference and the heat transfer coefficient (h_U),

$$q_{conv} = h_U(T_{PA} - T_A). \tag{4.11}$$

The heat transfer coefficient depends on the flow of fluid above the skin and the functional form changes with different flow regimes. I identify two states for h_U, natural convection and forced convection, corresponding to still and moving air. The latter must be sub-divided according to the nature of the flow, i.e. laminar or turbulent. The transition regions between different states are poorly understood and, for simplicity, I assume discontinuous transitions identified by the Reynolds number. This is a function of the wind speed (U), the characteristic length (Lc) and the kinematic viscosity of the air (ν);

$$Re = \frac{L_c U}{\nu}. \tag{4.12}$$

The characteristic length depends on the orientation of the seal to the air flow and can be taken as the seal's length (seal facing into the wind) or half its circumference (seal perpendicular to the wind). At $Re = 0$ heat transfer is solely by natural convection, whereas under the influence of wind ($U > 0$) natural convection rapidly becomes insignificant and I need only consider forced convection. The rate of forced convection is lower under laminar conditions than for turbulent air flow. I take the transition from laminar to turbulent flow to occur at $Re = 4 \times 10^5$ (Kays and Crawford 1993).

The literature contains relationships for the heat transfer (under different flow conditions) for a number of shaped surfaces, including flat plates and cylinders. For a hauled out seal the appropriate relationship depends on the orientation of the seal with respect to the local wind conditions. Since the flat plate relationships are less orientation specific I believe these are the more useful. The heat transfer coefficient for a flat plate depends on the temperature difference across the boundary layer and the physical properties of the boundary layer. The latter are subsumed in the composite terms ξ_N, ξ_L and ξ_T (for natural convection and forced convection with laminar and turbulent, respectively). Taking relationships for the heat transfer coefficient from Thomas (1992), I have a description of h_U

under all wind conditions,

$$h_U = \begin{cases} \dfrac{\xi_N}{{L_c}^{1/4}}(T_{SA} - T_A)^{1/2} & Re = 0 \\[2ex] \dfrac{\xi_L}{{L_c}^{1/2}}U^{1/2} & 0 < Re < 4 \times 10^5 \\[2ex] \dfrac{\xi_T}{{L_c}^{1/5}}U^{4/5} & Re > 4 \times 10^5. \end{cases} \tag{4.13}$$

The characteristic length for natural convection is the area of the surface (ψS) divided by its perimeter (p),

$$L_c = \frac{\psi S}{2(L_s + \psi S/L_s)} \qquad \text{if } U = 0, \tag{4.14}$$

where L_s is the seal's body length. The characteristic length, L_c, for forced convection depends on the orientation of the seal to the air flow. In order to choose between the length and width of the seal I assume that the seal orientates itself to minimise heat loss. From equation 4.13 it can be seen that this will be the larger of the two, i.e. the seal's body length.

In describing the model's representation of convective heat loss from a seal I have made use of a number of composite terms in the interest of clarity. They represent the physical properties of the fluid in relation to convective heat transfer and I here describe them in full;

$$\begin{aligned} \xi_N &= 0.54 k_a \left(\frac{g\beta Pr}{\nu^2}\right), \\ \xi_L &= 0.664 k_a \frac{Pr^{1/3}}{\nu^{1/2}} \\ \xi_T &= 0.037 k_a \frac{Pr^{1/3}}{\nu^{4/5}}. \end{aligned} \tag{4.15}$$

The acceleration due to gravity (g) was taken to be 9.812 $\mathrm{ms}^{-1}$and the coefficient of expansion of air (β) is simply the inverse of its temperature. The Prandtl number (Pr), the conductivity (k_a) and the kinematic viscosity (ν) are all temperature dependant properties of the air.

The evaporation of water from the surface of an object removes heat from that object and from the surrounding air. On leaving the water a seals pelt is wet and heat will be lost as the water evaporates. In dry air there is no further evaporation, once the water in the seal's pelt has dried, since seals lack sweat glands (Tarasoff and Fisher 1970). The rate of evaporation and the resultant heat flux (q_{evap}) depend on; the temperature and vapour pressure of the air, the wind speed and the pelt's water content. This implies that q_{evap} varies over the drying period as well as with changing weather conditions. The absence of empirical information on the heat transfer processes involved in evaporation from a seal's pelt and the detail of environmental data that would be required by a detailed model make it expedient to use a simple model. The total amount of heat required to dry the pelt can be estimated from the volume of water evaporated. The water content per unit area of pelt is estimated as its depth multiplied by its porosity (d_P and ϕ respectively) and by the density of water (ρ_w). The flux to the air is simply the pelt's water content multiplied by the latent heat of evaporation ($i_w = 2.48 \times 10^6$ Jkg^{-1}) and divided by the time to dry (t_{dry} in seconds). Thus, the evaporative heat flux to the air is

$$q_{evap} = \begin{cases} \dfrac{d_P \phi \rho_w i_w}{t_{dry}} & \text{when wet} \\ \\ 0 & \text{when dry.} \end{cases} \tag{4.16}$$

One consequence of this simple approach is the possibility that the pelt is cooled to below the air temperature, since q_{evap} is independent of the temperature difference between the pelt and air. In order to avoid anomalous values of q_{conv} I assume that in this case convection ceases.

4.4 Testing the model

4.4.1 Parameters

Where known, it is preferable to use the individual characteristics of the seal modelled. In the absence of this information, the surface area and the length are calculated from allometric relationships (Innes et al. 1990), and similarly the average blubber thickness (Ryg et al. 1993). The minimum heat transfer coefficient across the blubber (h_{CL}) is simply the conductivity of blubber, taken as 0.2 Wm^{-1}C^{-1} (Ryg et al. 1988), divided by the blubber thickness. Unless specified, it is reasonable to take the core temperature as 38C (Hansen et al. 1995). The upper limit to the heat transfer coefficient across the blubber layer (h_{CU}) is simply the product of the specific heat capacity of blood (4000 Jkg^{-1}C^{-1}Hokkanen 1990), the blubber thickness and the maximal blood flow rate. For a Baikal seal (*Phoca sibirica*) in thermoneutral conditions the subcutaneous blood flow rate has been measured at 2 kgm^{-3}s^{-1}(Neshumova and Cherepanova 1987). For sheep a fourfold increase in flow rate under conditions of heat stress has been observed (Hales 1973) and I therefore take the maximal flow rate for the seal to be 8 kgm^{-3}s^{-1}.

The depth of the pelt will depend on the conditions, since both wind and wetness will tend to compress the hairs into a thinner layer. For a dry pelt the hairs tend to 'curl up' (Tarasoff and Fisher 1970) despite the absence of arrector muscles (Ling 1970). Assuming that the individual hairs rise to an angle of 45^o (Øritsland and Ronald 1973) from the skin gives the maximum pelt depth as,

$$d_{PMAX} = L_h \cos 45^o. \tag{4.17}$$

Since there are no arrector muscles I assume that any wind results in a compressed hair layer. For a wetted pelt the compressed hair layer is estimated to be 1 mm (D. Tollit, personal communication) and I use this value for the compressed dry pelt also. The seal's pelt is a mixed layer of hair and either air or water and so its thermal properties must be an average of the properties of the materials. The porosity of the layer provides an appropriate weighting for the fluid properties. The porosity (ϕ) is the proportion of the layer composed of air or water and depends on the volume of hair in the layer (V_h);

$$\phi = 1 - \frac{V_h}{d_P} \qquad \text{where} \qquad V_h \approx n L_h \frac{\pi {d_h}^2}{4}. \tag{4.18}$$

The term n is the number of hairs per square metre and d_h the diameter of individual hairs.

The conductivity of the pelt is the weighted average of the conductivity of the hair strands (k_h) and either, the air (k_a) for a dry seal or water (k_w) for a wet seal. Thus;

$$k_P = \begin{cases} k_P = \phi k_a + (1-\phi) k_h & \text{when dry} \\ \\ k_P = \phi k_w + (1-\phi) k_h & \text{when wet.} \end{cases} \tag{4.19}$$

The conductivity of the hair strands is taken as 0.37 $\mathrm{Wm^{-1}C^{-1}}$ (Lage and Bejan 1991), while k_a and k_w are functions of the air and water temperature respectively.

The description of heat transfer through the seal's pelt requires values for the length and diameter of individual hairs, taken as 9 mm and 0.14 mm respectively (Scheffer 1964). I take the number of hairs per square metre to be 5.2×10^6 (Scheffer 1964). The absorptivity of the pelt differs for shortwave and longwave radiation; I take a_{SW} as 0.87 and a_{LW} as 0.97 (Watts 1992). For the emissivity (ϵ_P) I use 0.99, a value measured for a grey wolf (Welty 1978).

For a hauled out seal I take the proportion of the seal in contact with the air (ψ) to be 80 % (Leucke et al. 1975). There have been several measurements of the proportion of the metabolic heat lost through respiration (γ). Taking the lowest and highest as the limits gives, γ_L as 2 % (Gallivan and Ronald 1979) and γ_U as 19 % (Folkow and Blix 1987). Finally, I have assumed that it takes a seal one hour to dry (Watts 1992) and so $t_{dry} = 3600$ s.

4.4.2 The thermoneutral zone

Experimental data for the thermoneutral zone of juvenile common seals (*Phoca vitulina*) in air (Hansen et al. 1995) provides a means of partially validating the model. The thermoneutral zone is defined as the temperature range within which the seal is able to maintain its core temperature without having to increase its metabolic rate. The experiments were conducted in a metabolic chamber and so there is no solar heating or wind-driven cooling (I and U are zero). Furthermore the longwave radiation incident on the seal is now that emitted by the walls of the metabolic chamber. Assuming that the chamber's walls are at air temperature gives the flux as,

$$\epsilon_{wall}\sigma(T_A + 273)^4 \tag{4.20}$$

where the emissivity, ϵ_{wall}, is taken as 0.97 (Welty 1978). Metabolic rate was measured at air temperatures between -10 C and 32.5 C and the data (presented as multiples of Kleiber's predicted metabolic rate) are pooled for five seals. The metabolic rate within the thermoneutral zone was observed to be 1.6 times greater than that predicted by Kleiber's relationship, consistent with the animals being juvenile. The experiment spanned a period of about 40 weeks, during which time there was significant variation individual weight. In testing the model, I have therefore used a characteristic weight of 30 kg and a resting metabolic rate of 1.6 times Kleiber .

The lower critical temperature (T_{XL}) predicted by the model was taken to be that below which the metabolic rate was greater than the resting value (i.e. $M_T > 0$). The upper critical temperature (T_{XU}) was taken to be that above which the heat transfer coefficient lies outside its physiological bounds (i.e. $h_C > h_{CU}$). The model was run for a range of temperatures between -10 C and 38 C.

The model predicted T_{XL} and T_{XU} to be 5.1 and 23 C, respectively, for a 30 kg seal. The value of T_{XU} compares favourably with that observed by Hansen et al. (1995) (25.1 C) but the predicted T_{XL} is markedly higher than the observed value (-2.3 C).

For a 30 kg juvenile seal the model over-estimates the lower critical temperature by 7.4 C. Given the variation in weight (W) between the individuals and over the experimental period it is difficult to determine an appropriate value for use in the model. I, therefore, tested the sensitivity of predicted T_{XL} to variation in the weight of the seal. Decreasing W by 50% resulted in an increase of T_{XL} to 8.6 C, conversely a 50% increase in W decreased T_{XL} to 2.8 C. Another problem in applying the model to the data set is the lack of information on the condition of the animals (i.e. the blubber depth). Using a weight of 30 kg but a blubber thickness 50% greater than that predicted by the allometric relationship resulted in predicted values of T_{XL} and T_{XU} of -2.3 and 23.1 C. These are very close to those observed in the experiment.

The variability within the experiment of the weight of the seals (a key model parameter) and the lack of information on their condition makes a more rigorous test of the model difficult. The predictions of the model under realistic conditions ($W = 30$ kg and d_B 1.5 times higher than the allometric prediction) do compare well with the observations and there is, therefore, no reason to reject the model.

4.5 The interacting effects of weather conditions.

The experiment described by Hansen et al. (1995) looked at the effect of only one of the atmospheric parameters related to heat transfer; the air temperature. A full account of thermoregulation in air must take account of the heating effect of solar radiation (irradience), the convective cooling of the wind and the evaporative cooling whilst wet. The model incorporates all of these factors and I can, therefore, demonstrate their effect on the thermo-neutral zone of the juvenile common seals studied. In this section I shall assume a weight of 30 kg and a blubber layer 50% thicker than that predicted by the allometric relationship.

It would be expected, if the irradiance is kept at zero, that increasing wind strengths would increase both T_{XL} and T_{XU}, due to increased convective cooling. The model was run for temperatures between -10 C and 38 C with wind velocities in the range 0 to 60 ms^{-1}. Figure 4.1 A confirms that both boundaries of the predicted thermoneutral zone increase with wind speed, whilst the range initially decreases slightly and remains constant at wind speeds above 5 ms^{-1}. The cooling action of the wind is more clearly seen by plotting the equilibrium metabolic rate of the seal at -2.3 C (T_{XL} for no wind) against wind speed, Figure 4.1 B. The initial increase in metabolic cost is rapid but begins to plateau above 10 ms^{-1}, reaching a maximum of almost twice the resting rate. The discontinuity at 5 ms^{-1} is an artefact, being caused by the model's simple treatment of the transition from laminar to turbulent flow. The effect of extending the two flow regimes is shown by the dashed lines in Figure 4.1B. Although reality will be more subtle than the treatment of the transition used here, the simplification I have used is representative. The model's behaviour is consistent with empirical relationships for wind cooling in other animals. St-Laurent and Larochelle (1994), working on heat loss from a pigeon's head, found the cooling power to increase rapidly at low wind speeds and begin to level off above 25ms^{-1}.

We are all familiar with the powerful heating effect of the sun and would therefore expect solar heating to act as a counter-balance to the cooling wind. This was confirmed by running the model without wind but at increasing levels of solar heating. To illustrate the interplay of these two parameters the model was run as described in the previous section (incorporating the effect of different wind speeds) at increasing strengths of solar heating, Figure 4.2. In the absence of solar heating the seal's metabolic rate is greater than its resting rate (indicated by the bold line in the plot) at all non-zero wind speeds. As solar heating increases the metabolic rate decreases sharply for laminar flow conditions and more slowly under turbulent flow (the transition is marked by the obvious step). At mid-range irradiance values a plateau exists, corresponding to a region in which the seal is thermoneutral. Further increase in solar heating results in a situation where the seal is gaining excess heat from the environment and faces overheating unless it moves to a cooler environment (indicated in the plot by zero metabolic rate). Solar heating has much less effect at high wind speeds where the cost of thermoregulation is consistently high. Clearly the thermal balance of the seal will depend on the interaction of all three atmospheric parameters (temperature,

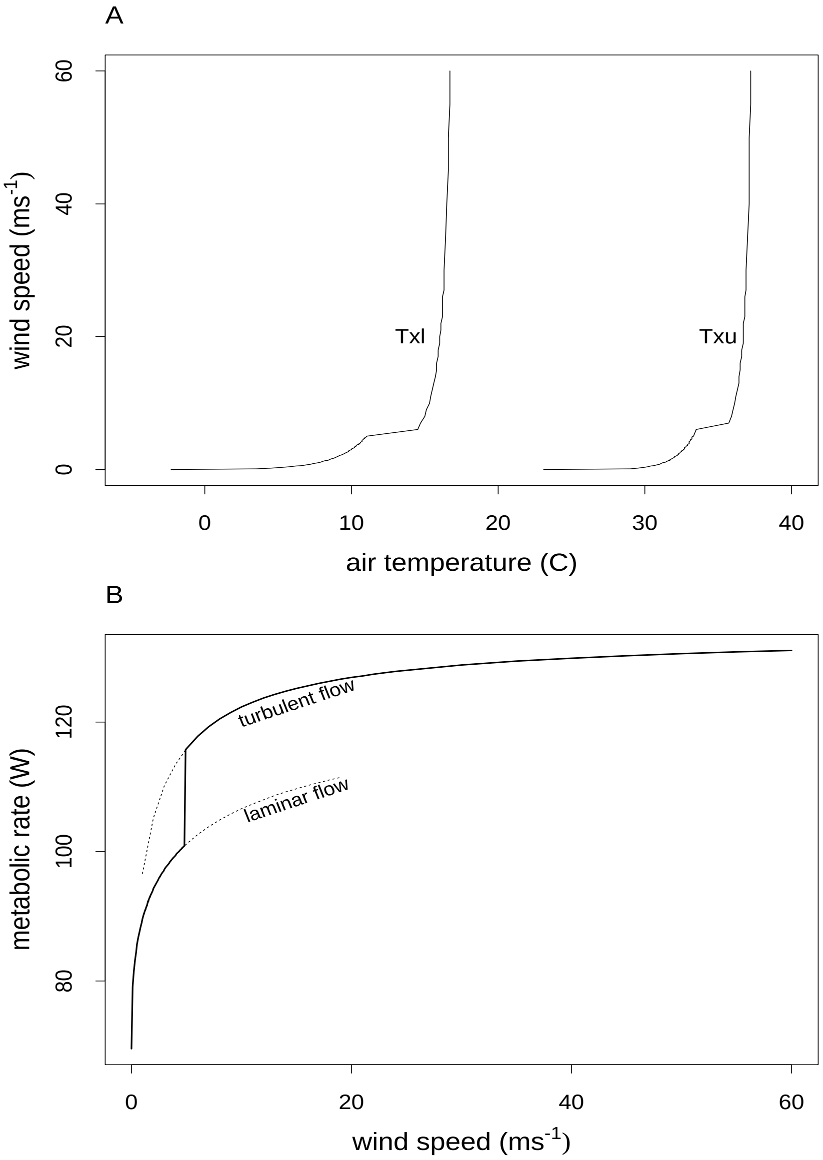

Figure 4.1: The effect of increasing wind speed on, A) the thermoneutral zone and B) the metabolic rate of a juvenile common seal. The thermoneutral zone is the range of temperatures between the lower critical temperature (T_{XL}) and upper critical temperature (T_{XU}), as plotted. The dotted lines in plot B) indicate the extension of the laminar and turbulent flow regions.

wind velocity and irradiance), as well as the seal's condition.

Evaporation of water from an animals coat has a powerful cooling effect and it has been proposed as a means to cool cattle in hot regions (Arkin et al. 1991). For a wet seal I would expect a large increase in the metabolic cost of thermoregulation at low temperatures, seen as a marked increase in the lower critical temperature. Indeed the model predicts the lower critical temperature for the wet seal to be 31 C (as opposed to -2.3 C when dry). Consequently the seal was still in thermal

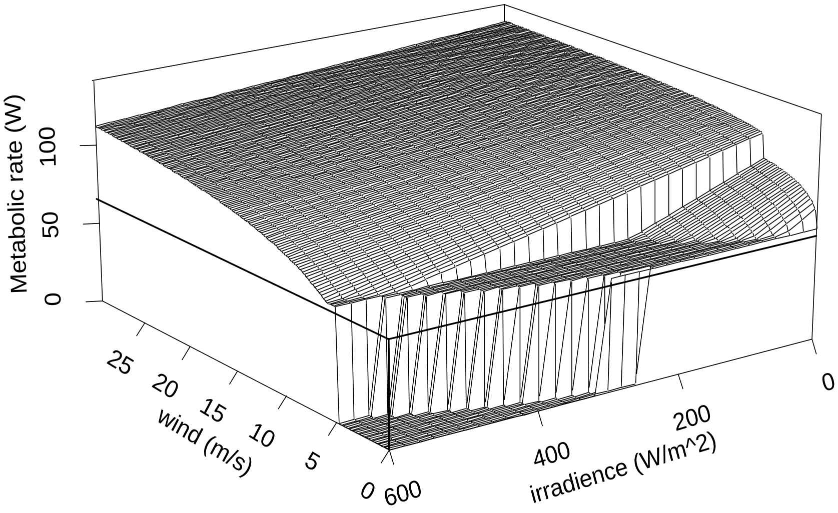

Figure 4.2: The counter-balancing effect between wind cooling and solar heating on the metabolic rate of a juvenile seal hauled out in air at -2.3 C, see text. The bold line indicates the resting metabolic rate of the seal. The metabolic rate is set to zero for situations in which the seal is unable to maintain its heat balance and would overheat. The discontinuity in the surface indicates the transition from laminar to turbulent boundary flow.

balance at air temperatures above 35 C. Since the heat flux due to evaporation from the coat is based on the water content I can make an easy comparison with the findings of Arkin et al. (1991). They measured a water content of around 225 gm^2 for the maximum recorded wettedness of 60 % and my calculated water content for a seal (259 gm^{-2}) is in very close agreement. Although drying of the cow's coat took over an hour most of the water was evaporated in the first 30 to 40 minutes, at a constant rate. This lends support to the simple approach I have taken to calculate of evaporative heat flux.

4.6 Implications for the timing of pupping.

Grellier et al. (1996) looked at the effect of weather conditions on the haul-out behaviour of common seals in Northeast Scotland. Since breeding and moulting increase the amount of time spent ashore they argue that these behavioural influences must be removed in order to look at the influence of weather conditions. Using data from six consecutive years they calculated the seasonal trend in haul-out counts for the summer months and found that it accounted for most of the variability. After removing the seasonal trend there was very little correlation between the residual counts and separate weather parameters. From this the authors inferred that behavioural patterns (foraging activity and breeding) are a more important influence on summer haul-out behaviour than the weather. I suggest that the timing of these behavioural patterns may actually be the evidence of the influence of weather conditions which the authors were interested in.

Reproduction represents a significant energetic burden to female seals. During gestation and lactation the mother must meet not only her own energetic costs but also those of her pup. Since lactation constrains foraging by the female seal, this energy demand must be met by mobilising energy reserves, i.e. the blubber layer (Bowen et al. 1992). In the common seal lactation lasts for 3-5 weeks following parturition (Bowen et al. 1992; Thompson 1988). Since common seal pups are able to swim shortly after birth lactating females have a limited opportunity to forage, but the pups are still dependent on their mothers milk to meet their energetic needs. Not only does lactation place a high energetic demand on females but also increases the amount of time they spend hauled-out. This combination of high cost and increased time spent ashore may create a pressure to minimise the cost, by timing pupping to coincide with favourable weather conditions. In Scotland common seals pup during June, with lactation lasting into the beginning of July (Thompson 1988). It, therefore, seems possible that the summer pupping of common seals in Scotland is a result of pressure to minimise the cost of reproduction.

In this section I seek to test the hypothesis that pupping in British common seals is timed to coincide with the most favourable conditions for hauling out. To do this I first parameterise the model to simulate a female adult common seal and a pup. I have taken the length of a reproductive female to be 1.35 m (Gardiner et al. 1996) and the length of a newborn pup to be 0.75 m (Markussen et al. 1989). In the absence of specific data for the weight, surface area and blubber thickness, I have resorted to the allometric relationships described previously.

The model requires data on the weather conditions; the air temperature, wind speed and solar irradiance. These I obtained from the UK Meteorological Office in the form of daily max/min temperature and mean wind speed recorded at Kinloss (station no. 1057) and daily mean irradiance recorded at Aviemore (station no. 0585). The data span the period May 1988 to May 1990 and provides representative conditions for the common seal population of the Moray Firth region of the North Sea, Figure 4.3.

The metabolic cost of hauling out depends on whether the seal is wet or dry. In the Moray Firth inter-tidal sand banks are used as haul-out sites and are only available for 4-6 hours on each tide (Grellier et al. 1996). Assuming that the seals haul-out for five hours on each tide I can calculate the average metabolic cost over that period.

The model was used to predict the metabolic rate, whilst hauled out, for an adult

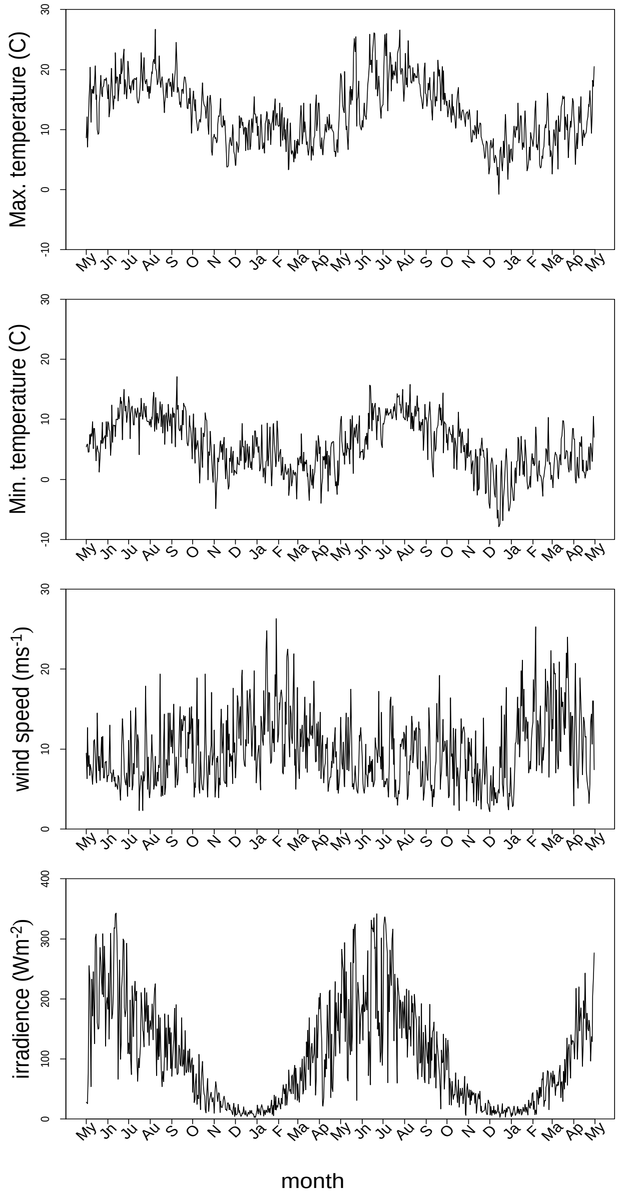

Figure 4.3: The weather conditions for the Moray Firth over a two year period, from May 1988 to May 1990. Maximum and minimum temperature and wind speed were recorded at UK Meteorological station 1057, Kinloss. The irradience was recorded at station 0585, Aviemore.

female and for a newborn pup, using mid-range temperature values. There were a number of days on which the conditions subjected the seals to excess heating. This is consistent with observations of common seals in temperate latitudes on the west coast of Canada (Watts 1992). On these occasions the author observed an increase in the proportion of hauled-out seals that were wet, implying that the seals were re-wetting their pelt to make use of evaporative cooling. It is beyond the scope of this study to take account of such behavioural adaptations and I simply assume that there are no thermoregulatory costs on these 'hot' days (i.e. basal metabolic rates apply). The average metabolic rate of the female seal shows a general decrease in the mid-part of the year (Figure 4.4 A) and is consistently above the resting rate. To emphasise the seasonal pattern I have

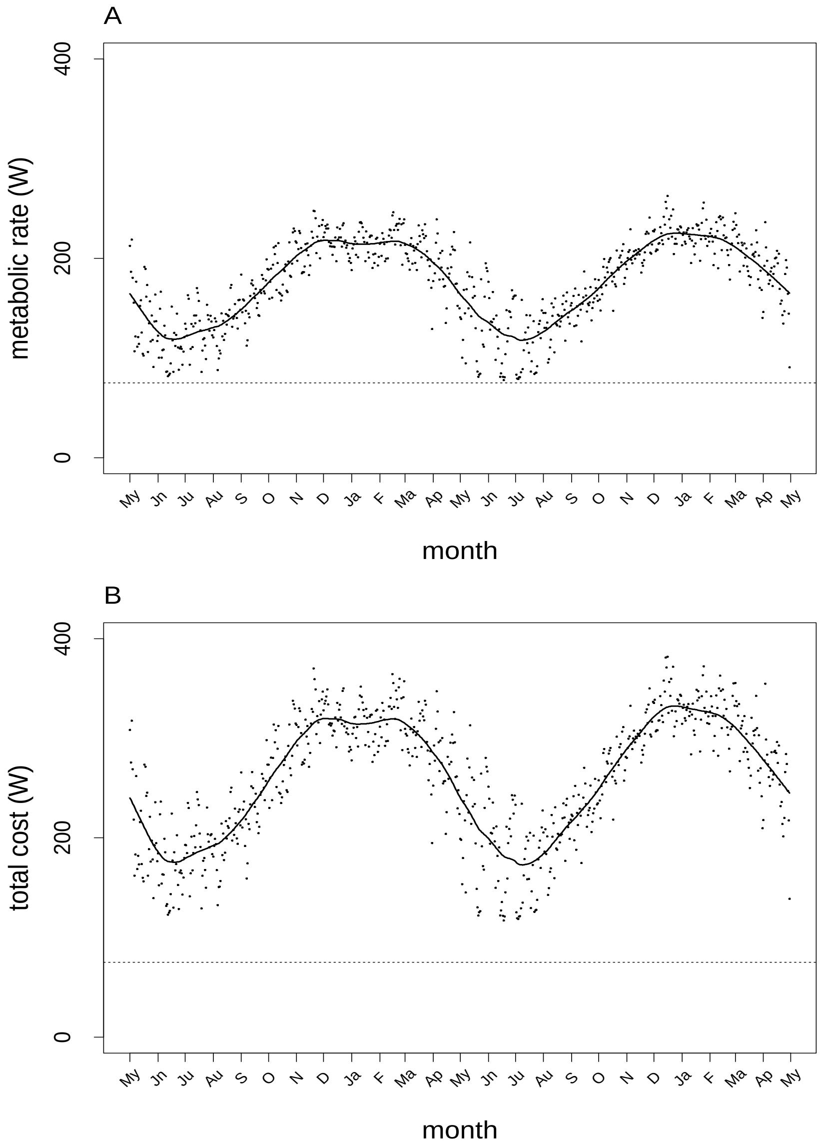

Figure 4.4: Seasonal variation in the predicted metabolic rate of a hauled-out female common seal (A) and the total cost of meeting her own haul-out cost and that of a pup (B). To illustrate the seasonal trends, smoothed relationships have been fitted (bold lines). As a reference point the mothers basal metabolic rate is shown (dashed lines).

fitted a smoothed trend line, which is illustrated. The seasonal variation becomes more marked if the metabolic costs of the pup are added to those of the female, Figure 4.4 B. The total metabolic cost to the hauled-out female during summer would be approximately double its resting rate, in contrast to winter when this would rise to over three times the resting rate. From an energetic point of view the optimal time for pupping would be June or early July, so that lactation coincides with the period of minimum cost of hauling-out.

4.7 Discussion

Ecological studies of the effects of weather conditions on the haul-out behaviour of seals in temperate regions have found some evidence that phocid seals haul-out less in unfavourable conditions (Smith 1965; Stewart 1987; Godsell 1988). In a study of the hauling out behaviour of common seals Pauli and Terhune (1987) found that counts increased during favourable weather, but noted the complicating influence of behaviour shifts during moulting. Another complicating factor was identified by Grellier et al. (1996) in that females spend more time ashore during pupping and lactation. They looked at the influence of weather conditions on haul-out numbers which had been corrected for this seasonal trend and found only a weak relationship with rainfall and cloud cover.

Rather than a separate influence which must be factored out, I believe that the timing of this period of increased haul-out provides further evidence of the impact of environmental conditions. During lactation the female common seal is subject to an energetic stress in meeting both her own needs and those of the pup, evidenced in the mass loss over this period (Bowen et al. 1992). Since lactation increases the amount of time the mother/pup pair spend hauled-out it would be energetically prudent if pupping coincides with the most favourable weather conditions. Using a general model of the heat balance of a seal in air I have tested this for common seals in the Moray Firth region of the North Sea, where pupping occurs in early June (Thompson 1988).

The model described in this paper was successfully tested against empirical observations on the thermoneutral zone of juvenile common seals. The model predicts that the cooling power of the wind, even where counterbalanced by solar heating, is sufficient to force active thermoregulation in a juvenile seal.

I used the model in combination with meteorological data for Northeast Scotland to predict the metabolic cost of hauling out for an adult female common seal and a pup. The predicted metabolic rates peak in mid-winter and are lowest in mid-summer. At most times of the year the model predicts some additional energetic cost associated with thermoregulation. Since the female must also meet the costs of her pup I summed the metabolic rates, giving a maximum cost in winter almost three times the female's resting metabolic rate and a minimum in summer of about double the resting rate. The model predicts that the most energetically favourable time to pup for common seals in the Moray Firth is June or early July, in order that lactation coincides with favourable weather.

I conclude from this that seasonal changes in weather conditions may act as a selection pressure on the timing of pupping. Although this is interesting from an ecological point of view, within the context of this thesis, the model's prediction that adverse weather can lead to a significant energetic cost during haul-out is more significant. In Chapter 6 I will look at the seasonal energy requirements of individual seals and it is clear from the results of this chapter that the cost of thermoregulation during haul-out periods must be taken into account.

Part III

Population Energetics and Food Consumption

Chapter 5

Estimating the impact of seal populations.

5.1 Introduction

Seals are near the top of the marine food chain and feed on many of the same fish species that are exploited commercially by the world fisheries. This has brought them into conflict with the fishing industry and seals have long been perceived to be a threat to fish stocks. In Chapter 1 I gave brief descriptions of three such seal/fishery interactions, including eastern Canada groundfish. The collapse of stocks of groundfish, such as cod, led to the closure of the fishery. This occurred at a time when the grey and harp seal populations were increasing (Hammill et al. 1995) and the fishing industry has been quick to connect the two. Although there is no doubt that the seals do prey on some of the fish species that have experienced such a dramatic fall in numbers, the impact of seal predation is by no means clear. In situations such as this, there is an obvious need to make a scientific assessment of the actual impact on fish stocks. Such fisheries modelling requires a knowledge of the level of predation inflicted by seals and other marine organisms.

The difficulty of direct measurement of the food requirements of wild seals has required alternatives to be devised. An early focus on the food requirements of captive seals has fallen out of favour with the recognition that the artificial activity patterns of captive animals compromise the applicability of the results to wild seals. Interest has shifted to the estimation of energy requirements using bioenergetic models and these studies provide the focus for this chapter. The underlying principle is that the impact of a seal population on the fish stocks it exploits can be assessed, given an estimate of the energy requirements of individual seals, information on the size and structure of the population and knowledge of the seal's diet.

A key study was the estimate of the energy requirements of the harp seal (Lavigne et al. 1982; Lavigne et al. 1985) in the western Atlantic. Harp seals in

European waters have also received attention, Markussen and Øritsland (1991) used a physiological based model (Øritsland and Markussen 1990) to estimate the energy requirements of harp seals in the Barents and White Seas. The seasonal energy requirements of individual ringed seals (an Arctic species) have been investigated (Ryg and Øritsland 1991) for a hypothetical population. The energy requirements of the grey seal population in the United Kingdom were estimated by Fedak, M. and Hiby, L. (reported in Anonymous 1986). With the express aim of estimating the consumption of cod by the Northwest Atlantic population, Hammill et al. (1995) derived an energy budget for grey seals. Although there has been no study on a common seal population in Britain, the energy requirements of two other common seal populations have been estimated; one in the Skaggerak, Denmark (Härkönen and Heide-Jørgensen 1991) and one on the west coast of Canada (Olesiuk 1993).

In this chapter I will review the different approaches these studies have used in relation to the elements involved in estimating the energy requirements of seals; the fixed costs (such as basal metabolism), the cost of activities, the amount of time spent on each activity and, lastly, the size and structure of the population. The estimated energy requirements reported in each study are then compared.

5.2 Fixed costs

5.2.1 Basal metabolism

In both papers on the eastern Atlantic harp seals (Lavigne et al. 1982; Lavigne et al. 1985) the basal metabolic rate (BMR) of adult seals was estimated using Kleiber's relationship (Kleiber 1947) and a fixed body weight of 106 kg. For juvenile seals an empirical relationship for basal metabolic rate was used. Most other studies have also used Kleiber's relationship to calculate the BMR for adult seals (Øritsland and Markussen 1990; Ryg and Øritsland 1991; Hammill et al. 1995; Olesiuk 1993), with a range of body weights appropriate to the different species. Two of the studies elevated the BMR for juveniles by an age dependent increment.

In contrast, one of the common seal studies (Härkönen and Heide-Jørgensen 1991) used an allometric relationship for the maintenance requirement of juvenile seals (Innes et al. 1987) and then calculated BMR for the adults by assuming that it is 71% of the rate for a juvenile of the same size.

5.2.2 Growth

Although all the studies took account of the elevated BMR of juvenile seals, a number of them also explicitly included a growth cost. Olesiuk (1993) calculated the daily energy requirement for growth for each sex- and age-class from the growth increment (predicted by the age structured population model). He assumed a fixed cost of growth (Innes et al. 1987), an approach also applied to grey seals (Anonymous 1986; Hammill et al. 1995) and harp seals (Lavigne et al. 1985). In the latter case a general relationship was used to describe the growth increments and adults were assumed to incur no growth cost. Based on a published cost of 9090 Kcal kg^{-1} and a weight increase of 2 kg yr^{-1} Härkönen and Heide-Jørgensen (1991) calculated an annual growth cost of 8×10^{4} KJ, for female juveniles and adult common seals. For male juveniles the cost was higher at 17×10^{4} KJ yr^{-1}, since a mass gain of 6 kg yr^{-1}was assumed.

5.2.3 Reproduction

For breeding harp seals Lavigne et al. (1982) estimated the cost of pregnancy and lactation separately. The metabolic rate during pregnancy was assumed to equal the basal rate, the negligible cost being inferred from details of the cost of pregnancy in cattle. For lactation the authors calculated the energy requirements of the pup, divided this by an efficiency of 80% for energy gain from milk and then by an efficiency of 63% for the transfer of energy from the mother to her milk. The result was a total cost for the lactation period of 1607 MJ, equivalent to 89 MJ day^{-1} over the 18 days of lactation. A similar method was used for common seals by Olesiuk (1993), giving an annual cost for pregnancy and lactation of 1060 MJ.

In contrast Markussen and Øritsland (1991) calculated the cost of reproduction for female harp seals from the weight loss (females do not feed during lactation), as did Ryg and Øritsland (1991) for ringed seals and Hammill et al. (1995) for grey seals. Following this approach for common seals, Härkönen and Heide-Jørgensen (1991) arrived at values for the cost of pregnancy and lactation of 290 MJ and 540 MJ, respectively.

5.2.4 Digestion and excretion

Estimating the digestive efficiency of seals is complicated by the variation in faecal and urinary losses with different diets (Keiver et al. 1984). In their original study Lavigne et al. (1982) used a value between 82.7% and 84.7%, but later revised this to 80% to allow for the very low efficiencies associated with some prey species (Lavigne et al. 1985). This value was also used for common seals by Härkönen and Heide-Jørgensen (1991), whereas Olesiuk (1993) assumed that faecal and urinary losses accounted for only 13% of ingested energy (Keiver et al. 1984).

There is a lack of published, species specific values for the specific dynamic action of seals. Faced with this most authors have used a value of 17%, which was measured in harp seals (Gallivan and Ronald 1981).

5.3 Activity costs

5.3.1 Swimming

Results from a study of the cost of swimming in captive common seals (Davis et al. 1985) were used directly by both of the studies on common seals (Olesiuk 1993; Härkönen and Heide-Jørgensen 1991). For harp seals, Øritsland and Markussen (1990) elevated the resting metabolic rate by fixed factors (based on unpublished observations) to represent calm swimming and migratory swimming. Lavigne et al. (1982) initially calculated the cost of transport (the metabolic rate of a swimming seal divided by its speed) from a simple hydrodynamic model, but faced with a discrepancy between the results and experimental observations (Øritsland and Ronald 1975) they resorted to direct use of the experimental data. Since ringed seals are somewhere in size between common seals and harp seals, (Ryg and Øritsland 1991) elevated the metabolism for diving seals by a factor such that the swimming cost was between observed costs for captive harp and common seals. The metabolic rate was then taken as the higher of this value or the estimated minimum heat production necessary to maintain thermal equilibrium. This comparison of swimming cost to minimum heat production has also been applied to grey seals (Hammill et al. 1995), using a similar scaling for the metabolic rate of a swimming seal to its basal rate.

5.3.2 Hauling out

Only three of the studies took account of thermoregulation (Øritsland and Markussen 1990; Ryg and Øritsland 1991; Hammill et al. 1995) and two were looking at seal populations in Arctic regions. The rest assumed that the seals never encountered conditions requiring them to thermoregulate.

Øritsland and Markussen (1990) used a detailed physiological model to determine the heat balance and, thus, the thermoregulatory cost for each size class (both in air and water). The results indicated seasonal variation in the cost of thermoregulation as well as a difference between age classes. The highest cost was 20% of the total energy requirements for females during the summer. The ringed seal study (Ryg and Øritsland 1991) simply assumed that the metabolism of a seal in air was 1.5 times greater than its basal metabolic rate. Hammill et al. (1995) assumed that hauled-out grey seals had a metabolic rate higher than basal and compared this to a calculated minimum heat production, taking the higher value in calculating the haul-out cost.

5.4 Population energy requirements

5.4.1 Time budgets

In order to calculate the total amount of energy spent on different activities some estimate of the amount of time spent on each is necessary. Daily time budgets generally included periods of rest (varying from 25% to 50% of the day) and swimming at different speeds, although (Olesiuk 1993) used a single swimming classification which accounted for 60% of the seal's time. Only Hammill et al. (1995) considered seasonal variation in time allocation, with differences between the breeding and moult periods and the rest of the year.

A slightly different approach for the total cost of locomotion is to estimate the distance a seal swims and multiply by the cost of transport. This was done for common seals in the Skaggerak (Härkönen and Heide-Jørgensen 1991), but considering it to be an overestimate the authors resorted to an educated guess for the cost of swimming.

5.4.2 Population size and structure

To calculate the per capita energy requirement of a ringed seal population, Ryg and Øritsland (1991) used a published age distribution for ringed seals in western Canada and assumed that the age-structure was stable. Similarly, Härkönen and Heide-Jørgensen (1991) used published age structures, from two years, for common seals in the Skaggerak, which in turn were calculated from stock data. The results from a previous publication were also used by Hammill et al. (1995) for the grey seal populations on Sable Island and in the Gulf of St. Lawrence, both off Eastern Canada.

Other studies used population models to calculate the age-structure. Lavigne et al. (1985) calculated the age structure for harp seals in the western Atlantic using different mortality rates. The results were then compared with published age structures for exploited seal populations. A range of values were used for the age of maturity and fertility and the sex ratio was assumed to be 1:1. Based on census information for the common seal population in the Strait of Georgia (western Canada) Olesiuk (1993) calculated the birth rate, the mortality and, hence, the seasonal change in numbers. The population was assumed to be below its carrying capacity, skewing the age distribution towards juveniles. For a hypothetical harp seal population Øritsland and Markussen (1990) used a Leslie matrix to calculate the age and sex structure, based on a sex ratio of 1:1 for newborns.

Population sizes appropriate to the species and region, of each study, were generally taken from published stock assessment studies.

5.4.3 Estimates of energy requirements

The easiest way to compare the energy requirements calculated in the different studies is to look at the daily energy requirements (DER) of an individual. Values from the different studies are shown in Table 5.1, although the exact criteria vary slightly. For harp seals in the western Atlantic a range of estimates were produced using different population sizes and age structures. The other harp seal study produced separate estimates of DER for male and female adults (shown in the table). The ringed seal study calculated average per capita DER throughout the year and the yearly range is shown.

Species	Region	DER (MJday^{-1})	Reference
harp seal	Western Atlantic	26.4 to 31.6	Lavigne et al. (1985)
harp seal	Barents & White Seas	46.7 to 56.9	Markussen and Øritsland (1991)
ringed seal	-	7.62 to 14.2	Ryg and Øritsland (1991)
common seal	western Canada	14.9	Olesiuk (1993)
common seal	Skaggerak	19.6	Härkönen and Heide-Jørgensen (1991)

Table 5.1: Previous estimates of the per capita daily energy requirements (DER) for different seal populations.

There are significant differences between the DER estimates from the different studies. The most obvious division is between the estimates for harp seals and those for the (smaller) ringed and common seals. It is not unreasonable to attribute this to the size difference; a typical adult harp seal weighs over 100 kg as opposed to around 70 kg for an adult common seal. The difference between the two estimates for harp seals is, however, as great as the difference from the smaller seals. The authors of the more recent study (Markussen and Øritsland 1991) attribute this to the different assumptions made about activity costs. Another key difference is the inclusion in the later study of thermoregulatory costs. The two studies on common seals (Olesiuk 1993; Härkönen and Heide-Jørgensen 1991) differ by a factor of only 1.3 despite the very different approaches taken, Olesiuk attributes the difference to the calculation of maintenance requirements. Both studies resulted in similar partitioning of energy demand between the different costs; 68-73% on maintenance, 19-26% on activity, 1.4-2% on growth and 4-5% on reproduction.

5.5 Discussion

The studies described here have all taken slightly different approaches to what is essentially the same problem. The general use of Kleiber's relationship to calculate maintenance costs, with an appropriate modifier for juveniles, is well supported by empirical evidence (see Chapter 2) and provides the corner stone for estimating the energy requirements of a seal. Indeed, maintenance costs proved the largest portion of the annual requirements in most of the studies.

Following maintenance costs, the cost of activity (swimming) generally accounted for most of the rest of a seal's requirements. Unfortunately, this is also the aspect of these previous studies which has had most recourse to conjecture and surmise. The assumed cost of swimming has generally been based on a crude extrapolation of empirical observations coupled with a time budget consisting of best estimates. With advances in telemetry both detailed information on swimming speeds during diving and on the allocation of time between diving, resting and hauling-out is now becoming available. Using this, it should be possible to improve upon previous calculations.

Only one of the studies (Markussen and Øritsland 1991) made use of a detailed, physiological model for estimating individual energy requirements. This resulted in a thermoregulatory cost being predicted, for juvenile and adult harp seals, that varied between summer and winter. At its highest (a female adult in summer) this cost was predicted to be 20% of an individual seal's energy requirements. Although the need to take account of thermoregulation in an Arctic species is more obvious it may well be appropriate for species in temperate regions and should be investigated. The work described in Chapter 4 points to common seals in Scotland facing a significant thermoregulatory cost whilst hauled-out.

Chapter 6

Seasonal variation in individual energy requirements.

6.1 Introduction

In the previous chapter (Chapter 5) I discussed the differing approaches taken by previous studies of seal bioenergetics. A number of the features of these suggest a need for further work. All the studies made simple assumptions about the cost of swimming to individual seals and yet found this to be the second largest component of the energy budget, after maintenance costs (e.g. Härkönen and Heide-Jørgensen 1991). The assumptions were based on isolated empirical data for different species and, until recently, there has been no synthesis of the information provided by the different studies of the swimming energetics in pinnipeds. Using the detailed, mechanistic model described in Chapter 3 I was able to explain a number of apparently anomalous features in the empirical data. The key to this lay in the interaction of hydrodynamic and thermoregulatory constraints. One of the conclusions was that the optimal swimming speed of seals depends on both individual size and the water temperature. This, in turn, implies that the energetic cost of foraging may vary seasonally, a factor that has not previously been considered.

In addition to a simple representation of the cost of swimming, the majority of the previous studies assumed that the seals are within their thermoneutral zone at all times and do not incur any thermoregulatory costs during haul-out periods. Although observational evidence of an influence of weather conditions on the haul-out behaviour of seals remains inconclusive (Grellier et al. 1996), avoidance of adverse conditions has been seen in temperate as well as polar species (e.g. Smith 1965 and Pauli and Terhune 1987). Unfortunately, experimental work on the thermal balance of seals in air has generally focused on the effects of temperature alone (e.g. Hansen et al. 1995), neglecting the interaction with wind speed and solar heating. In Chapter 4 I described a comprehensive, mechanistic model of the heat balance of a hauled-out seal. For an adult female common seal (hauled-out in the Moray Firth, Scotland) the predicted metabolic rate varied markedly between seasons, being almost twice as high in winter than summer. On most days the predicted metabolic rate was higher than the basal rate, due to the cost of thermoregulation. The model was used to explain the timing of breeding, it occurs when the extra cost of thermoregulation would be lowest. This provides indirect evidence that thermoregulation costs are significant for common seals in Scotland and must be looked at seasonally.

The development of detailed models of specific aspects of the energetics of individual seals has high-lighted some of the overly simplistic assumptions made in previous studies of seal energy requirements. Furthermore, these same models create the opportunity to estimate the energy requirements of seals at any time of the year and so make a more exhaustive assessment of seasonal variation. Seasonal changes in the diet of seals and the energy content of their prey have been taken into account previously (e.g. Olesiuk 1993), but this has not been paralleled by consideration of the seasonal variation in energy requirements.

In this chapter I use the models described in Chapters 3 and 4 to estimate the seasonal energy requirements of individual seals. The common seal population resident in the Moray Firth region of the North Sea provides a particularly expedient case study. This population is the subject of a long term study by University of Aberdeen, which has yielded a detailed description of the activity patterns of the seals (e.g. Thompson and Miller 1990; Thompson et al. 1994). Combined with the detailed information on diving behaviour now available (e.g.Bjørge et al. 1995) this creates an opportunity to make a comprehensive investigation of the seasonal energy requirements of common seals.

6.2 Common seals in the Moray Firth.

The Moray Firth is an inshore region of the North Sea (Figure 6.1), forming a ragged triangle bounded by the coastline between Fraserburgh (in the south-east) and Helmesdale (in the north). The sides of this triangle are incised by three deep water estuaries; the Dornoch Firth, the Cromarty Firth and the Beauly Firth. The region is home to a resident breeding population of common seals (*Phoca vitulina*) which hauls-out on inter-tidal sand and mud banks in the inner Firths and at Ardersier (east of Inverness) (Thompson et al. 1994). To a lesser extent, sites in Loch Fleet and Findhorn Bay (to the north and the east of Inverness respectively) are also used. Foraging trips, although spanning up to 6 days (Thompson and Miller 1990), are generally close to the haul-out sites (Tollit et al. 1998). For the majority of seals tracked the foraging range lay within 20 km of the haul-out site, although one seal travelled over 70 km from its haul-out site. Common seals are evidently more parochial in their movements than their larger cousins, the grey seals, which are also found in the Moray Firth. Grey seals on the east coast of Britain have been observed to move regularly between haul-out sites in the Farne Islands, the Orkneys and a number of places between (Hammond et al.

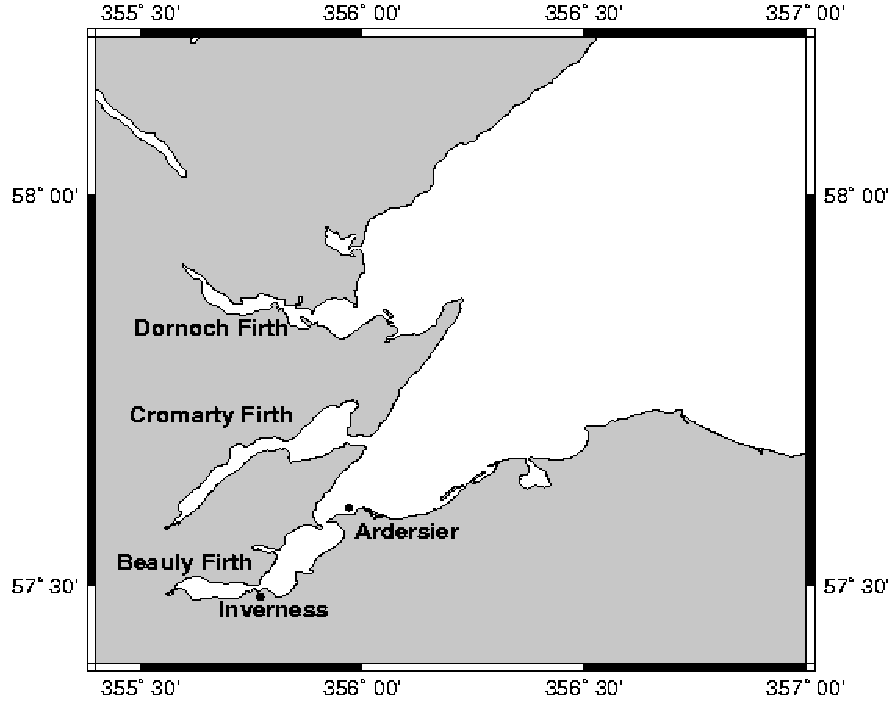

Figure 6.1: The Moray Firth region of the North Sea with Inverness shown as a reference point. The other labels refer to key haul-out sites for the resident common seal population.

1993; McConnell et al. 1992). Given the limited movements and the distance to the nearest breeding colonies (in Orkney and the Firth of Tay) there is the added attraction that the common seals can be assumed to form an isolated population. Although a few juveniles have been observed to travel between the Moray Firth and Orkney (Thompson 1993), this is not significant in looking at population energetics.

For the work described here I shall use three size classes representing juveniles, adult females and adult males. Based on plasma progesterone concentrations Gardiner et al. (1996) classify female common seals from the Moray Firth that are greater than 1.25 m in length as sexually mature. For male common seals in Danish waters the length at maturity is 1.30 m (Härkönen and Heide-Jørgensen 1990), based on testes weights. I have, therefore, classed any seal greater than 1.25 m as an adult and any less than that as a juvenile. Although adult common seals may reach lengths of 1.6 m, length at age plots (Corpe 1996) suggest 1.35 m and 1.45 m to be typical lengths for adult female and male seals, respectively. The length of the juvenile (1 m) is based on a one year-old seal. The weight, surface area and average blubber thickness of the seals were estimated from published relationships (Innes et al. 1990; Ryg et al. 1993). In parameterising the heat balance models I have used Kleiber's relationship (Kleiber 1947) to calculate the basal metabolism of the three size classes, but have doubled the rate for the juvenile (Lavigne et al. 1986). The morphometrics and basal metabolic rates of the three size classes are given in table 6.1.

Size class	L (m)	W (kg)	d_B (mm)	BMR (W)
juvenile	1.0	24.4	27.4	74.3
female adult	1.35	62.2	31.4	75.1
male adult	1.45	77.8	32.4	88.8

Table 6.1: Details of the morphometrics of the three size classes of common seal used in this chapter. The body lengths (L) were selected as being typical to the class. The mass (W), blubber thickness (d_B) and basal metabolic rate (BMR) were taken from published relationships, see text.

The Moray Firth is generally shallow (less than 60m), but with a deeper channel along the southern coast (Adams and Martin 1986). There is little difference between surface and bottom water temperatures, but these do vary seasonally between a spring minimum of 5 C and a late-summer maximum of 12 C. Monthly water temperatures are shown in Figure 6.2.

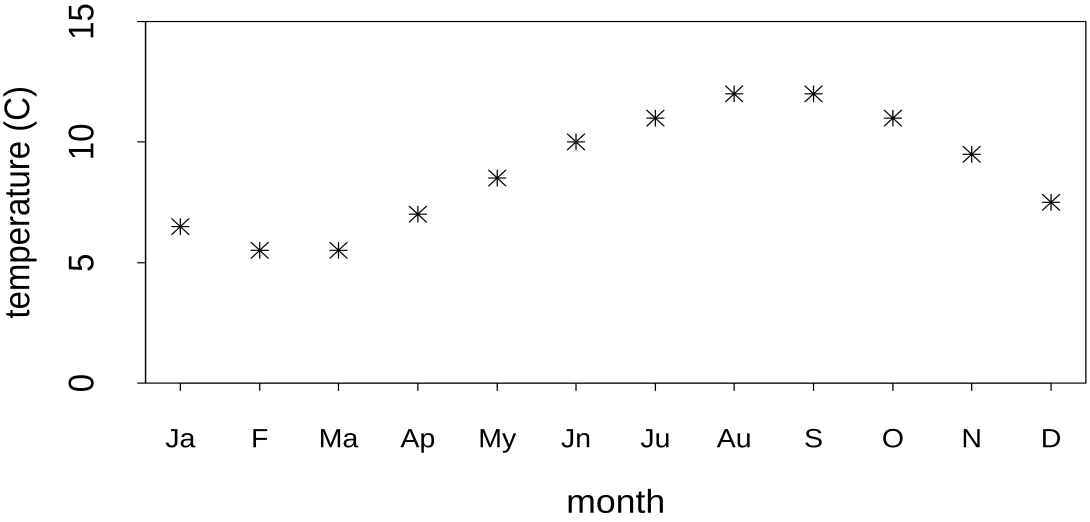

Figure 6.2: Typical monthly water temperatures for the inner Moray Firth.

The UK Meteorological Office coastal weather station at Kinloss (station no. 1057) records data on the air temperature and wind speed, while the nearest station which records solar irradience is Aviemore (station no. 0585). The daily recordings for a two year period are shown in Chapter 4 (Figure 4.3).

6.3 The energetic cost of activities

One of the limitations of the model described in Chapter 3 for the swimming cost of seals is the abrupt transition from stationary to turbulent flow as the seal speeds up. In reality the boundary flow over the seal will be laminar at very low speeds, becoming turbulent as the speed increases, and this will affect the heat transfer mechanics. I have, therefore, adopted the approach to flow transition described in Chapter 4, along with the appropriate heat transfer relationship for laminar boundary flow. Although making the model more generally applicable this adaptation made little difference to the model's behaviour. For an adult common seal the transition from laminar to turbulent flow occurred around 0.1 ms^{-1}; below this the metabolic rate increased linearly before reaching the rate predicted by the original model.

6.3.1 Foraging

The costs of foraging and of resting in the water were predicted using the model described in Chapter 3, as functions of the seal's size and the seasonal water temperature. Previously I suggested that the optimal swimming speed for a seal, V_{opt}, is that which minimises the cost of transport (COT). Although this appears reasonable for a seal making "travelling" dives, the optimal speed for a foraging seal requires more careful consideration. Thompson et al. (1993) extended work done on the optimal time allocation for diving animals (Housten and Carbone 1992) to the foraging dives of seals. Based on telemetry studies, they suggest that foraging common seals are acting to maximise their energy efficiency. For slow moving prey they found that the swimming speed that maximised energy efficiency was V_{opt} (i.e. that which minimises COT).

Advances in telemetry mean we now have a picture of the, previously hidden, diving behaviour of wild seals. Bjørge et al. (1995) present dive records from an adult common seal in the Froan Islands, Norway, under three classes: travelling dives, foraging dives and mating display dives. Whilst foraging in the coastal waters the seal swam continuously during dives (which were generally to the sea-bed) and the surface periods between dives were short. The swimming speed of the seal during the dives was highly variable, ranging from 0.5 to 3 ms^{-1}. It would appear that prey capture requires bursts of fast and slow swimming and it is not sufficient to assume that they swim at V_{opt}. The importance of looking at foraging costs averaged over diving bouts (as opposed to individual dives) has been emphasised by de Leeuw (1996), in reference to diving ducks. The need to include the stationary periods at the surface is obvious, but the variability of swimming speed during the dives must also be considered. Due to the non-linear nature of the cost of swimming at different speeds (see Chapter 3, Figure 3.6) even short bursts at high speed may have a significant effect on the overall cost of the dive.

I have followed the same procedure to calculate the cost of the three different types

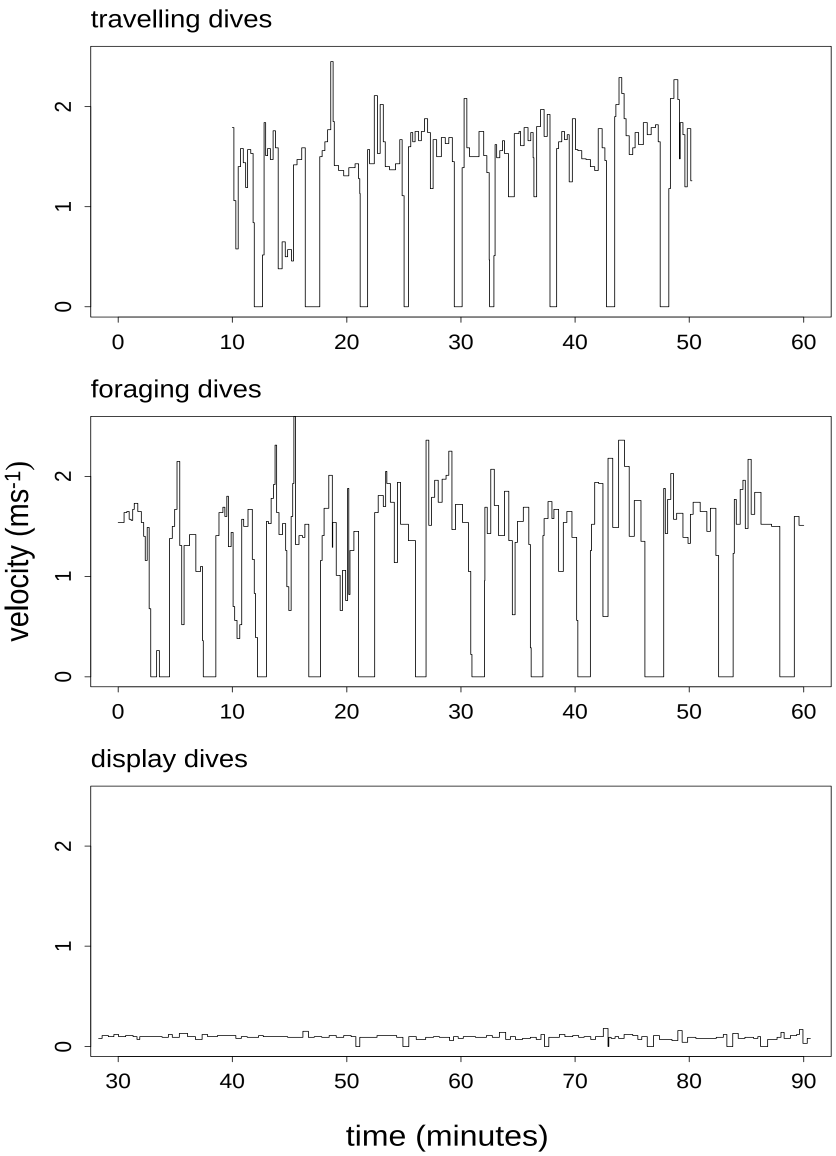

Figure 6.3: Swim speed records for an adult male common seal engaged in three different activities (adapted from Bjørge *et al.* 1995, see text).

of diving (averaged over a bout of dives), but will defer discussion of display costs. I divide the dive records, covering between 10 and 18 dives, (Bjørge et al. 1995, their Figures 2 ,3 and 6) into discrete periods in which the seal can be considered to swim at a constant speed, Figure 6.3.

Using the model of swimming costs I can calculate the metabolic rate associated with each of these speeds, for each size of seal. Multiplying each metabolic rate by the time for which it applies gives the total cost of the diving bout. The seal's average metabolic rate for foraging is simply this total cost divided by the period of the bout. The predicted metabolic rate during travelling and foraging dive bouts are shown in Figure 6.4, for the three size classes of common seal. The average metabolic rates for whole bouts are also shown (horizontal lines).

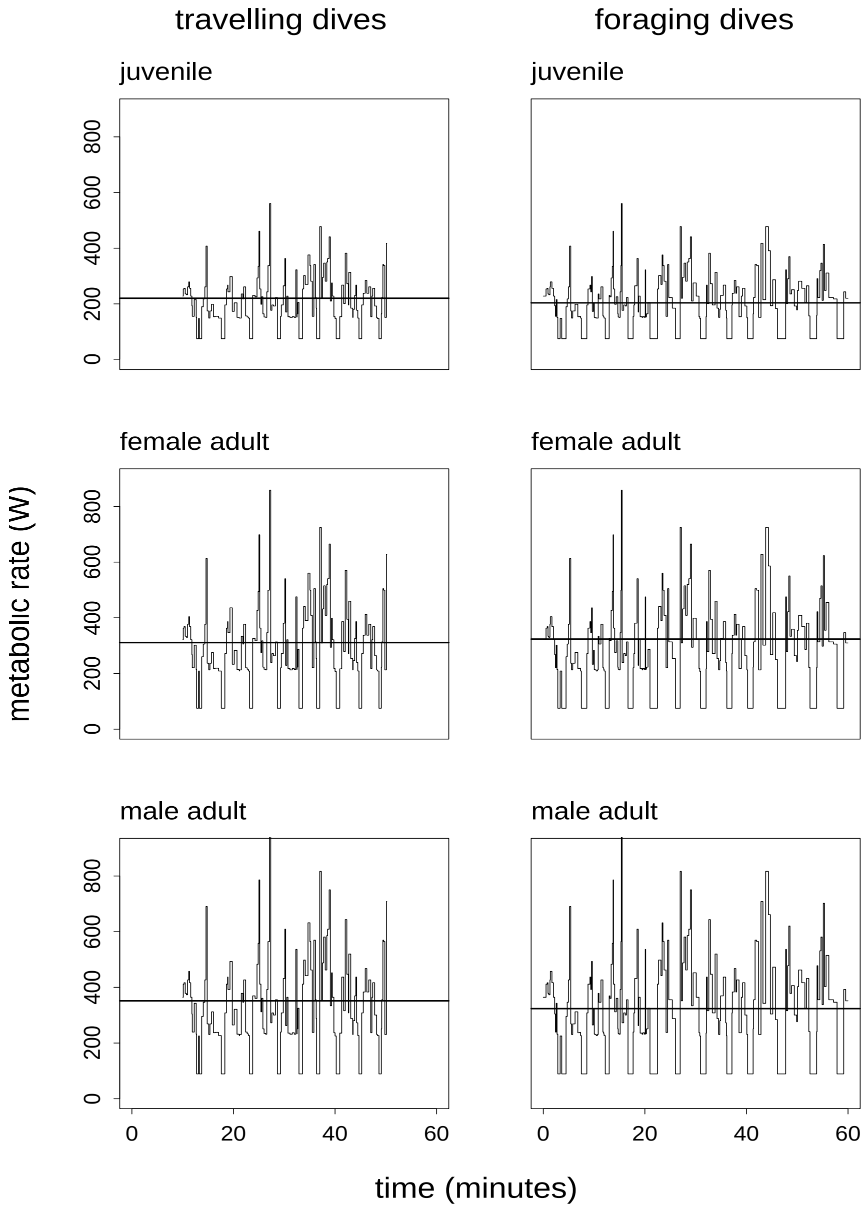

Figure 6.4: The predicted metabolic rate for different sized seals during bouts of travelling and foraging dives. The horizontal lines indicate the average for the whole sequence of dives.

Repeating this procedure, using water temperatures appropriate to the Moray Firth (Adams and Martin 1986), provides me with a monthly metabolic rate for travelling and foraging dives. These are shown (for each of the size classes) in Figure 6.5, along with the metabolic rates (M_{opt}) corresponding to the optimal swim speed V_{opt}. For all three size classes, the metabolic rate whilst travelling and foraging is significantly greater than M_{opt} and both are greater than the basal metabolic rate (also shown). For both the adult classes, the predicted metabolic rate during dives is over 3.5 times the basal rate, this is slightly lower for the

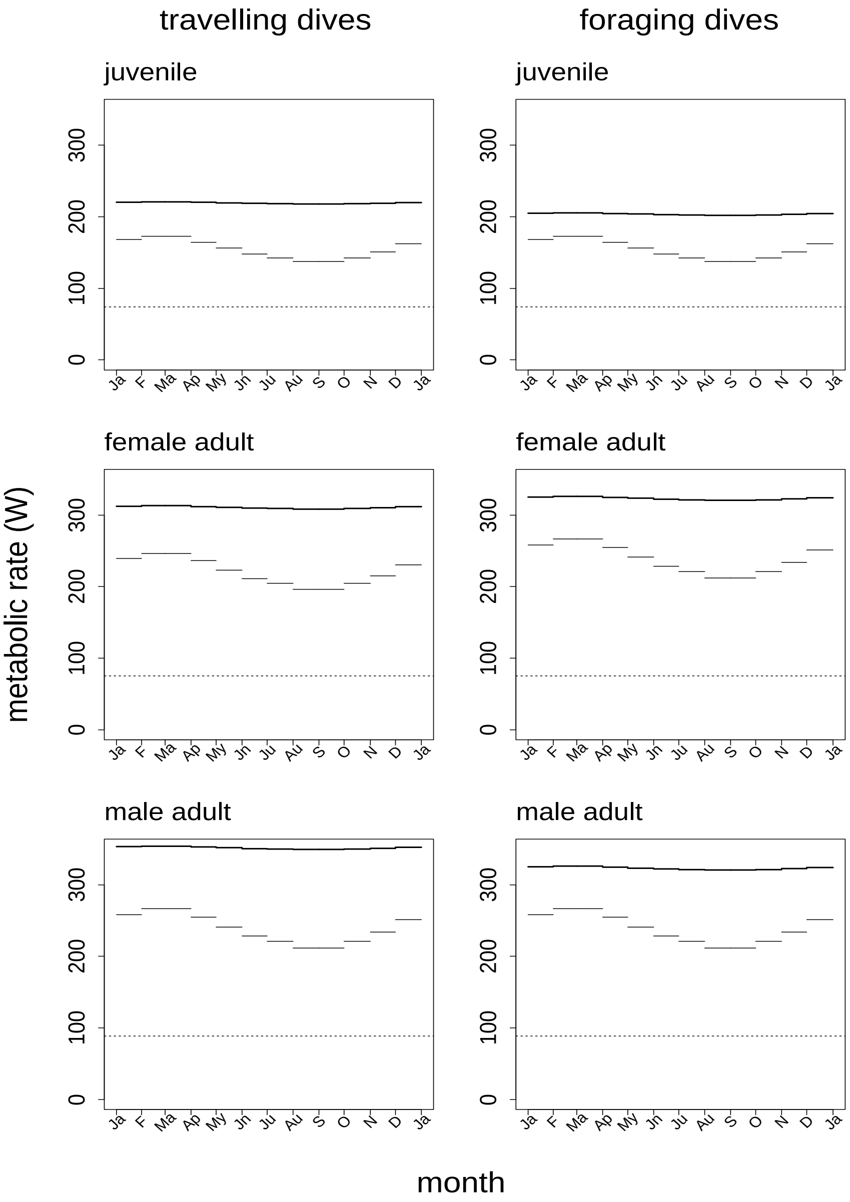

Figure 6.5: The seasonal variation, for three size classes of common seal, in the average metabolic rates for travelling and foraging dive periods (heavy line). The metabolic rate corresponding to the optimal swimming speed (see text) are shown by the thin lines and the basal metabolic rates by the dotted line.

juvenile since its basal rate is elevated. Although M_{opt} shows some seasonal variation, the calculated foraging costs vary little between each month. The reason for this can be seen (using the adult male as an example) by plotting the cost of swimming curves for the warmest and coldest water temperatures, Figure 6.6. There are three features to note; firstly, the rate at rest is independent of temperature, secondly, above a moderate speed the metabolic rate again becomes independent and, finally, the non-linearity means that bursts of fast swimming will skew the average swimming cost. The average metabolic rate is, therefore, dominated by the rate at rest (which applies for about a quarter of the diving

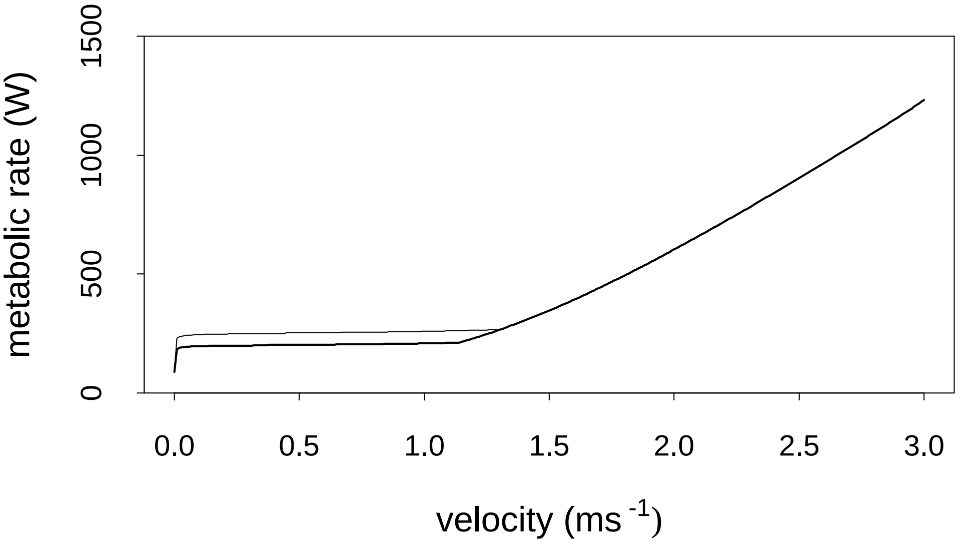

Figure 6.6: The predicted metabolic rate of an adult male common seal swimming in water at two temperatures. The heavy line corresponds to the annual maximum water temperature for the Moray Firth and the thin line to the minimum.

period) and the bursts of high cost associated with fast swimming, both of which are independent of temperature and therefore season.

The final step in calculating the cost of foraging requires information on the duration of the foraging trips and the distance between foraging sites and the haul-out sites. In the Moray Firth, common seals generally forage within 10 to 20 km of their haul-out site (Tollit et al. 1998) and these foraging trips typically last about 48 hours (Thompson and Miller 1990). Taking a distance of 15 km and a travelling speed of 1.3 ms^{-1} (the speed averaged over the whole foraging dive record in Figure 6.3) implies a $6\frac{1}{2}$ hour round trip to the foraging ground. If the seal spends 48 hours offshore then 13% of the foraging trip is spent travelling. I assume that the seals do not rest at sea and that the rest of the trip is spent actively foraging. (Coltman et al. 1997) present an 18 hour dive record for a foraging common seal which contains no extended surface periods. The metabolic cost for a foraging trip is simply the weighted average of the travelling and foraging costs. Since there is little difference between the cost of these two activities the resultant average will not be very sensitive to the assumptions I have made.

6.3.2 Resting in water

The model for swimming costs predicts that (for all the sizes and monthly water temperatures) the metabolic rate of a seal at rest in water is equal to its basal metabolic rate. Since the seals in the Moray Firth use sand banks, the availability of the haul-out sites is dictated by the tide state. Common seals in this area forage in the outer Firth for an extended period before returning to the haul-out sites in the inner Firths. I follow Thompson (1993) in assuming that foraging is restricted to the outer Firth area and that during the time spent in inshore regions the seals are resting in the water. There is, therefore, no additional cost associated with spending time in-shore.

6.3.3 Haul-out

Using meteorological data for 1989 and the model of heat balance in air, described in Chapter 4, I have predicted the metabolic rate during haul-out periods throughout a year (for the three size classes). The metabolic rates of the seals are shown in Figure 6.7, along with the monthly average metabolic rates (indicated by the horizontal bars). The model predicts that at most times of the year there is a thermoregulatory cost associated with hauling-out, regardless of size. During the summer the metabolic rates remain below twice the basal rate for the adult seals. Since the basal rate of the juvenile is elevated the cost of hauling-out is proportionally lower than for the adults. In contrast to the cost of foraging the thermoregulatory cost of hauling out shows a marked seasonal pattern.

6.3.4 Male mating displays

Following the weaning of their pups around the beginning of July, female common seals resume their foraging trips and, coincident with this, the males begin to perform aquatic mating displays (Van Parijs et al. 1997). The aquatic displays consist of characteristically shallow dives (Bjørge et al. 1995; Coltman et al. 1997), during which they perform a vocal mating display (Van Parijs et al. 1997).

Since display dives are confined to adult males in the breeding season (July) only a single cost determination is necessary. The dive record for a displaying male common seal is shown in Figure 6.3 and the most striking feature is the very low swimming speed. To calculate the metabolic rate of a male performing display dives I applied the same method used for the other dive types (see section 6.3). For an adult male common seal the average metabolic rate while displaying is 200 W. This is a little over twice the basal metabolic rate and significantly lower than the rate during foraging. Of the three dive types investigated here, display dives are by far the most energetically economic. Since displaying supplants foraging, the slow swim speeds may be a means of minimising the cost and hence the weight loss experienced by the males (Walker and Bowen 1993). It has been suggested that a competitive advantage is conferred on the male that can afford to dedicate the most time to displaying (Coltman et al. 1997) and this would favour diving behaviour that minimises energy use.

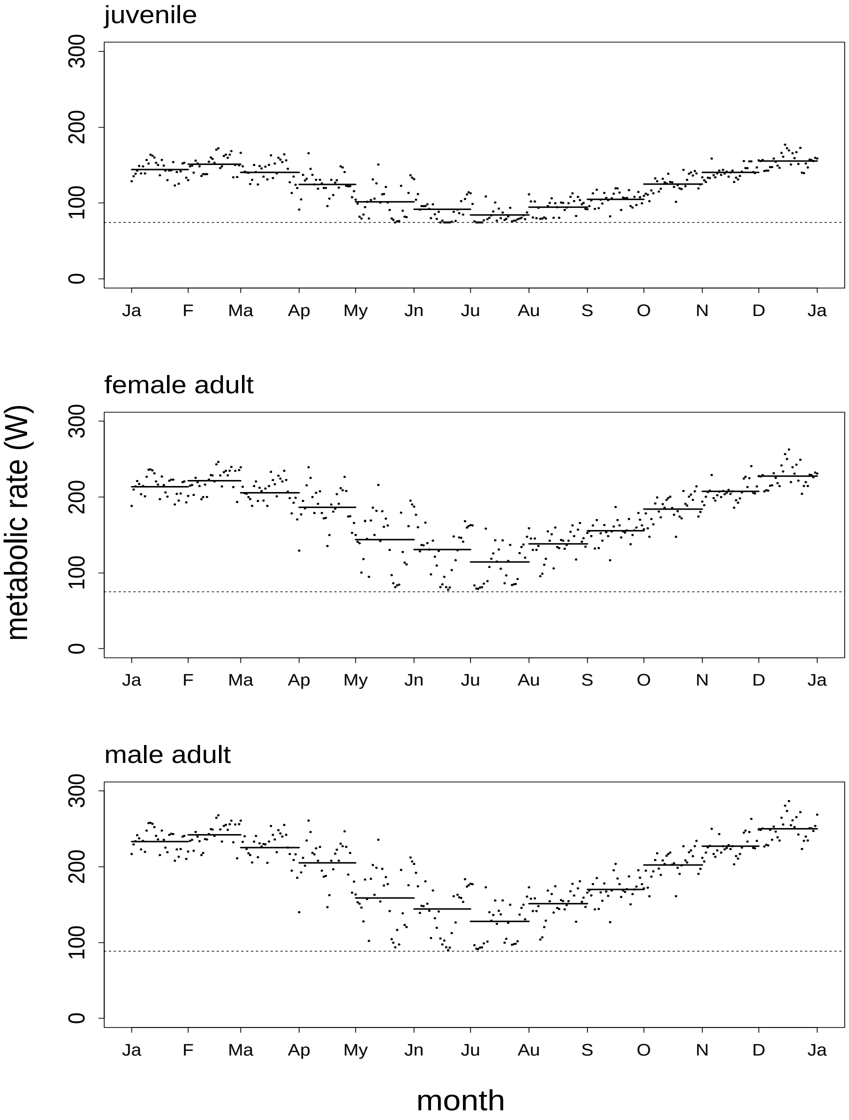

Figure 6.7: The predicted metabolic rate of common seals hauled out in the Moray Firth, weather data were taken from 1989. The horizontal bars show the monthly average metabolic rate for each of the three size classes.

6.3.5 Fixed costs

By its definition the basal metabolism of a seal is independent of its activities and its environment. For all adult seals I have used Kleiber's relationship (Kleiber 1947) to calculate the basal metabolic rate. Juvenile seals are known to have elevated metabolic rates and (based on pooled data from several phocid species) Lavigne et al. (1986) suggest that twice "Kleiber" is appropriate. More recent determinations of the basal metabolism of juvenile seals are generally consistent with this scaling (Nordøy et al. 1990; Markussen 1995) and I have used it.

The assumption that seals do not exert hourly control over the energy they spend on growth implies that the cost of growth accounts for the elevated, resting metabolic rate measurements of juvenile seals. I do not, therefore, include any additional growth cost. This assumption is supported by concurrent measurements of the metabolic rate and growth rate of young harp and grey seals (Worthy 1987).

Until seal pups break their post-weaning fast all their energy requirements are met by the transfer of energy from the mother to the pup. Prior to parturition the energy transfer is internal and occurs across the placenta. Post parturition the pup is dependent entirely on its mother's milk to meet its energy requirements. It follows that the energetics of pre-weaning pups are most appropriately considered as maternal investment by breeding females. Based on a study of common seal mothers and pups on Sable Island, Bowen et al. (1992) put forward a figure of 93 MJ for the energy content of a newborn pup (with an average mass of 10.6 kg) and 714 MJ for the energy loss by mothers during the first 19 days of lactation. It should be noted that the latter figure includes the mother's maintenance costs. In order to calculate the maternal energy cost of reproduction I must first estimate the mother's own costs for the 19 day period and subtract this from the energy loss value. The time budget for calculating the mothers cost is discussed in the next section, but the resultant estimate of the cost for the first 19 days of lactation is 531 MJ. Since lactation actually lasts about 24 days (Bowen et al. 1992), I have increased the maternal investment cost for 19 days by the appropriate factor, arriving at a total cost for the lactation period of 670 MJ. The cost of pregnancy comprises the energy content of the newborn pup and the maintenance requirements of the foetus. I follow Lydersen (1995) in calculating the latter from a simple relationship ($18.4W^{1.2}$ MJ) based on the mass of the newborn pup (W). The total cost of pregnancy (406 MJ) is spread over most of the year and I assume a gestation period of eight months, the active gestation period for ringed seals (Lydersen 1995).

6.4 Seasonal energy requirements.

So far no clear picture of seasonal variation in energy requirements has emerged. The cost of foraging appears to remain almost constant through the year in contrast to the cost of hauling-out, which varies greatly. In order to calculate the actual energy requirements of the seals throughout the year I must apportion their time to these different activities.

6.4.1 Time budgets

Information from the radio tracking of individual seals in the Moray Firth makes it possible to describe their activity budgets in broad terms. Data for males and females tracked during the summer (but outside the pupping and mating periods) were used to estimate the proportion of time spent hauled-out, inshore and offshore (Thompson, P., unpublished data). I follow Thompson et al. (1994) in assuming that, whilst inshore, seals spent the time resting in the vicinity of the haul-out site and that foraging was restricted to the time spent offshore. Taking the average of the proportion estimates gives the summer activity budget for the common seals as: 22% of their time hauled out, 19% inshore and the remaining 59% spent offshore.

Thompson et al. (1992) report that the mean proportion of time spent hauled out dropped in the winter to 15%. Assuming that the seals spend the extra time in the water foraging (offshore) gives a winter activity budget of: 15% hauled out, 19% inshore and 66% offshore.

Females are constrained in their movements during lactation, by the limited swimming abilities of the pups. Consequently during the initial 10 to 24 days (mean = 18 days) the females remained in the vicinity of the haul-out sites and spent between 6 and 10 hours hauled-out each day (Thompson et al. 1994). Taking a daily haul-out period of 9 hours per day as typical, results in an activity budget for lactating females of: 38% hauled out and 62% inshore. Although lactation in common seals in another population has been observed to last 24 days (Bowen et al. 1992), the females resumed feeding after about 19 days. In the Cromarty Firth lactating females reverted to spending time offshore between 10 and 24 days after pupping (Thompson et al. 1994), which occurred around June 18th. With regards to the activity budget of breeding females I will take the period of constraint due to lactation to be 19 days.

Mature male common seals also alter their behaviour in relation to reproduction (Van Parijs et al. 1997), with significant amounts of time spent in performing display dives. Mass loss in male common seals has been recorded during the breeding period (Walker and Bowen 1993; Reilly and Fedak 1991) and this has been linked to a switch from foraging to aquatic display (Coltman et al. 1997; Van Parijs et al. 1997). There was no evidence that males in the Moray Firth were reducing the amount of time spent hauled out during this 25 day period. I will, therefore, assume that the proportion of time spent inshore and hauled-out remain the same, but for the first 25 days of July the time previously spent foraging is spent performing display dives.

6.4.2 Individual energy requirements

The energy requirements are divided into four groups: basal costs, foraging costs, the cost of hauling out, and reproductive costs (for breeding adults). Although resting inshore was considered as a separate activity, the predicted metabolic rate for this never exceeded the basal rate and there was no cost. To avoid the complication of differing month lengths I have calculated the daily energy requirements for each of the cost groups for each month, and these are shown in Figure 6.8. It should be noted that in calculating the costs the appropriate basal metabolic rates were subtracted from the predicted, activity specific, metabolic rates discussed in earlier sections.

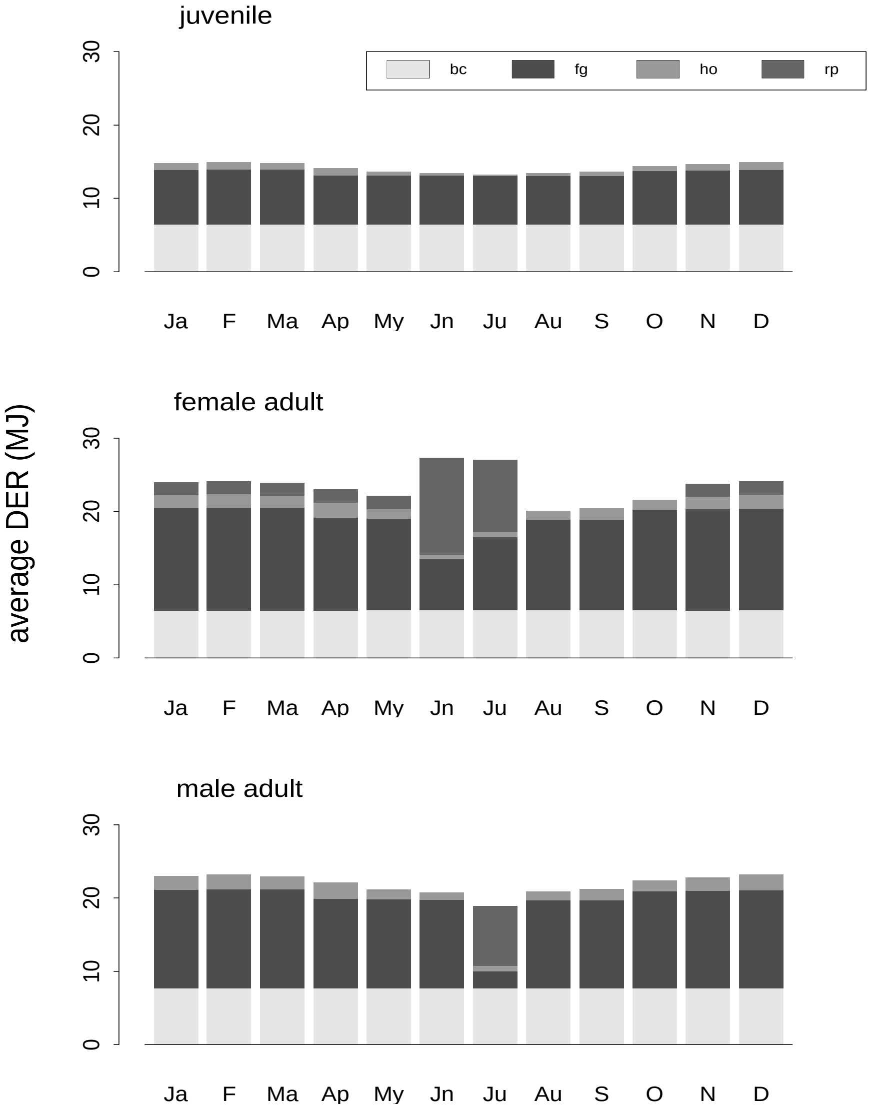

Figure 6.8: The seasonal energy requirements of common seals in the Moray Firth. The daily energy requirement for each of four categories is shown; basal costs (bc), foraging costs (fg), haul-out costs (ho) and reproductive costs (rp).

The total daily energy requirement (DER) of the juvenile seal shows little variation between months, basal, foraging and digestive costs being essentially constant. Although the seasonal changes in the cost of hauling out are still visible they are only ever a small fraction of the total costs for the seal. The total cost is dominated by the basal cost and the cost of foraging, which are approximately equal.

Apart from the changes in June and July associated with breeding, the picture for the adult seals is similar. Foraging costs for the adult seals generally exceed the cost of maintenance and in most months are approximately twice the basal cost. For breeding female seals the cost of foraging is reduced in June and July as they remain around the haul-out sites, suckling their pups. The total DER for this period is, however, higher than at other times of the year due to the high costs of lactation (around twice the mother's maintenance costs). Reproduction costs associated with gestation (November through to mid-June) are only a small proportion of the mother's total energy requirements. Behaviour changes associated with breeding lead to a shift in the energetic costs of a male adult common seal. Foraging costs become much reduced as the seal switches from foraging dives to displaying. The cost of these mating displays is slightly lower than the foraging cost and the seal's total energy requirements drop slightly in July.

6.5 Discussion

In this chapter I have applied the detailed models of the metabolic cost of swimming and of hauling-out, to an investigation of the seasonal energy requirements of individual seals. As a case study I have chosen to look at common seals resident in the Moray Firth region, Scotland. Combining predictions from the model described in Chapter 3 with details of the dive characteristics of common seals, I have calculated the average metabolic cost for a typical foraging trip, at different times of the year. Similarly, I used the thermoregulation model described in Chapter 4 to calculate the seasonal variation in the cost of hauling-out. In addition to calculating the costs of different activities I have estimated the fixed costs of maintenance, digestion and reproduction, from the appropriate published information. Knowledge of the activity patterns of common seals in the Moray Firth has made it possible to calculate the monthly energy requirements of juvenile and adult seals.

The results of this investigation suggest that the total daily energy requirements of common seals varies little through the year. Although the thermoregulation cost associated with hauling-out does vary, this is only ever a small fraction of total costs. The only exceptions to the lack of seasonality are the changes in June and July (for adults) associated with reproduction. The high cost of lactation increases the female's energy requirements above the monthly average. The opposite is true for males and the switch from foraging to aquatic display during July results in a drop in total energy requirement. Outwith the breeding season the energy requirements of all three size classes are dominated by maintenance costs and the cost of foraging, neither of which vary significantly with season.

There are little data available on the energy requirements of wild seals, against which we can make comparisons. Reilly and Fedak (1991) did measure the energy expenditure of a male adult common seal during the breeding season. The seal showed the mass loss associated with a switch from foraging to display activity (Coltman et al. 1997) and had an average daily energy expenditure of 52.5 MJ.

This is about twice as high as my estimate for the daily energy requirements of a male adult common seal during the breeding season. Since the seal studied by Reilly and Fedak (1991) was somewhat larger I calculated the daily average cost for a 1.55 m male (during the breeding season) but even allowing for digestive efficiency and specific dynamic action the result is only 33.5 MJday^{-1}. In these calculations I did not take account of any additional costs which might be associated with: vocalisations, mating encounters with females or aggressive encounters with males. A dramatic increase in the prevalence of neck wounds among mature male common seals (Thompson 1988) has been observed during the breeding season and these were assumed to be the result of fights between rival males. Such aggressive behaviour is likely to be costly (in energetic terms) and may account for the discrepancy between my predictions and the observation of energy expenditure in a wild seal. In the absence of data for other times of the year and other size classes it is difficult to make a more rigorous assessment of the estimates of daily energy requirement I have reported in this chapter.

The energy requirements predicted here are considerably higher than either of the previous estimates for common seals (Olesiuk 1993; Härkönen and Heide-Jørgensen 1991), discussed in the previous chapter. The key difference is the high foraging cost that has emerged from the detailed investigation of the energetic cost of this activity, described in section 6.3. Previously, swimming was thought to account for only about a quarter of a seal's energy requirements, but I have shown it to be a much greater proportion. Indeed, it represents as much as two thirds of the costs for adult seals outwith the breeding season.

Although the energy requirements of individual seals vary little through the year, this is not to say that prey consumption by the seal population does not differ between seasons. In the next chapter I build on the work described here and move on to looking at the impact of the common seal population in the Moray Firth on local fish species.

Chapter 7

Estimating the impact of common seals in the Moray Firth

7.1 Oh no, not another energy budget !

The energy requirements of common seal populations in both Pacific Canada and the Skagerrak, Denmark have already been subject to investigation (Olesiuk 1993; Härkönen and Heide-Jørgensen 1991). Given this, it would appear that estimating the energy consumption of the Moray Firth common seal population is a simple matter of re-applying the results of these studies (Tollit 1996). It is, however, my opinion that significant improvement can be made on the energy requirement estimates of previous studies. Having highlighted some of the limitations of these previous studies in Chapter 5 I went on to investigate the seasonal energy requirements of individual seals in Chapter 6. Taking a detailed look at the foraging costs of common seals I showed that this is higher than was previously thought and accounts for up to two thirds of a seal's average daily energy requirements. Consequently the energy requirements of individual seals are also higher. At the beginning of Chapter 6 I suggested that there may be significant seasonal variation in energy requirements. However, it transpired that this is generally not the case. The exceptions are the costs associated with breeding that are faced by adult seals.

In this chapter I will take the estimates of the energy requirements of individual seals described in the previous chapter as a platform from which to estimate the seasonal energy consumption of the common seal population in the Moray Firth. Information on the diet of common seals can be gained from studying the contents of faecal samples. The work done in the Moray Firth (Pierce et al. 1991; Thompson et al. 1991; Tollit and Thompson 1996; Thompson et al. 1996) gives a detailed picture of the diet of the common seal population. Using estimates of the abundance of individual species within the diet, by biomass, Tollit (1996) calculated the contribution, by energy, of each species. In combination with an estimate of energy consumption, this can then be used to estimate the consumption of individual fish species.

7.2 The size and characteristics of the seals

In Chapter 2 I used three size classes corresponding to a juvenile common seal and male and female adults. In this chapter I expand the juvenile class and use four different lengths to characterise the size range. I have again made use of published relationships for calculating the weight and surface area of the seals (Innes et al. 1990). Comparison of the length/weight relationship with data from seals captured in the Moray Firth (as part of the radio tracking programme conducted by University Aberdeen) shows there to be good agreement (Thompson P., unpublished data).

As part of the recording protocol a pig-fat meter was used to measure the blubber depth of captured seals. This was calibrated against samples of fresh blubber of known depth (Tollit, D., unpublished data), to obtain a correction factor of 0.951 (SD=0.186 n=10). The calibration implies a very close correspondence between measured and actual blubber thickness. Since the sample size of the calibration was very small, I take it to indicate that the pig-fat meter is an effective means of measuring blubber depth. I have, therefore, used the measured blubber thickness values directly, Figure 7.1. There is no clear separation between the data for male and female seals. The minimum thickness appears to remain constant with increasing weight, whilst the maximum thickness increases. Adult seals of both sexes experience marked weight loss associated with reproduction (e.g. Bowen et al. 1992; Walker and Bowen 1993) and this would result in a seasonal trend in blubber thickness. Unfortunately, there are insufficient data to separate this seasonal variation and I have resorted to fitting the data as a single set. The lines in the figure are the published relationship (thin line) used elsewhere in this thesis (Ryg et al. 1993) and a linear regression line for the combined data (bold line). The linear regression ($d_B(\mathrm{m}) = 0.015 + 1.12 \times 10^{-4} W$, $\mathrm{R}^2 = 0.187$) is significant at a probability of less than 10^{-4}. The allometric relationship from Ryg et al. (1993) consistently overestimates the blubber thickness of the Moray Firth common seals. Given that the allometric relationship was fitted to data for seals taken mostly from cold water regions this is not surprising. Since the pig-fat meter readings are specific to common seals in the Moray Firth I will use the regression relationship for calculating blubber depths in this chapter.

If the seals in the Moray Firth are indeed thin, it follows that their surface area may also be reduced, in comparison to the predictions of a published relationship between surface area and weight (Innes et al. 1990). Using girth measurements of the common seals (Thompson, P. unpublished data) I calculated the surface area of the torso by approximating it to two cones and two rostra. In the absence of detailed measurements of flipper size, was unable to calculate total surface area from measurements. Since there is no blubber on the flippers,the difference in surface area due to the seal's reduced blubber layer would be expected to occur

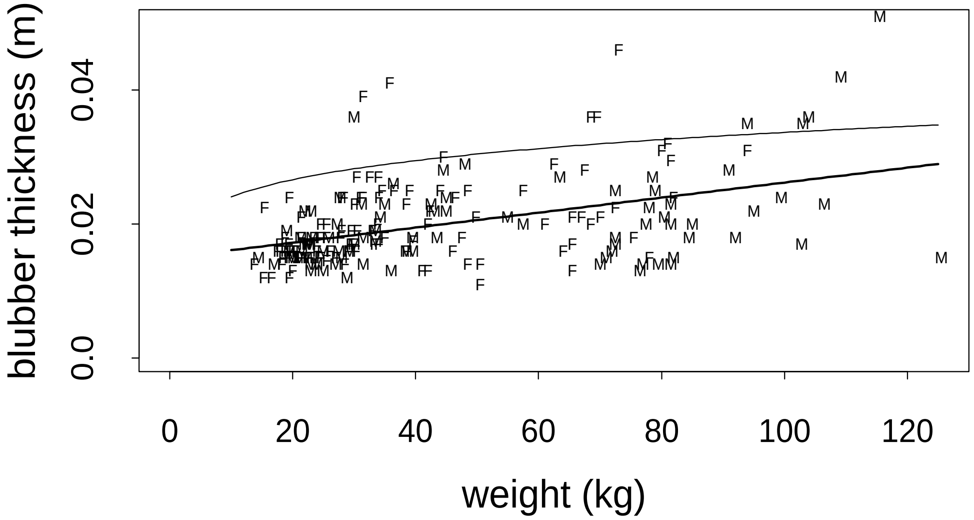

Figure 7.1: The blubber thickness of male (M) and female (F) common seals in the Moray Firth. The allometric relationship for blubber thickness from Ryg *et al.* (1993) is plotted (thin line), along with a linear regression relationship (bold line).

in the torso. I, therefore, estimated the flipper surface area from a published relationship (Innes et al. 1990). The estimates of total surface area were consistently lower than those predicted by the allometric relationship and re-examination of the data used by Innes et al. (1990) shows that their regression equation overestimated the maximum surface area of the four common seals included (their Figure 3.). I will therefore use a regression relationship for the estimated surface areas ($S = 0.118W^{0.51}$) to calculate the surface area of common seals in the Moray Firth.

The revised size characteristics for common seals in the Moray Firth are shown in Table 7.1.

7.3 Energy consumption by common seals

7.3.1 Revised individual energy requirements

Following the same approach I described in the previous chapter, I have recalculated the seasonal energy requirements using the new body characteristics (i.e. reduced blubber thickness and surface area) and included the new size classes. Figure 7.2 shows the monthly average daily energy requirement (DER) for three of the size classes (corresponding to those in Figure 6.8). Despite considerable

Size class	L (m)	W (kg)	(S m^2)	d_B (mm)	BMR (W)
juvenile	0.9	17.5	0.556	17.0	58.1
juvenile	1.0	24.4	0.664	17.7	74.3
juvenile	1.1	32.8	0.780	18.7	92.9
juvenile	1.2	43.1	0.903	19.8	114.0
female adult	1.35	62.2	1.10	22.0	75.1
male adult	1.45	77.8	1.24	23.7	88.8

Table 7.1: Details of the morphometrics of the size classes of common seal used in this chapter. The body lengths (L) were selected as being typical to the class. The mass (W) and basal metabolic rate (BMR) were taken from published relationships. The blubber thickness (d_B) and surface area (S) were calculated using regression relationships, see text.

changes to the scaling of two of the body parameters, there is very little difference between the energy requirements calculated using relationships from the literature and those calculated using relationships specific to the Moray Firth common seals. The only change is a slight increase in the amount of energy required for thermoregulation during haul-out periods. At most, this represents a 5% increase in the average DER. There is no difference in the energy required for foraging, for any size class or any month. This is consistent with the finding that the cost of foraging is independent of water temperature changes (section 6.3), since the altered parameters will principally affect the seals thermal balance.

7.3.2 From energy requirements to consumption.

In order to calculate the actual energy intake of individual seals I must account for the efficiency with which ingested energy is made available for meeting the seal's energy requirements. A significant proportion of the energy content of ingested food is lost in an animal's faeces and urine. Keiver et al. (1984) measured the faecal and urinary losses of grey seals and report a mean of 83% of the energy content of the food. In the absence of comparable measurements for common seals I use this value. In addition to the loss of energy in faeces and urine, heat is generated as a waste product of digestion, often referred to as specific dynamic action (SDA). In the absence of an estimate specific to common seals I assume that SDA is 17% of ingested energy, a value recorded for the larger harp seal (Gallivan and Ronald 1981). Combining these efficiencies indicates that the amount of energy that must be ingested is 1.45 times greater than the seal's energy requirement.

Adult seals undergo periods of fasting associated with lactation and mating display (for females and males, respectively) and their energy requirements during these periods must be met from body reserves. In order to maintain their av-

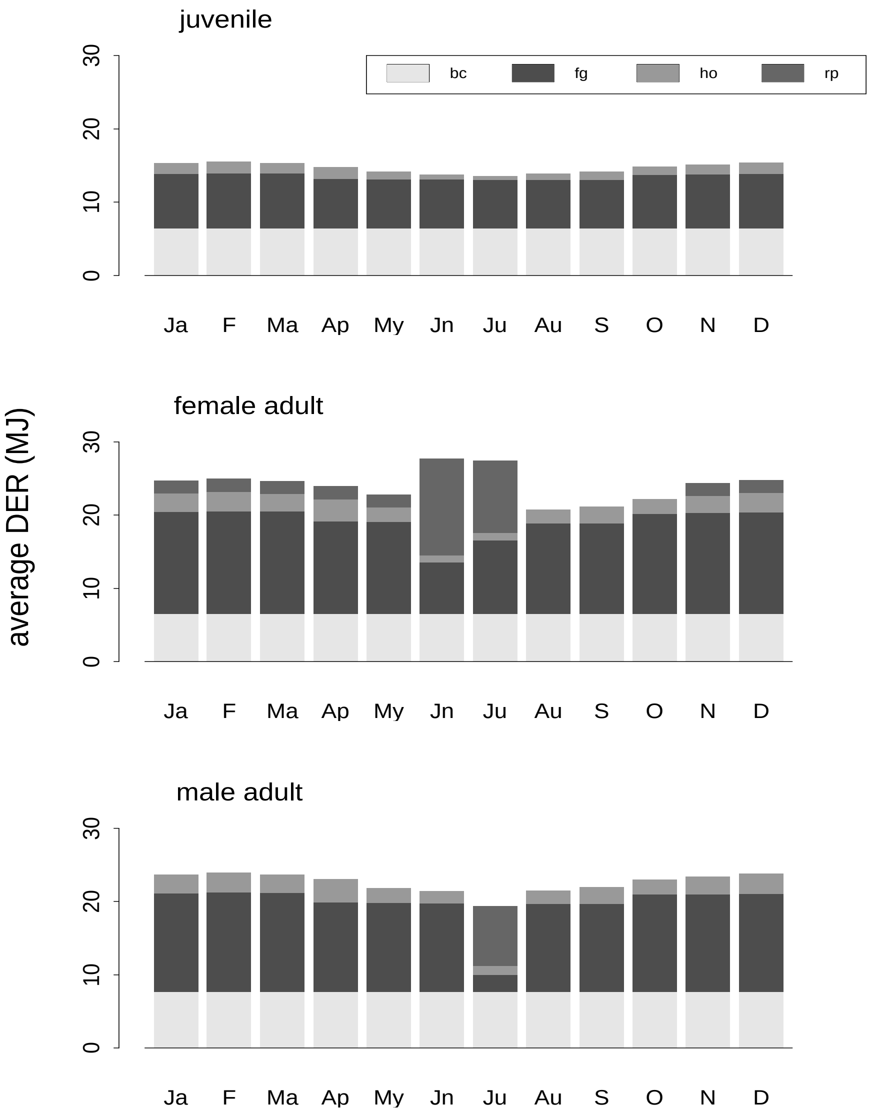

Figure 7.2: Revised seasonal energy requirements of common seals in the Moray Firth, using specific body parameter relationships (see text). The daily energy requirement for each of four categories is shown: basal costs (bc), foraging costs (fg), haul-out costs (ho) and reproductive costs (rp).

erage condition they must regain the mass lost during these fasts later in the year. Ringed seals have been found to recover their mass in the three months following the fasting (Ryg et al. 1990). In order to calculate the daily average energy intake for the adult seals, I have calculated the intake required to meet their energy requirements for the respective periods of fast. I have then averaged this over the three months following breeding (August to October). The resultant daily average energy consumption for each month is shown in Figure 7.3 for adult male and female common seals, and for a juvenile (of 1 metre length). The drop in energy intake in the adult seals during the breeding season is obvious, as is

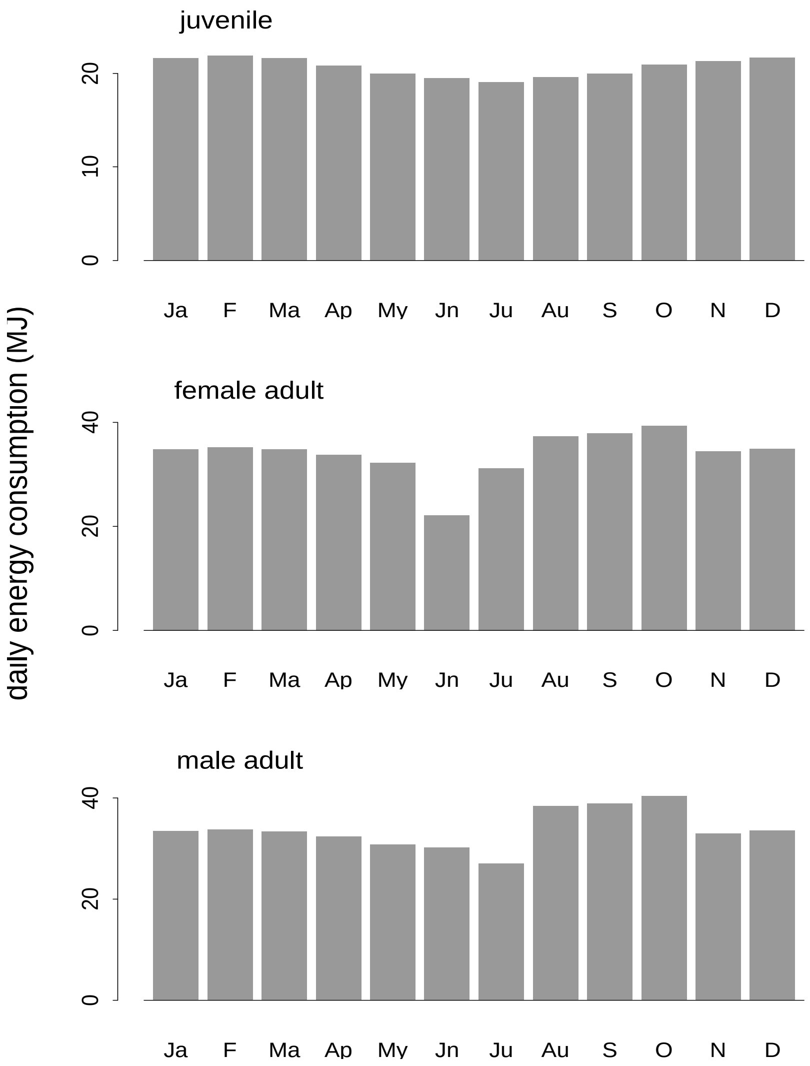

Figure 7.3: The seasonal energy intake of three size classes of common seal in the Moray Firth. The average daily energy intake for each month is shown.

the increase in the following three month recovery period . In the juvenile seal a slight increase in energy intake in the winter can be seen.

7.4 Population size and structure

In order to estimate the energetic requirements of a population it is necessary to know its size and structure, in terms of age classes and sex ratio. One approach that has been used (Øritsland and Markussen 1990) is to derive a population structure from a model. Unfortunately, there is only limited information available on the size and sex structure of the Moray Firth common seal population. There is also a lack of information on the birth rate and mortality of the population, removing the possibility of accurately generating the population structure from an appropriate model.

The data on blubber depth in Figure 7.1 can be used to estimate the sex ratio of the population. The data implies a 0.81:1 ratio of males to females, but since the capture programme is potentially biased I am wary of placing faith in this estimate. In the absence of any other information I follow Thompson et al. (1995) and assume a sex ratio of 1:1 throughout the population.

Thompson et al. (1995) present frequency distributions of seal lengths obtained by two methods. Long term study of the population has been based on a capture/release programme. This has yielded a biased sample of 199 animals from the population. In addition, an aerial survey of haul-out sites was made in 1994. Following calibration against identifiable rocks, this yielded length estimates for a sample of 166 individuals. The two different samples have somewhat different distributions , the distribution obtained by capture being more uniform than that from the aerial survey. If all seals longer than 1.25 m are pooled the proportion of adults and juveniles are similar in the two cases (≈43% adults for the aerial survey and ≈50% for captures). Pooling the bottom three length classes from the aerial survey provides a standard subdivision of juveniles (into length classes of 0.9, 1.0, 1.1 and 1.2 m). The length distributions are now broadly similar (Figure 7.4) and I shall use the distribution obtained by aerial survey.

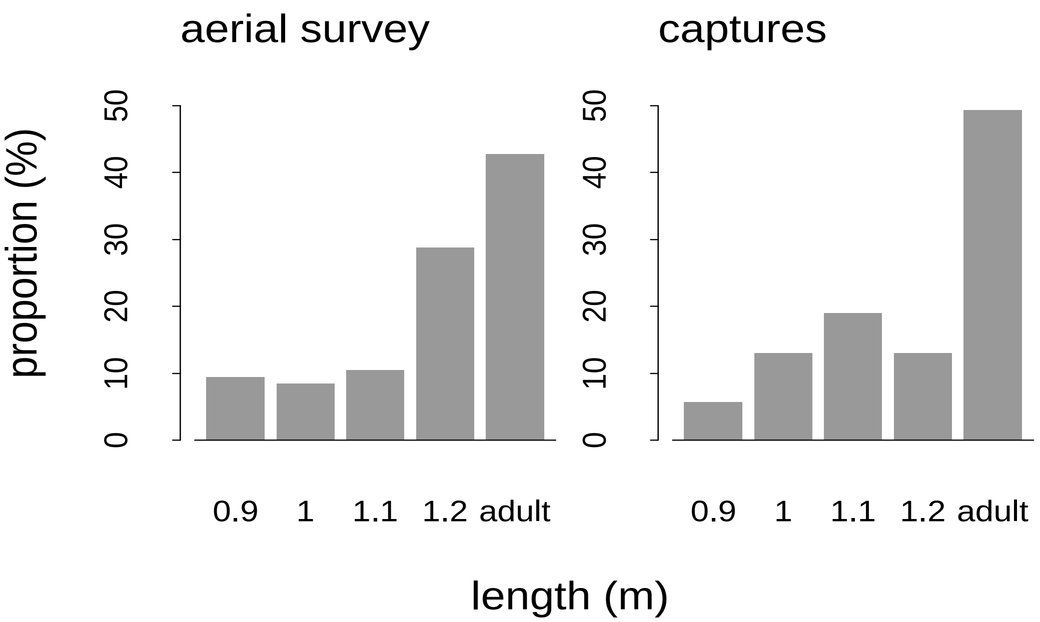

Figure 7.4: Length distribution of the Moray Firth common seal population, obtained by two methods, see text.

The population can be considered to be isolated, the nearest breeding colonies of common seals being in Orkney and the Firth of Tay. Although juveniles have been observed to travel between the Moray Firth and Orkney (Thompson 1993), this movement of individuals is not significant in looking at population energetics. The size of the population in the Moray Firth has been monitored for a number of years by University of Aberdeen. A combination of counts of hauled out animals and information on the behaviour of radio-tagged individuals was used to produce an estimate of the population size in 1993 (Thompson et al. 1994). The mean count of 1007 was adjusted to 1653, to take account of the proportion of the population not hauled-out, this was compared with an estimate of 1398 produced using a bounded count method (Olesiuk et al. 1993). The authors argue in favour of the higher estimate. In addition, they estimated the error bounds to be ±182 seals.

7.5 Population energy demand

For a given population size and structure (proportion of the population in each size class) it is a simple matter to calculate the total energy consumption of the common seal population from the intake estimates in section 7.3. Using the estimated population size for the Moray Firth results in a per annum energy intake for the common seal population of 17.3×10^6 MJ ($\pm1.91\times10^6 MJ$).

There are a number of uncertainties involved in arriving at these estimates of population energy consumption and their sensitivity to the assumptions involved must be examined. Firstly, it is clear from section 7.3 that revising the body parameter relationships had little effect on the estimates for the average DER of individual seals. It follows that the estimate of population energy intake will also be insensitive to these changes and it is indeed only 3% higher. In section 7.4 two estimates of the population structure were discussed. Switching from the aerial survey estimate to that based on the capture programme results in an increase in the estimated energy intake of less than 1%. I elected to assume that the sex ratio is 1:1, but have repeated the calculations using a ratio 0.81:1 male to females for the adult seals (see section 7.4). There was no difference in the estimates of the population energy intake (to 4 s.f.). The most significant uncertainty in the estimate of the population energy intake is clearly the population size itself. Since the energy intake is directly proportional to the population size, a 10% increase in the latter would cause a 10% increase in the former.

An estimate of the energy intake of a seal population tells us very little in itself. Of more use is an estimate of the consumption of fish by the seals. In the next section (7.6.1) I will describe the available information on the diet of common seals in the Moray Firth before calculating the consumption of individual prey species by the seals (section 7.6.2). Since the diet data are resolved into summer and winter it is convenient to do the same in estimating fish consumption. I have, therefore divided the year into two seasons; summer (April to September) and winter (October to March). The estimated population energy requirement for the Moray Firth common seals is 8.36×10^6 KJ for summer and 8.95×10^6 KJ for winter (only 7% higher than the summer).

7.6 The impact of common seals on fish stocks

7.6.1 The diet of Moray Firth common seals

There are two approaches to studying the diet of wild seals. The first is stomach content analysis, the second is recording the fish hard parts in seal faeces (or scats). Stomach content analysis requires the direct sampling of a proportion of the population. This is both costly and (in some countries) a politically sensitive approach. This method has biases (Pierce et al. 1991), but it is not necessary to discuss them here. The second method is non-invasive, requiring only the collection of the seal faeces. There are a number of problems with this method (Pierce et al. 1991), the most obvious being that samples can only be obtained where a seal has defaecated on land. Given that some seal species spend only a few weeks of the year on land, it is only appropriate for those which haul-out regularly such as the common seal. Even with the common seal, foraging trips last a number of days (e.g. Thompson and Miller 1990) and so any faecal samples will only indicate what prey was captured in the later part of the foraging trip. The identification of prey species relies on them having indigestible hard parts which will be detectable in the faeces. In the case of fish the otolith is used and for cephalopods the beak (e.g. Pierce et al. 1991). The situation is further complicated by differential digestion of otoliths both, from different species, and of different sizes from the same species. The nature of these biases and some methods by which they can be compensated are discussed in detail by Tollit (1996).

Allowing for the problems associated with estimating the diet of common seals from faecal samples, the work done in the Moray Firth using faecal sampling (Pierce et al. 1991; Thompson et al. 1991; Tollit and Thompson 1996; Thompson et al. 1996) gives a detailed picture of the diet of common seals in this region. Sampling has been carried out at the different haul-out sites since 1989. Tollit (1996) used measurements of the otoliths and beaks, corrected for digestion, to estimate the individual prey weights consumed and, therefore, the abundance within the diet by biomass. Using information on the calorific density of the different species the contribution, by energy, of each species was estimated.

The dietary data indicates that common seals are catholic in their choice of prey, consuming a wide range of species (Tollit and Thompson 1996; Pierce et al. 1990). In summer the key species are sandeels, octopus and herring. Less important in summer are sprat, *Salmo* sp. (i.e. seatrout and salmon), cod, whiting, dab, flounder, plaice and squid. In winter the key species change slightly, being; herring, sprat, whiting and sandeels. The only other species of significance in winter are cod and flounder. The dominance of species within the winter diet is not consistent between years. In most years sandeel are by far the dominant prey species, followed by whiting. In the winters of 93/94 and 94/95, however, the dominant species were sprat and herring (the clupeids) and this has been linked to high abundances of clupeids in the inner firths (Thompson et al. 1996). Given these patterns Tollit (1996) pooled the summer data into an average summer diet, but pooled the winter data separately for "good" (high clupeid) years and "bad" (low clupeid) years, the results are given in table 7.2.

Prey species	Season		
	summer	clupeid winter	non-clupeid winter
herring	6.56	27.9	4.45
sprat	0.52	42.1	1.2
salmonid	1.55	-	-
cod	2.35	2.08	5.49
whiting	2.49	0.13	17.49
sandeel	65.1	23.0	63.7
dab	0.31	-	-
flounder	3.68	3.66	1.35
plaice	1.22	-	-
octopus	10.8	-	-
squid	2.85	-	-
other sp.	2.51	1.08	6.34

Table 7.2: The prevalence of prey species in the diet of common seals in the Moray Firth, from Tollit (1996). Values are percentage of diet by energy.

7.6.2 Estimating fish consumption

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. Combining information on the energetic requirements of the population (section 7.5) and the diet of the seals allows estimates of fish consumption to be made. The greater the detail in the information used the more detailed the estimates. In particular it is desirable to incorporate the seasonal differences in the diet discussed above.

The proportion of the seal population's energy intake that is met by each prey species can be calculated by dividing the appropriate diet proportion estimate (from Table 7.2) by the energetic density of the prey species. Estimating the mass of fish consumed by the seal population is then a simple matter of multiplying this value by the seal population's energy intake. In order to be consistent I have used the energy densities Tollit (1996) used to calculate the diets. These were taken mostly from Hammond et al. (1994) but the value for salmonids was provided by J. Hislop (MLA, Aberdeen). Consumption estimates are presented in Figure 7.5 for summer and, both, good and bad winters (in which clupeids and sandeels are respectively dominant), see section 7.6.1.

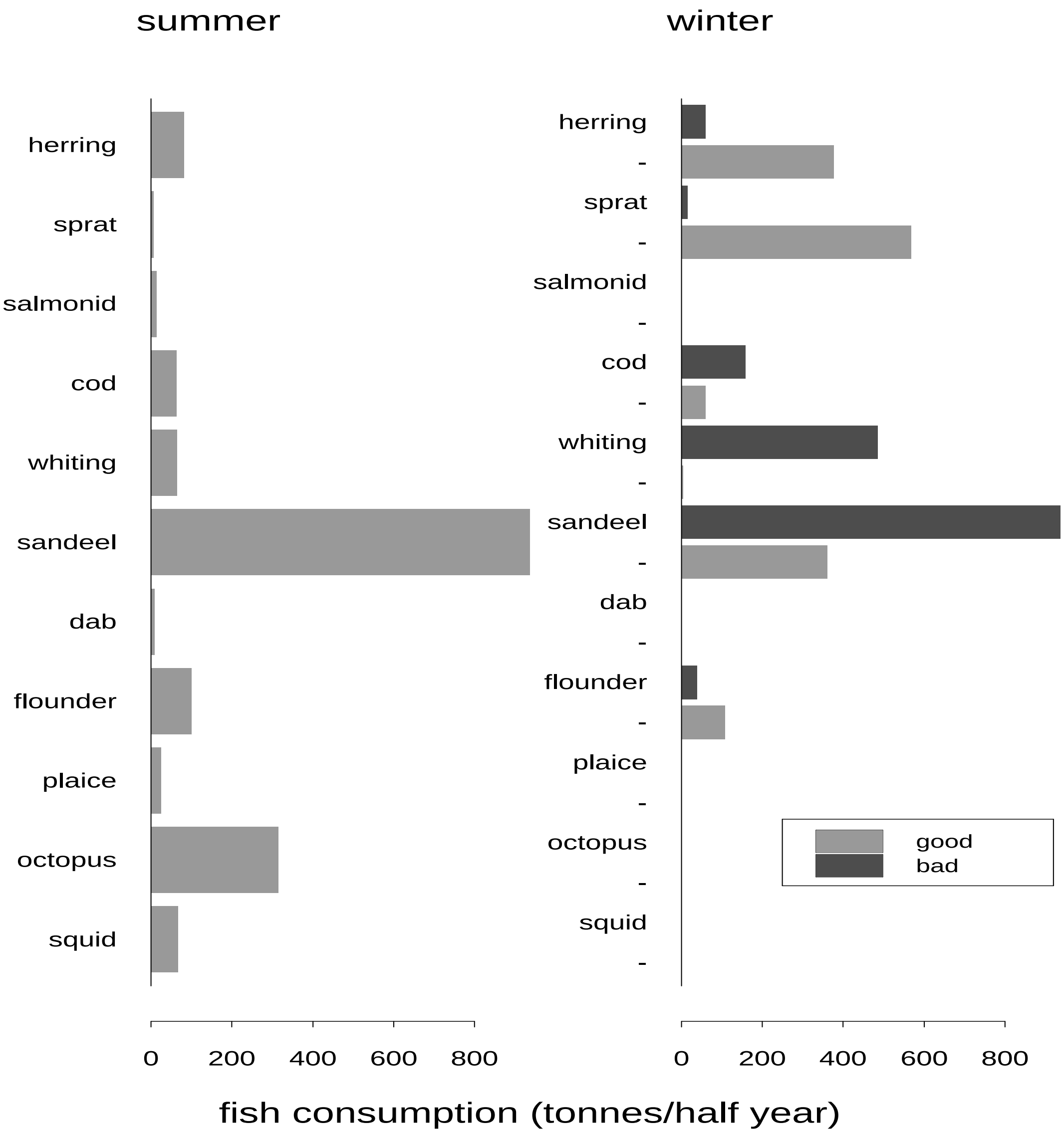

Figure 7.5: Estimates of half yearly fish consumption by the Moray Firth common seal population. Two estimates are given for winter; a winter in which clupeids dominate (good) and one in which sandeels do (bad), see text.

Consumption of sandeels in summer is estimated at 952 tonnes whilst in winter it is 360 or 997 tonnes (depending on whether clupeids are prevalent). These figures combine to give two estimates for annual consumption of 1312 and 1949 tonnes. The combined estimated consumption of clupeids (herring and sprat) for the summer is 83 tonnes and for winter is 954 tonnes for a good year or 76 tonnes for a bad, giving yearly estimates of 1037 and 159 tonnes. Whiting is important as an alternative winter prey in non-clupeid winters, the yearly consumption estimates are 549 tonnes in bad years and only 68 tonnes otherwise. Cod appears to play a similar role in the seal's diet; the yearly consumption estimates being 223 tonnes in non-clupeid years and 123 tonnes otherwise. Octopus is the other important prey species with an estimated yearly consumption of 314 tonnes, despite being absent from the winter diet.

One other prey group is of note, due to their importance commercially, the salmonids. They are only reported in the diet during summer and based on their average prevalence in the diet, I estimate that common seals in the Moray Firth consume 15 tonnes annually. The variability in their occurrence in the diet is considerable, in some years they were absent whilst in others they represented as much as 7% (by energy) of the summer diet. Using the maximum value I estimate that 68.6 tonnes of salmonids were consumed in the summer of 1995. Unfortunately, the biases involved with faecal sampling are particularly acute with salmonids. Seals have been observed to decapitate salmon before consuming them (Rae 1960) and if the head is not consumed their consumption will not be detected in the faeces. This would result in their being under-represented in the diet estimates. The otoliths of salmonids are relatively soft and therefore erode heavily during digestion, making identification to species impossible. Based on estimated lengths of fish consumed Tollit (1996) suggests that the otoliths found in seal faeces may have been sea trout and not the more commercially important salmon.

7.7 Discussion.

The only previous study of the impact of common seals in British waters on local fish species (Tollit 1996) used a previously published estimate of the average daily energy requirement (DER) of individual seals. Both previous studies of DER for common seals (Olesiuk 1993; Härkönen and Heide-Jørgensen 1991) made simple assumptions about the costs of activities. In Chapter 6 I described the seasonal energy requirements of common seals in the Moray Firth. This highlighted the limited seasonality in the average DER of seals and the gross underestimation of DER by the previous studies of common seal energetics. Given this and the availability of detailed information of the diet of common seals in the Moray Firth I believe that a detailed estimation of the consumption of prey species was appropriate.

Data from the recapture programme (run by University of Aberdeen) suggested a discrepancy in the published relationships for two body parameters that I had used previously. Using relationships specific to the common seals in the Moray Firth I recalculated the energy requirements. I found there to be little difference in the average DER estimates, with at most a 5% increase. From the DER it is easy to calculate the amount of energy that must be ingested to meet these costs. A little care is required for the adult seals since both sexes go through periods of fasting associated with breeding. The periods of fasting and recovery introduce a greater degree of seasonal variation into the energy consumption estimates (for the adult seals) than was seen in the individual's DER.

Demographic information about the common seal population is somewhat limited. Although a good estimate of the population size (in 1993) has been made (Thompson et al. 1994), there is no accurate information on the sex ratio or age structure. I assumed a 1:1 sex ratio, but repeated the calculation with a ratio based on the data in Figure 7.1 and saw no change in the population energy intake. Two estimates of the length distribution of the population are available. Again, the choice made very little difference in the estimate of the population energy intake (just 1%) and I have used the distribution obtained by aerial survey. The estimate of the population energy intake appears to be quite robust to the assumptions involved in its derivation, with the exception of the population size. This concurs with the findings of Härkönen and Heide-Jørgensen (1991) for the energy requirements of common seals in the Skaggerak.

The energetic requirement of the population was translated into estimates of the consumption of different prey species. Since the estimate of the seal population size is subject to an error of 11% the consumption estimates will carry at least this degree of uncertainty. In order to assess the potential impact of this perdition on the fish populations the standing stock of fish must be known. Fish research surveys of the Moray Firth have been conducted by the Scottish Office Agriculture, Environment and Fisheries Department (SOAEFD) and the resultant estimates of biomass are reported in Tollit (1996). The survey conducted in June 1992 suggests a clupeid biomass of 7,824 tonnes. Even taking the highest estimate (1037 tonnes), consumption by seals is only 13% of this biomass. Unfortunately the size and behaviour of sandeels make them less suited to acoustic fish surveys (Greenstreet S., pers. comm.). That said the biomass in June 1992 was estimated at 8,444 tonnes. An additional complication in assessing the direct predation by seals on sandeels (which are preyed on by other species in the seal diet) is the occurrence of secondary consumption, which can account for up to 20% of the occurrence in the seal diet (Tollit 1996). The maximum estimate of sandeel consumption (1949 tonnes) represents 23% of the estimated biomass.

The work reported here suggests that predation by seals may have a significant impact on local fish stocks. A full assessment of the nature of this impact would require a multi-species approach and is beyond the scope of this study. I would hope that this work could be used in such a study in the future.

Chapter 8

Modelling the foraging behaviour of seals

8.1 Introduction

I have already touched on seasonal and between year differences in diet, which suggest that prey-switching occurs (Thompson et al. 1996). To be able to take account of this within a predictive assessment of the impact of seals on fish stocks, it is necessary to understand the foraging strategies employed by the seals. Although there has been a great deal of modelling effort directed at foraging behaviour, there has been no investigation of the foraging strategies of seals. I do not propose to review the extensive literature on foraging studies here, but would suggest Stephens and Krebs (1986) as a useful starting point for the interested reader. Seals forage in a complex environment, exploiting heterogenously distributed prey. Some species, such as the southern elephant seal, spend months at sea, foraging over large areas of open ocean (Le Boeuf et al. 1988). Although satellite tracking of tagged animals has increased our knowledge of the seal's movements there is a paucity of data on the distribution of their prey. The less wide-ranging Moray Firth common seal once again proves to be an excellent case study. Not only is there data on the movements of seals and on their diet, there have also been acoustic surveys of the distribution of key fish species in the Firth (conducted by SOAEFD). The regular return to the haul-out sites in the inner Firths is a slight complication, but is balanced by the small geographical area covered in the foraging trips (Tollit et al. 1998).

In this chapter I describe a model of the foraging of an individual common seal. A novel approach to representing the foragers movement and the distribution of prey was developed. The behaviour of the model is investigated using a simplified version that uses a square arena. The model is then applied to the more complex environment of the Moray Firth.

8.2 An event-driven approach

The mechanics of a foraging model and in particular the way in which the environment is defined will depend on the nature of the prey species. Traditionally foraging models have tended to be based on a grid of fixed nodes. Individual prey items or patches of prey are distributed on these nodes and the forager is moved from node to node. If the prey is highly dispersed the forager will traverse large barren regions within the foraging arena. In this case movement from node to node in fixed time-steps becomes inefficient with respect to the model run-time. An alternative is to take an event driven approach and move the model from event to event (the time-step is now variable), where an event is any location or time which results in a change in the forager's movement or 'status'. Events could include; an encounter with prey, reaching the edge of the arena or a need to meet some physiological requirement such as rest. To implement such an approach the model determines the location of the next event, then calculates the interval between events (according to the distance travelled etc.) and finally updates the status of the forager. This approach, although more subtle to design, means that the model spends time only on defining events and avoids detailed description of the time spent between them.

A second complication arises where the prey species is itself mobile. It is clearly easier to work with a fixed distribution of prey or food patches and a mobile predator. It has been shown (Thompson et al. 1993) that for fast moving prey it is more efficient for the predator to remain stationary and allow the prey to move past. Common seals would appear to occupy a more complicated middle ground with prey that is mobile within the scale of a foraging trip but is not moving sufficiently to make a sit and wait strategy favourable. Tracking the individual movements of both the forager and its prey would be a considerable under-taking, even where the prey is aggregated into groups. A simpler approach is to use a probability distribution to calculate the distance that must be travelled through a region of known prey abundance before an encounter occurs. If a uniform distribution is used to generate the random encounter distances, then the average distance to encounter is a function of prey density and the foragers effective search width (Renshaw 1991). This approach simulates a random prey distribution within regions of fixed prey density. Regional variation in prey abundance can be represented by dividing the arena in to a number of sub-regions (boxes) of known total abundance. The boxes do not constrain the movements of the forager, but simply determine the likelihood of a prey encounter. If the forager enters a box it hits prey only if the encounter distance is less than the distance to traverse the box (a function of the entry point and the direction of travel). Otherwise it passes into the next box and the procedure is repeated.

Multiple prey species with different distributions and different detectabilities can be easily incorporated. Each box simply has an abundance value for each species and each species has an effective search width associated with it. An encounter distance is predicted for each species and the shortest is tested against the traverse distance to determine whether prey is hit.

8.3 The forager

The model requires a description of the seal as a forager. Many of the physiological characteristics depend on the seals size, which in turn implies that seals of different size may differ in their foraging characteristics. An obvious example of this is the metabolic rate, a higher metabolic rate raising the amount of energy a seal must gain from foraging to 'profit' from it. It is therefore appropriate to model different sizes of seal, representing male and female adults and juveniles.

The swimming speed of a forager is a key parameter, since it determines the search rate and may also affect the capture rate. Radio tracking of common seals in Norway showed velocity to vary during individual foraging dives (Bjørge et al. 1995). In Chapter 6 I calculated the cost of foraging for different sized seals. The average costs for a sequence of dives were considerably higher than the simple costs I had suggested at the end of Chapter 3. There is no technical reason why the model could not allow for variation in the seals swim speed and calculate the metabolic cost using a sub-model (based on that described in Chapter 3). This would, however, increase the complexity of the model considerably and, since it is not clear what the benefits would be, I have adopted a simpler approach. In Chapter 6 I calculated the metabolic rate averaged over an entire foraging trip for different sized seals, using a swimming speed of 1.3 ms^{-1} for all. In this chapter I shall make use of the resultant metabolic rate for a foraging common seal male (length = 1.45 m) and assume a constant swimming speed of 1.3 ms^{-1}.

Although they forage underwater, seals are required to return to the sea surface to breath. This decreases the proportion of the seal's time which is available for hunting. It is reasonable to assume that the dive duration is limited by the amount of oxygen the seal is able to store. This gives rise to the aerobic dive limit, a function of size. It would seem from observations of larger seal species that the notion of an aerobic dive limit is too simplistic (Boyd and Croxall 1996). To avoid becoming entangled in this confusion, I have simply assumed that dives and the subsequent surface period are of fixed length. For a foraging common seal (Bjørge et al. 1995) the dive record shows the average dive length and surface recovery period to be 221 and 79 seconds, respectively. The proportion of the foraging time that is actually available to the seal for hunting will depend on the depth, since the time spent swimming back and forth to the surface depends on the distance.

Common seals in the Moray Firth make extended foraging trips and it seems unlikely that they would limit themselves to filling their stomachs with food before returning to haul-out. Instead, digestion will be an on-going process during foraging. Since digestion requires the stomach and intestine to be perfused with blood Krockenberger and Bryden (1994) suggest that in elephant seals digestion occurs in bursts and is not combined with active dives, this is supported by dive records (Crocker et al. 1997). The model seal, therefore, ceases foraging once its gut is full and digests that prey load before resuming. In order to calculate the time of these digestion stops the seals stomach capacity and its rate of digestion must be known. Unfortunately, there is little detailed information available on these parameters. Markussen (1993) studied the stomach evacuation time of captive common seals and found that for variable meal sizes (0.5 to 2.1 kg) there was still some food left in the stomach after 5 hours. Assuming that the evacuation time is 5 hours gives digestion rates of 0.0278 to 0.117 gs^{-1} and I have used the upper limit. I have taken the seals stomach capacity to be 5 % of its body weight (Kastelein et al. 1990).

8.4 The distribution of prey species

The Marine Laboratories, Aberdeen (SOAEFD) have conducted acoustic surveys of the spatial distribution of fish species in the Moray Firth. The surveys were conducted in June 1992, September 1993 and January 1994 (Simon Greenstreet, personal communication) and provide synoptic pictures of the abundance and location of three of the key species in the diet of common seals; sandeels, herring and sprat. The results from the analysis of the acoustic survey provide estimates of the biomass density (for each species), recorded for boxes of 5 minutes latitude by 5 minutes longitude. The distributions show a high degree of heterogeneity and also marked inter-survey variation (Thompson et al. 1996).

In fisheries terms these acoustic surveys represent a fine scale picture but there are problems in using these data for a study of individual foraging behaviour. The data grid approximates to boxes of 46 km^2, within which nothing is known of the distribution of the fish. Clearly, there is a gulf between this and the fineness of scale needed to model the individual movements of a seal. Radio tracking studies suggest that foraging trips by common seals in the Moray Firth generally extend less than 50 km from the seal's haul-out site (Tollit et al. 1998). Direct use of the fisheries data would assume that prey was homogeneously distributed over areas similar to that which is likely to be covered by an entire foraging trip. One of the approaches to overcoming this problem of scale would be interpolation of the fish data, but it is not clear how this should be done. The biomass estimates were obtained by line transect survey and the current gridding of the data represents the finest scale which avoids autocorrelation in converting the track based acoustic data into spatial density estimates. I found that using encounter probabilities overcame this to some extent and was also beneficial for the reasons I mentioned above.

Converting the biomass density estimates to density of numbers is a simple matter. For this I have taken the length of a sandeel to be 12 cm (Hislop, Harris, and Smith 1991) and for sprat and herring I have used 12.5 and 18.3 cm, respectively (Misund 1993). Coull et al. (1989) give length weight relationships for a number of species, their relationships imply that the sandeel weighs 11.1 g, the sprat 13.7 g and the herring 48.1 g. The results of these conversions are summarised in Table 8.1. The variation between the years is marked as is the range of box densities within a survey. If we consider the high densities found in some boxes

Survey	species	n	Min	Max	Mean
June 1992	sandeel	100	0	48.3	6.65
	sprat	100	0	19.7	0.784
	herring	100	0	171	3.191
September 1993	sandeel	93	0	22.62	1.65
	sprat	93	0	29.3	2.24
	herring	93	0	58.1	2.85
January 1994	sandeel	76	0	8.86	0.461
	sprat	76	0	132	4.27
	herring	76	0	4.58	0.153

Table 8.1: A summary of the fish density estimates (no.m^{-2}) calculated for the three fisheries surveys (see text). The number of boxes covered by each survey (n) is given.

a problem rears its head. The result of this approach is best described as 'fish soup', since the resultant prey distribution would be close to a fish every 10 cm^2 over a 46 km^2 area. Figure 8.1 shows two tracks from the foraging model, with a square arena. The first is the movements of the seal if there is no prey, in the second the prey density is uniform (for each prey species) and is equal to the mean densities (fish per m^{-2}) for September 1993. When the mean September fish densities were used the seal moved less than a metre from its starting point in five days. It averaged 2543 prey encounters and a net energy gain of 161 MJ (n=50). Even if spacing of the fish in the water column were accounted for, the prey distribution is clearly unrealistic and would result in a seal 'bumping' into

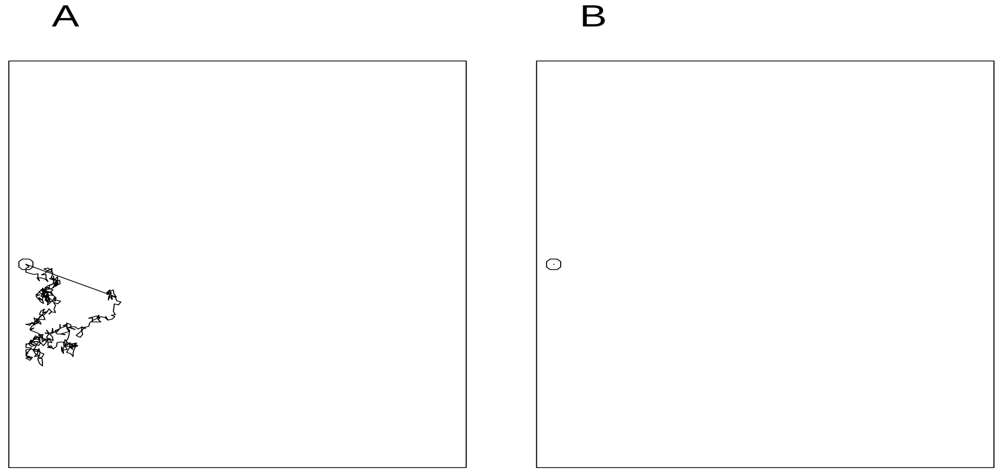

Figure 8.1: The movements of the seal predicted by the foraging model with A) no fish and B) a uniform fish distribution based on the September survey (see text). The arena is 100 km by 100 km and the start point is indicated by the circle.

a fish whichever way it turns.

In using the available fisheries data the shoaling behaviour of fish in the water column must be considered and the crude density estimates must be converted into the number of shoals in a given area. By grouping the number of fish per box into shoals the number of prey units is reduced and a 'sensibly' patchy prey distribution achieved. Misund (1993) provides detailed information on the size and structure of herring and sprat shoals in the North Sea and I made use of these. The average shoal size for herring and sprat was 52 and 51 thousand fish (for 1988 and 1989 respectively) and I have used an average shoal size of 51.5 thousand fish for both species. For sandeels I calculated a typical shoal size of 14 thousand fish from data for the waters around Shetland (P. Wright, personal communication). The results of this second stage in the interpretation of the fish survey data are summarised in Table 8.2. The variability remains high but the number of prey 'units' per box is much reduced. Repeating the model runs described above with these new values, a more reasonable amount of movement by the seal is observed, Figure 8.2. The number of encounters has dropped to a mean of only 44, but the average net energy gain remains similar at 121 MJ (n=50). The aggregation of the prey into shoals appears to be successful but raises questions about: variability in shoal size, the detectability of shoals and the degree to which a seal is able to exploit a shoal once located.

Survey	species	n	Min	Max	Mean
June 1992	sandeel	100	0	34.8	4.78
	sprat	100	0	3.70	0.152
	herring	100	0	33.3	0.620
September 1993	sandeel	93	0	16.3	1.19
	sprat	93	0	5.69	0.435
	herring	93	0	11.3	0.54
January 1994	sandeel	76	0	6.38	0.332
	sprat	76	0	25.6	0.829
	herring	76	0	0.888	0.0297

Table 8.2: A summary of the shoal density estimates (no.$m^{-2} \times 10^4$) calculated for the three fisheries surveys (see text). The number of boxes covered by each survey (n) is given.

8.5 Some preliminary results

In this section I will describe the results from a preliminary investigation of the effect on the seal's foraging performance of; fish capture time, water depth and shoal exploitation. The fish capture time is the amount of time it takes the seal to capture individual fish, once it has located a shoal. The shoal exploitation is the weight of fish taken from each shoal. In order to avoid any unusual effects

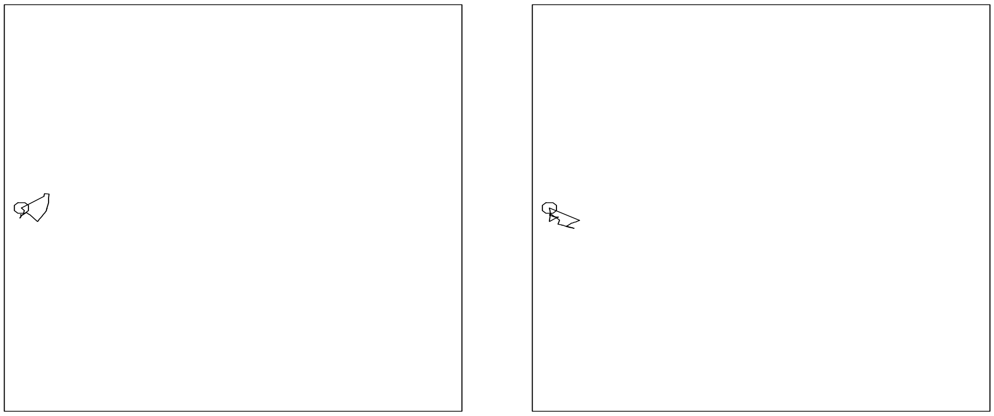

Figure 8.2: The movements of the seal predicted by the foraging model with the fish aggregated into shoals (two simulations are shown). The mean shoal densities from the September survey were used for all three fish species (see text). The arena is 100 km by 100 km and the start point is indicated by the circle.

caused by the triangular shape of the Moray Firth, I used a square arena for the simulations reported in this section (the arena width was fixed at 100 km so that the longest distance was approximately the same as the Moray Firth). I also assumed that prey density is uniform across the arena and used the average shoal densities calculated for the three fish species from the September data. A routine was included in the model to calculate the time and energy required for the seal to return to its start point (on the edge of the arena) by the most direct route. For each parameter combination 50 simulations were run and in all the simulations the seal followed a random walk with a leg distance of 1 km.

The first parameter investigated was the capture time for each fish taken from a shoal (once it has been located). The depth was set to zero and the shoal exploitation to 1 kg. The latter means that for each prey encounter the seal consumed 1 kg of fish, regardless of species. Figure 8.3 shows the effect of increasing the capture time on the final energy balance of the seal (the energy gained minus that used for the trip). The median energy balance decreases steadily and is approximately linear over the range 0 to 30 seconds per fish. A single value was used for all three fish species and was arbitrarily set to 10 seconds for the rest of the work. Improvement of this situation requires knowledge of the fine scale pursuit and capture techniques used by seals for different fish species, information not currently available.

It is reasonable to expect the final energy balance of the seal to decrease if the water depth is increased, since the amount of time available for foraging decreases. Assuming that the prey occurs at maximum water depth I ran a set of simulations with increasing water depth and the final energy balance does indeed decrease,

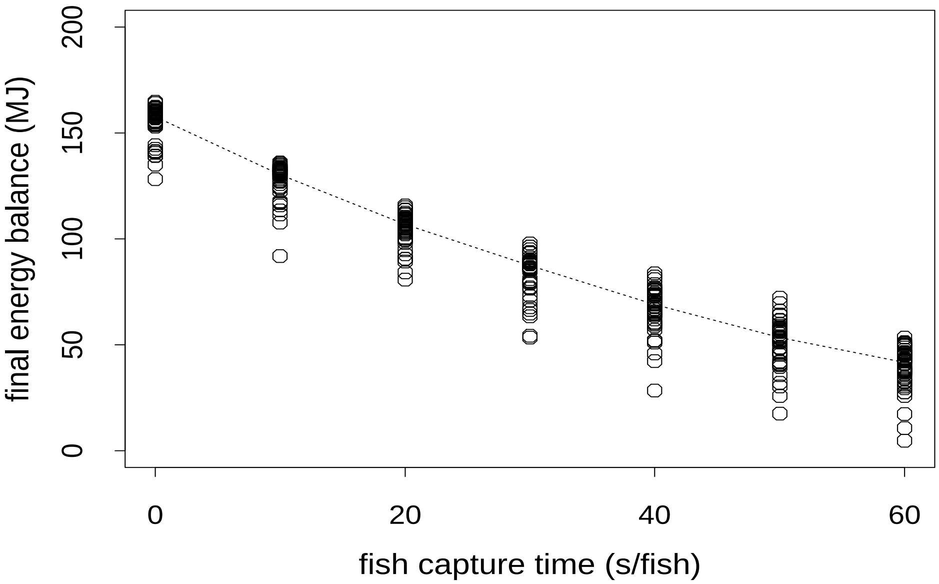

Figure 8.3: The effect of increasing the capture time (for each fish consumed) on the seal's foraging performance for a 5 day trip. For each capture time 50 simulations were run and the dotted line joins the medians.

Figure 8.4, although not dramatically. The median energy balance approximates to a linear relationship with dive depth. I used a depth of 30 m for subsequent simulations since this appears to be a typical foraging depth for common seals in the Moray Firth (Tollit et al. 1998).

The final parameter for which the sensitivity was tested, using the square arena and a homogenous prey distribution, was the shoal exploitation. This number is the weight of fish (irrespective of species) that the seal is able to consume upon encountering a shoal of fish. Figure 8.5 shows the effect of increasing the shoal exploitation (from 100 g to 3890 g) on the final energy balance of the seal. The upper bound on the shoal exploitation was chosen to equal the seal's stomach capacity. Unsurprisingly, the energy balance increased with increasing shoal exploitation. The median values of the energy balance appear to follow a saturation curve, with a rapid increase between a shoal exploitation of 100 g and 1 kg and a slower increase thereafter. This pattern may be a result of using a capture time for individual fish, extracting more fish from a shoal increases the time required and therefore the energetic cost. A more detailed investigation would be required to establish the mechanism. The choice of a default shoal exploitation of 1 kg of fish per shoal appears fortuitous since it lies within the range for which the seal's performance is less sensitive to the assumed exploitaiton. I have continued to use 1 kg as the standard value.

All of the results described thus far used the average prey densities recorded by the September 1993 survey. The frequency distributions of the final energy balance for

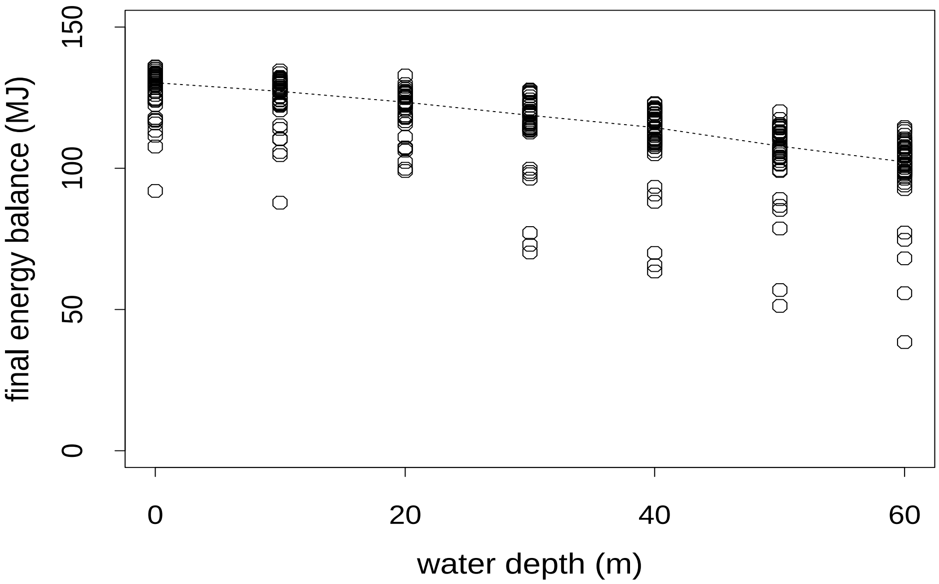

Figure 8.4: The effect of increasing the water depth on the seal's foraging performance for a 5 day trip. For each depth 50 simulations were run and the dotted line joins the medians.

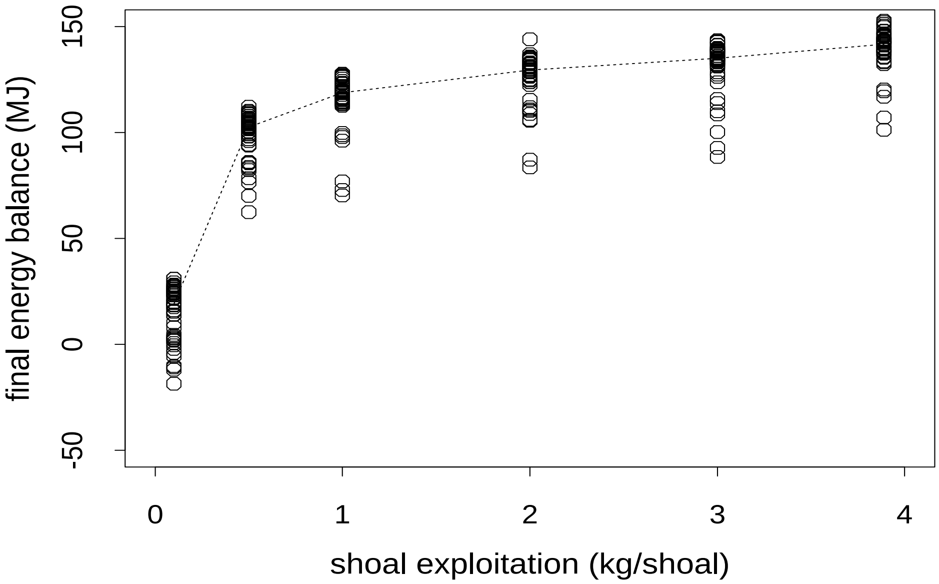

Figure 8.5: The effect of increasing the shoal exploitation on the seal's foraging performance for a 5 day trip. The shoal exploitation is the weight of fish the seal is able to consume for each encounter with a fish shoal. For each parameter value 50 simulations were run and the dotted line joins the medians.

50 simulations lasting 5 days are shown in Figure 8.6 for all three fish surveys. For all of these, the prey was assumed to be homogenously distributed with densities equal to the mean values for the respective survey. All three distributions are broadly similar with medians between 105 and 120 MJ and some skewing toward lower values.

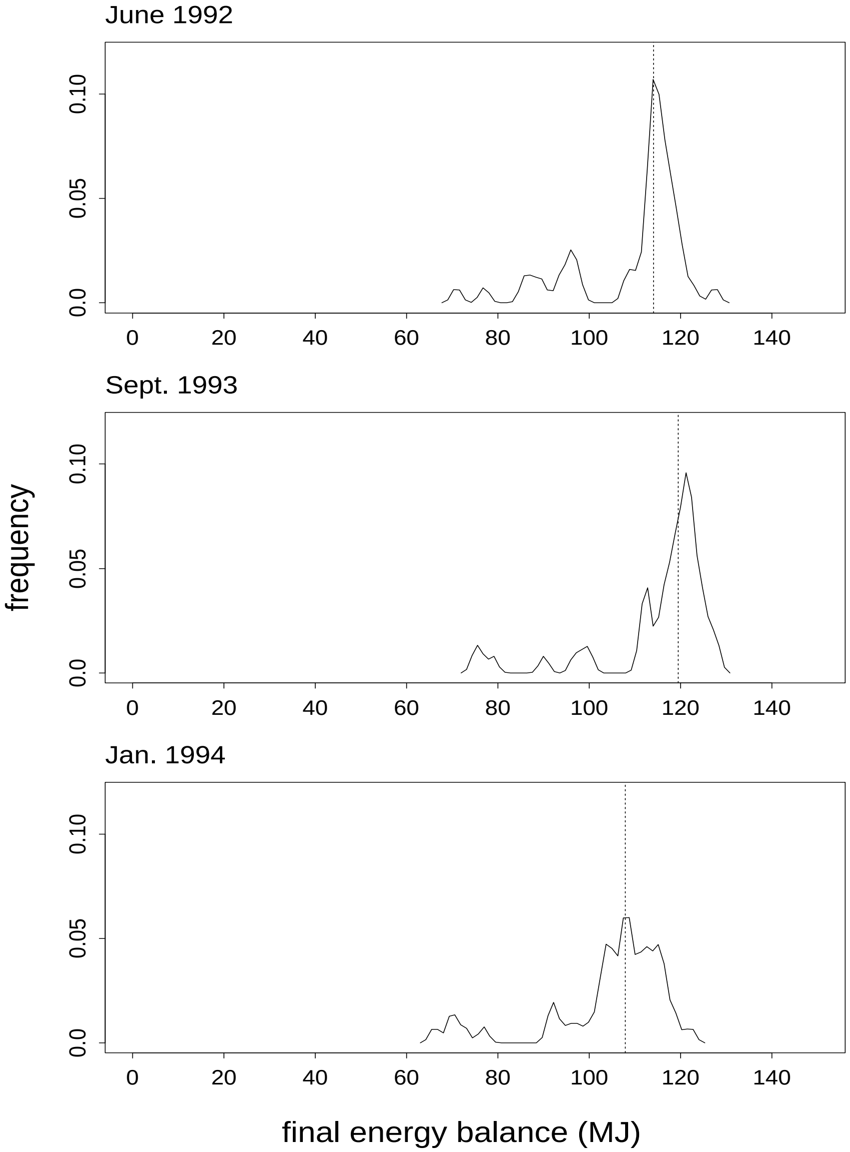

Figure 8.6: The foraging performance of a seal in a square arena under different homogenous prey conditions. The plots show the frequency distributions for sets of 50 simulations run using the average shoal densities calculated from each set of survey data.

8.6 The Moray Firth

In this section I will briefly describe initial simulations for a seal foraging in the Moray Firth. As a simplification I used the box structure of the fisheries data to define the coastline, although a more realistic coastline could be substituted. The parameter values were as described in the previous section, except for the prey distribution which was no longer assumed to be heterogenous. The start point was chosen to approximate the position of one of the haul-out sites (Ardersier) used by common seals in the Moray Firth. The complex shape of the new arena meant that the return procedure used previously, to get the seal back to its start point, could not be used. Example tracks from two simulations are shown in Figure 8.7.

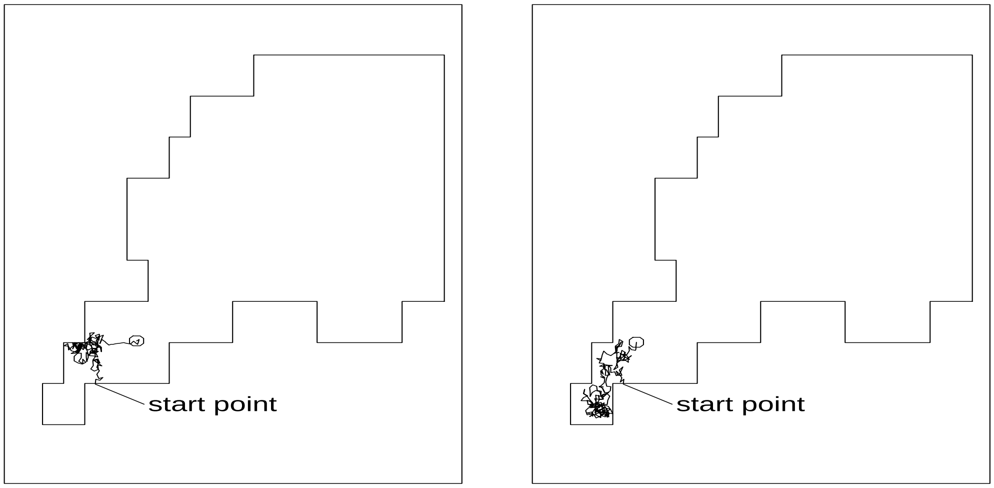

Figure 8.7: Two predicted tracks for a seal foraging in the Moray Firth. The start point for the simulation is indicated and the seal's position after 5 days is marked by a circle. For both simulations used the shoal density distribution calculated from the September 1993 survey data (see text).

The frequency distributions, of the final energy balance of the seal, for simulations run with the three prey distributions are shown in Figure 8.8. For each month 50 simulations were run and each of these represented 5 days. Compared to those from the square arena (Figure 8.6) there is greater variation between the three months. The performance of the seal in June is actually better in the Moray Firth simulations. The most obvious feature of the results for September and January is the large degree of spread and the absence of a pronounced peak in the distribution. In both months the seal generally performs less well than in the square arena and this is reflected in medians of about 25 MJ.

All the simulations described so far used a random walk with each leg a fixed distance of 1 km. For heterogenously distributed prey the step length is unlikely to affect the foraging performance of the seal, but this is not necessarily true for heterogenously distributed prey. Figure 8.9 shows the results from simulations

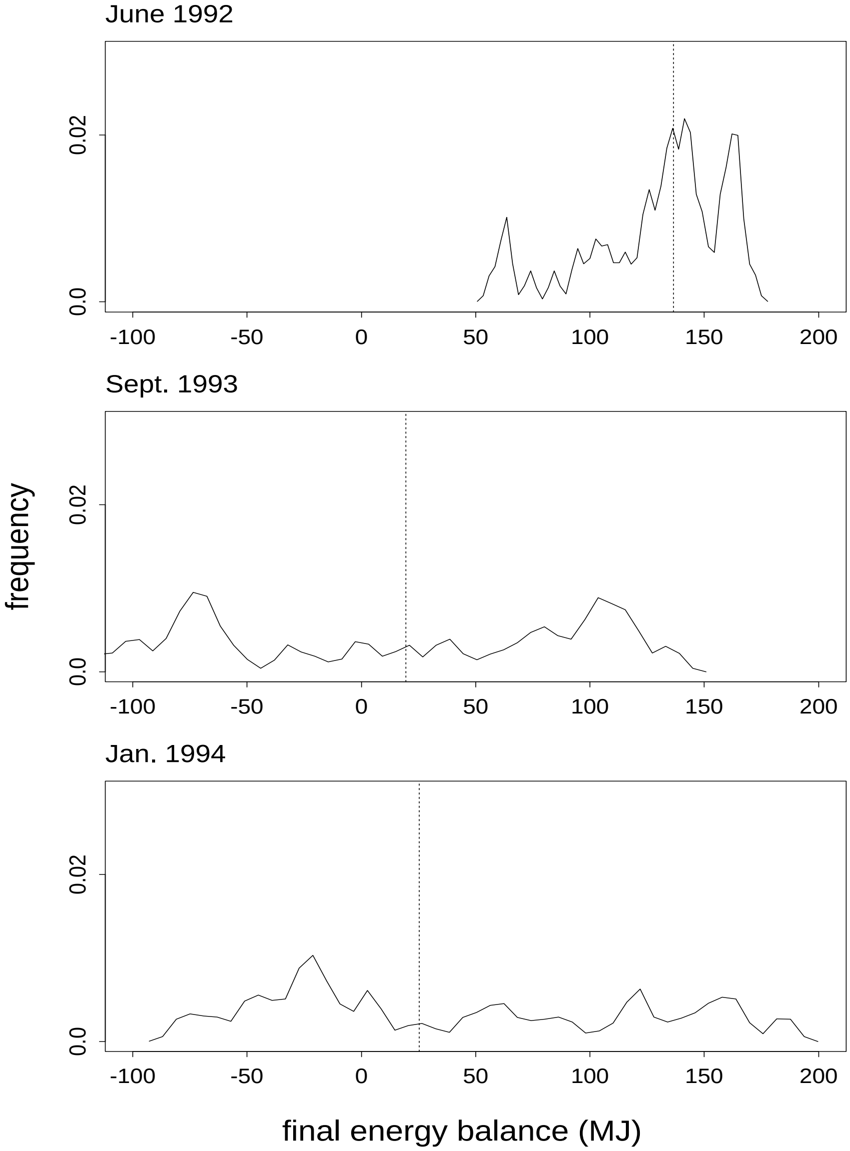

Figure 8.8: The foraging performance of a seal in the Moray Firth under different prey conditions. The plots show the frequency distributions for simulations run using the shoal density distributions calculated from each set of survey data. For each distribution 50 simulations were run.

done using each set of prey data and an increasing step length for the random walk movement rules. There is no obvious improvement in the foraging performance of the seal in any of the months.

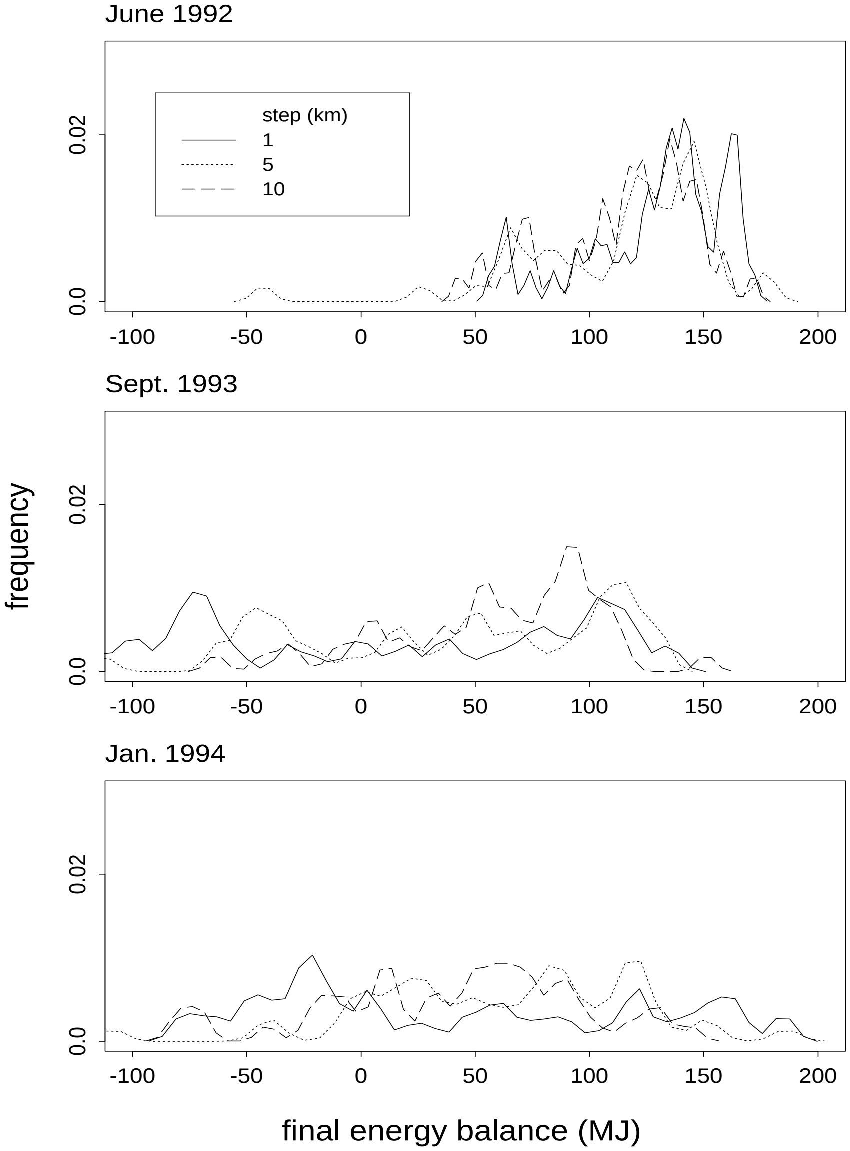

Figure 8.9: The effect of increasing the step length of the random walk on the foraging performance of a seal in the Moray Firth. The plots show the frequency distributions for simulations run using the shoal density distributions calculated from each set of survey data. For each distribution 50 simulations were run at step lengths of 1, 5 and 10 km.

8.7 Discussion

In this chapter I have described the development of a model of the individual foraging behaviour of a common seal. The model makes use of acoustic survey data on the distribution of three key prey species (sandeels, herring and sprat) in the Moray Firth. The successful incorporation of these data into the model required careful interpretation. Simply converting the biomass densities in to fish numbers resulted in unrealistically high prey densities. It was, therefore, necessary to aggregate the fish in to shoals, reducing the density of prey units.

To avoid any effects associated with the boundary shape of the Moray Firth I used a square arena for the preliminary investigations of the models behaviour. I concentrated on the capture time for individual fish, the water depth and the amount of fish the seal catches when a shoal is encountered (shoal exploitation). The energy balance of the seal at the end of a five day foraging trip decreased with both increasing capture time (for individual fish) and increasing water depth. Neither of these results are surprising since they both decrease the time available to the seal for benthic prey searching. The effect of varying the shoal exploitation was more interesting, with the average final energy balance apparently fitting a saturation curve. Although this requires further investigation, I would suggest that it results from the use of a capture time for individual fish (over and above the time required to locate a shoal). Some trade off will occur between the additional energy gain of taking more fish and the reduction in time available for searching at depth. It would be desirable to improve upon the simple assumption of a fixed capture time for individual fish, regardless of species, but this would require detailed information on the seals fine scale hunting techniques and this is not currently available.

The model was applied to the Moray Firth, with heterogenous prey distributions based on the survey data. The final energy balance provides a crude test of the success of a foraging strategy, since the seal must return with an energy surplus in order to meet its costs during intervening periods of haul-out. The simulations for June showed the seal doing well and consistently ending the trip with a large enrgy reserve. The predicted foraging performance was highly variable in the other two months. This suggests that a random walk foraging strategy is an ineffective method of locating patchy prey, as has been demonstrated previously (e.g. Benhamou 1992; Benhamou 1994). Increasing the distance step in the random walk made little difference to the performance of the seal. More efficient ‘area-restricted’ search rules were proposed by Benhamou and Bovet (1989), which operate by making the sinuosity of the search path proportional to foraging performance. Klinokinesis is one such mechanism (Benhamou 1992; Benhamou 1994) and would seem a good choice for a ‘next simplest’ strategy to test.

There are several features of the model that require development. One of the most obvious is the need to include a realistic representation of the bottom topography of the Moray Firth. This should not present any technical difficulties but may have a significant effect on the foraging performance of the seal. The assumption of uniform depth I made for the work described here does provide a basic scenario against which more realistic simulations could be tested. The PASCAL implementation of the model is included in the Appendix in the hope that it may prove useful to someone wishing to go further with this interesting research topic. Although I was unable to develop the model fully, the preliminary work described in this chapter produced some interesting results and shows the potential of such work.

Part IV

Overview and Discussion

Chapter 9

Discussion.

9.1 An overview

9.1.1 Part I

In the first part of this thesis I had two aims; to place the work described in its broader context and to provide the reader with an overview of the current state of knowledge of the energetics of seals.

In Chapter 1 I have outlined the motivation behind the work, both from an ecological and political perspective. Although the energy requirements of seals have an ecological significance, the principal motivation for this work has been the contribution that an understanding of seal energetics can make to improved management of fisheries. I described three different seal fishery conflicts, from different regions, to illustrate both the political nature of the problems and the ecological complexity. As fisheries management models continue to move towards a multi-species approach they are beginning to incorporate the predation mortality inflicted on the focus species by seal populations. The success of this will depend on the realism of the estimates of fish consumption by the seal population. These estimates rely on a knowledge of the energetics of the individual seals and past attempts to model this (and their limitations) are discussed in Chapter 5. Given the changing focus of fisheries modelling, the comprehensive and detailed study of seal energetics I have presented here seems particularly timely.

The literature on the biology and ecology of seals is vast and a comprehensive review lies beyond the scope of this thesis. Instead, I have attempted to distil what is known about those aspects of seal biology related to their energetics, into the concise review that forms Chapter 2. I have grouped the studies into five categories relating to the energy requirements of individual seals; maintenance, thermoregulation, locomotion, growth, reproduction and digestion. For each section I have described the state of knowledge, drawing principally on empirical studies but, where relevant, I have also covered previous theoretical studies. The empirical information contained in Chapter 2 provides a foundation for the modelling work described in later chapters.

9.1.2 Part II

The energetics of individual seals provide the focus for the second part of the thesis more specifically, it is the energetics of two key activities that are addressed.

I began with locomotion and in Chapter 3 described a model of the metabolic cost of swimming in seals. Although there have been a number of experimental studies of the energetics of swimming seals and sea lions, two features of the observed relationships have awaited satisfactory explanations. The first is a very rapid increase in metabolic rate at low velocities and the second concerns the overall rise in metabolic rate with velocity, which is slower than the rise in hydrodynamic drag force. The key to the success of the model in explaining these features lies in the incorporation of both hydrodynamic and thermal processes. Constructing the hydrodynamic component proved to be relatively straightforward, thanks to detailed information provided by previous experimental studies. The thermal component of the model incorporates both free and forced convection and takes account of the effect of hair on free convection, an aspect not previously considered. Using data from the literature I was able to evaluate all but two of the parameters needed to test the model's predictions against metabolic rate data for phocid seals, otariids, penguins and minke whales. I demonstrated that the model is able to reproduce both unusual features of the data; namely the step in the metabolic rate between resting and slow swimming and the overall rise in metabolic rate being slower than the increase in the drag force (as a function of velocity). The work suggests differing costs of propulsion for different modes of swimming and, more importantly, shows the metabolic costs of propulsion and thermoregulation in a swimming homeotherm to be inter-linked. Potentially, this is of ecological significance since the swimming speed that minimises the cost of transport for an animal will change with changes in water temperature.

In Chapter 4 the scene changed to a seal 'hauled-out' on land and I described a model of the thermal balance of the seal. The detailed model applies the principles used to such good effect in the previous chapter to a seal in air. There were a number of changes necessary, starting with the obvious simplification that seals are effectively sedentary during haul-out periods. The surface heat exchange is more complicated than for an immersed seal, in addition to convective heat transfer, radiative heat exchange and evaporative cooling must be considered. Testing the model proved less straightforward, since experiments on the thermal biology of seals in air have generally focused on the effect of air temperature and have neglected the interacting influence of the wind and solar irradience. Using data on the thermoneutral range of captive common seals a partial validation was possible and indicated no reasons to reject the model. If the weather conditions experienced by a hauled-out seal result in excess cooling it may seek to avoid the energetic cost of thermoregulation by altering its behaviour and a reduction in the time spent ashore would be expected. This provided an alternative means of investigating the legitimacy of the model's predictions. Evidence that local weather conditions influence the haul-out behaviour of harbour seals remains inconclusive. One of the complications is the seasonal increase in the time spent hauled-out by females with pups. During this period the mother must meet both her own energy requirements and those of her pup. It would, therefore, be advantageous to the female seals if pupping coincides with favourable weather conditions. I used the model to predict the combined cost for a common seal mother and pup pair hauling-out in the Moray Firth, Scotland. The model predicts that there is an energetic cost resulting from thermoregulation at all times of the year, but this is at its minimum in June and July. The predicted, energetically optimal period for lactation, coincides with the timing of pupping in this seal population. I concluded that, for common seals in Scotland, the timing of pupping is influenced by thermoregulation and that this adds to the body of evidence suggesting that thermoregulation influences haul-out behaviour in this small phocid species.

9.1.3 Part III

In part three the focus of the work becomes progressively broader, moving from the energetic cost of specific activities, first to the seasonal energy requirements of individual seals and then to the impact of a seal population on the local fish stocks. I begin in Chapter 5 with a brief review of previous studies of the energetics of seal populations. Despite the number of studies and the different approaches taken, I identify a number of limitations and show that there is considerable potential for improvement. For Chapter 6 and Chapter 7 it was necessary to focus on a specific seal population and I used the common seal population of the Moray Firth as my case study. There are a number of reasons for this choice but one of the principle ones is the extent of knowledge about the population. A long term study by University of Aberdeen has yielded a wealth of information on the behavioural ecology of the seals, including details of the movement patterns of individuals (obtained by radio tracking). Parallel to this, the diet of the seal population has also been studied, based on the occurrence of fish hard parts in the seals' faeces. The combination of seasonal information on the movements of the seals and detailed information on the diet creates an enticing opportunity for an investigation of population energetics.

In Chapter 6 I used the models described in Chapter 3 and Chapter 4 as a starting point and (in conjunction with information on the behaviour of seals) went on to investigate the seasonal energy requirements of common seals. One of the key energetic costs identified by previous studies (see Chapter 5) is the cost of activity, i.e. swimming. Advances in telemetry have made available detailed records of depth and swim speed during bouts of dives. Taking three such records for common seals I used the model described in Chapter 3 to predict the metabolic rate of a seal throughout these dive bouts. Taking the average for a sequence of dives I produced estimates of the cost of foraging and travelling for adult and juvenile common seals, and also the cost of aquatic mating displays (for male adults). Using this combination of observed swim speed and predicted metabolic rate I showed that the cost of both foraging and travelling is independent of season, in contrast to the speculative prediction made at the end of Chapter 3. The model of the thermal balance of a seal in air (Chapter 4) was used to calculate the cost of hauling out for the different size classes of seal. For all seals the cost of hauling out in winter was considerable, dropping somewhat in summer. Using time budgets for the Moray Firth seals and an estimate of the reproductive costs of an adult female common seal I estimated the seasonal energy requirements of three size classes of seal. For all three, the energy requirements were dominated by maintenance and foraging, both of which were generally independent of the time of year (the exceptions being the cessation of foraging by breeding adults). The cost of hauling-out was relatively low for all three size classes, since it accounts for less than a quarter of their time budget, but the seasonal variation in the cost of this activity is still perceptible. Only for the adult female was there a significant change in the total energy requirements, corresponding with lactation and its high energetic cost. Although the male adult switched from foraging to the less costly aquatic displays during the breeding season, there was only a slight reduction in the total energy requirement.

In Chapter 7 I began by discussing the size characteristics of the Moray Firth common seals. Measurements of the blubber thickness of seals (caught as part of a mark and recapture programme) indicate that the published relationship used elsewhere in this work consistently overestimates the blubber thickness of these common seals. Estimating the surface area from length and girth measurements of the seals I found that this was also somewhat lower than the values predicted by a published relationship for surface area as a function of weight. I, therefore, repeated the estimation of energy requirements described in Chapter 6, using relationships specific to the common seals in the Moray Firth, for these two body parameters. Overall, the values and the pattern were very similar. The cost of hauling-out was slightly higher, consistent with the seals being thinner and less well insulated. In order to calculate the consumption of fish by the population it was first necessary to turn my estimates of energy requirements into energy intake. This involved taking account of; periods of fasting for adult seals (during the breeding season), the seals digestive efficiency and the heat increment of feeding. For the juvenile seals the energy intake varied only slightly between winter and summer. For both the male and female adults the intake dipped in mid-summer (the breeding season) and peaked in the autumn, due to a post-fast recovery of body condition. By making some assumptions about the size and structure of the seal population I then estimated the total energy intake of the population. This estimate proved to be surprisingly robust to the assumptions about the size of the seals and to those about the structure of the population. The estimate was only sensitive to the population size, to which it is directly proportional. Finally, I used the estimate of population energy intake to predict the quantity of individual prey species consumed. The diet information was resolved into an average summer diet and two different winter averages, for years dominated by clupeid species and other years. Although information on the size of the fish populations is limited I estimated that seals consume, at most, 13% of the standing stock of clupeid species and up to 23% of the sandeel stock. Probably the most commercially important fish species in the Moray Firth is the salmon. Although this is only ever a small part of the seals diet, an estimated annual consumption of up to 69 tonnes may represent a significant impact (since the economic value of individual fish is high). Unfortunately, the diet study was not able to distinguish between salmonid species and it is possible that most of the fish consumed were the less commercially important sea trout.

Chapter 8 looked at the extension of the population consumption work described in Chapter 7 to a more predictive study of the impact of common seals. This is based on a model of the individual foraging behaviour of a common seal. The novel structure of the model is described along with preliminary investigations of the models behaviour. A square arena and a homogenous prey distribution were used and the seal was assumed to execute a random walk search. The prey distribution was based on acoustic survey data for three key species in the Moray Firth. The data was initially converted from biomass densities to the density of individual fish. This proved unrealistic and the fish were grouped in to shoals, reducing the prey unit density. The seal was assumed to take a fixed mass of fish from each shoal encountered (the shoal exploitation value). Increasing the handling time (per fish) or the water depth decreases the amount of time the seal is able to spend searching for prey and the seal's foraging performance decrease. Increasing the shoal exploitation initially improved the seal's performance, but a plateau is reached at a moderate value. In the initial simulations the seal consistently ended a five day foraging trip with a large energy deficit. Neither increasing the prey density, nor increasing the seal's search width resulted in a significant improvement in performance. From this I inferred that the seal's performance was limited by the time required to process the prey and not by the effort required to locate shoals. Increasing the digestion rate dramatically improved the seal's foraging performance, confirming that processing time was the limiting factor. The model was then applied to the Moray Firth, this time with a heterogenous prey distribution. The final energy balance was highly variable for simulations run with the same prey distribution. The seal's performance under different prey distributions (corresponding to data from three different acoustic surveys) also varied. A number of interesting features of the model are demonstrated and provide a good platform for further work.

9.2 The author's reflections

The advances in telemetry have brought marine mammal science into a new era. For the first time detailed information is becoming available on the behavioural ecology of these aquatic predators. In addition to this, long term studies are producing descriptions of the diet of seals, for a number of species and regions. The wealth of information now available makes it possible to take a far more comprehensive look at seal energetics. In carrying out the work reported here it was my aim to capitalise on this situation and look at the energetics of seals on a finer time scale than had previously been possible.

The most significant piece of work has proved to be the mechanistic model of the metabolic rate of swimming seals described in Chapter 3. I originally anticipated that it would be a simple matter of constructing a hydrodynamic model of a swimming seal. This merely re-emphasised the unusual features of the observed relationships between metabolic rate and swim speed. Unsatisfied with the explanations that had previously been put forward, I concluded that another metabolic process was involved. Since the rate of heat loss from a surface changes with the speed of fluid flow over it, I realised that the thermal balance of a seal would alter with swimming speed and so expanded my model to include the seal's thermal balance. This novel approach proved essential in explaining the odd features of data-sets from a number of marine homeotherms. I was now in possession of a predictive model of the metabolic cost of swimming. A preliminary look at the ecological significance of this work suggested that the optimal swimming speed of a seal may be a function of both its size and the temperature of the water.

To complement this model of the cost of swimming I needed a predictive model of the cost to a seal of hauling-out on land, in order to investigate energetics throughout the year. I was able to use the same principles that had been successfully applied to modelling the thermal balance of a seal in water. A number of adaptations were necessary to take account of the different heat transfer processes that occur in air (Chapter 4). Although mine is not the first model of thermoregulation in a seal, no previous model has (to my knowledge) taken full account of these processes, in particular the evaporative cooling experienced by a wet seal. The predictions of the model show that even in a temperate region common seals experience weather conditions that require them to actively thermoregulate. Unfortunately, ecological evidence of the influence of weather conditions remains inconclusive. One of the complications is the change in frequency of haul-out associated with breeding and moulting. I used my model to predict the combined cost (for a common seal mother and pup) of hauling-out throughout the year, in order to test the hypothesis that pupping is timed to coincide with the most favourable weather conditions. The results confirmed that pupping in the Moray Firth (for common seals) does indeed occur at the most energetically favourable time, i.e. that which minimises the energetic burden on the mother of increased hauling-out. This adds to the evidence that common seals in temperate regions do experience conditions in which they must actively thermoregulate to maintain their body temperature.

No previous study of the energetics of a common seal population had taken into account the seasonal variation in the energy requirements of individual seals. They had also based their estimates of swimming costs on simple extrapolations from empirical data and had failed to consider any thermoregulation costs for hauled-out seals. The information gained from the long term study of the common seal population in the Moray Firth and the models of swimming and haul-out costs I had constructed put me in a position to address these deficiencies (Chapter 6). The availability of detailed dive records for a common seal made it possible to more accurately predict the metabolic cost of travelling, foraging and male display dives. These predictions showed that the seals were not optimising their swim speed on the basis of minimising the cost of moving a given distance, as I had suggested earlier. Both travelling and foraging dives were energetically more costly and, what is more, the cost was independent of water temperature. The cost of foraging for bottom feeding common seals does not vary with season.

Although the cost of hauling-out varies considerably throughout the year it only ever accounts for a small portion of a seal's energy requirements, as they generally spend less than a quarter of their time hauled out. In consequence, the total daily energy requirements of a seal varies little with season. The exception to this is the increased energy demand that lactation places on a breeding female. Inclusion of the breeding costs of a male seal has previously been neglected in studies of seal energetics. Although the male seal reduces its energy requirements slightly when it switches from foraging to display dives this energy saving is not great. The most significant conclusions from this part of the work is the general lack of seasonal variation and the high proportion of the energy requirements of seals that are due to the cost of foraging. Indeed, they generally exceed the cost of maintenance which was previously thought to be the largest cost. This prediction arises as a direct result of the detailed approach to estimating foraging costs, described above.

Having made a detailed calculation of the energy requirements of common seals in the Moray Firth it seemed logical to combine these with information on the diet of the seals and estimate the consumption of fish by the population. To convert the energy requirements of the seals into the actual intake of energy required the cessation of feeding associated with breeding (applicable to both male and female seals) to be taken into account. This, and the subsequent recovery period, introduced a greater degree of seasonal variation for breeding seals. The estimate of the energy intake for the whole population was encouragingly robust to changes in the assumptions I had made about the body condition of the seals and the population's structure. The estimate was only sensitive to changes in the population size, to which it is directly proportional. The large seasonal changes in the consumption of individual prey species is attributable to the changes in their prevalence in the diet and are not a product of my energetics model. An assessment of the impact of predation by seals on local fish stocks lies beyond the scope of my thesis, but I hope that such work would benefit from what I have achieved.

Improving the synoptic picture of the impact of common seals in the Moray Firth would require a predictive model capable of taking account of the large seasonal variation in the abundance of some fish species with the area. Such a model requires an understanding of the mechanisms and rules by which a foraging seal operates. With this in mind I have developed a model of the foraging behaviour of an individual seal, which I believe could throw light on possible mechanisms and this is described in Chapter 8. Incorporation of data on fish distributions from acoustic surveys performed by SOAEFD (MLA, Aberdeen) provided some unexpected challenges. I have obtained some interesting results for an adult seal using a random walk search strategy. In particular, for the estimated digestion rate, the seal's foraging performance is limited by the time required to process the fish it catches and not by the effort required to locate its prey. An accurate determination of the stomach capacity and digestion rate are clearly important, although empirical data on this are limited. The work done provides a good platform for a more comprehensive investigation of this fascinating topic and it is a cause of frustration that I have had to draw a line under my contribution. Such a comprehensive study would merit a thesis in its own rite.

9.3 Further work

One of the truisms of scientific research is that it raises more questions than it answers. It is, therefore, appropriate that each study generates fruitful avenues for further work.

A useful refinement to the model of the thermal balance of a seal in air would be the inclusion of the effect of rain. This is less than straight forward, since the simple approximation of evaporation would no longer be adequate. A more detailed representation would require information on factors such as vapour pressure as well as data on rainfall. A more straightforward extension of the work is suggested by the observed cline in the timing of pupping on the Pacific coast of America (Temte et al. 1991), pupping occurring earlier further south. Given the necessary meteorological data it would be a simple matter to investigate a possible link between the timing of pupping and the suitability of weather conditions for periods of extended haul-out.

One of the most obvious expansions of this energetics study would be its application to other common seal populations. Multi-species fisheries modelling is now reaching the stage where the impact of higher predators, such as seals, are being explicitly included. For the North Sea MSVPA (Multi-species virtual population analysis) model this has been done for grey seals. Given sufficient data on the size of the common seal populations in the coastal regions of the North Sea and on their diet, it would be relatively straight forward to estimate the predation mortality this species inflicts on the major prey species.

The foraging model described in Chapter 8 is something of an unfinished symphony and there is huge potential for further work. The first step would be the application of a more effective search strategy than a random walk and there are any number of possible search strategies that can be devised. One of the most interesting aspects is incorporating the benefit of the seals knowledge. It is reasonable to assume that a mammalian predator uses some form of mental map as a framework for its foraging decisions. This fascinating area, raises such questions as; the time-scale on which the seal updates the map and the manner in which it first builds it. It also introduces the role of conspecifics. Do seals share information (either voluntarily or involuntarily) and is there a possible benefit in frequent of hauling-out ?

Personally, I think the influence of the tides on the foraging ecology of common seals in the Moray Firth may be an interesting topic. There are two aspects to this, the first is the limited availability of the sand banks on which they haul-out and the second the separation of the haul-out sites from the foraging grounds. The haul-out sites are generally in the inner Firths and the seals forage in the outer Firth. Between the two lie constricted regions creating moderate tide races, a good example is the narrowing of the Inverness Firth between Chanonry Point and Fort George. These tide races may act as tide gates which the seals must take account of in their movements between haul-out site and foraging ground. This suggestion is somewhat speculative and it is possible that the seals avoid the strongest tide flows by hugging the inside shoreline, Chanonry Point is popular for dolphin spotting since they often swim past very close to the shore.

So Long And Thanks For All The Fish

Douglas Adams

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Part V

Appendix

Appendix A

Foraging model PASCAL code

A.1 Introduction

This appendix contains the entire program code for the model of a seal foraging in the Moray Firth. The code is divided between four files: a header file (edf.h), the main file (edf.p), a file of modules (edf_mod.p) and a file of utility routines (edf_utils.p). The header file (section **??**) contains declarations for global variables, procedures and functions, in addition to a list of constants. The structurally defining procedures and functions are contained in the main program file (section **??**). The module files more generic routines (sections **??**), these are standard to all implementations. The final group of routines are designated as utilities (section **??**) and included routines such as hitline (which determines whether a trajectory passes bisects a line) and the random number generator (ran3) which was taken from Press, Flannery, Teukolsky, and Vetterling (1989). The program was run on a UNIX workstation and the files were complied and linked by a Makefile (section **??**).

A.2 Header file

```
{***header file for  event driven foraging model ***}
{***}
{***   Alasdair Hind            last update 20-5-98 ***}


#include <TurboP.def>
#include <WinLib.def>
#include <PlotLib.def>

const   FrameHgt=0.8;   FrameWdth=0.8;
        OpWinTop=10;    OpWinLeft=100;
        OpWinWidth=502; OpWinHeight=502;
```

```
        WinBorder=2;

        pi=3.141592653; blank=' ';

        longmin=-4.3336;        latmin=57.416;    {*lng/lat lim of boxes*}

        xinc=4990;      yinc=9265;                     {*m/coord box dim*}
        xmax=99800;     ymax=92650;                       {*coord limits*}
        dmax=136176;                   {*max dist. = sqrt(xmax^2+ymax^2)*}

        xbox=20;        ybox=10;                    {*space dim in boxes*}

        nruns=50;                                        {* no of runs  *}
        nouts=100;                                {* no of writes to res*}
        resdir='res-edf/';

        noofsq=200;                                        {*xbox x ybox*}

        unidepth=30;                              {* water depth -const *}
        hox=17465;      hoy=18530;                {*x,y coord of ho site*}
        initb=5;                                       {* first bearing *}

        detectsl=10;   detectst=10;   detecthg=10;{*search wdth for fish*}
        fwgtsl=11.1;   fwgtst=13.7;   fwgthg=48.1;{*wgt of indiv fish: g*}
        evalsl=5.72;   evalst=6.64;   evalhg=6.64;{*E density fish: Kj/g*}

        wgtsheat=1000;                            {* # shoal eaten: fish*}
        handt=10;                                       {* handling t: s*}

        hidet=0;

{* ADULT MALE common seal *}
        ing=0.69;                            {*digest eff g->E: fraction*}
        digestr=0.185;                            {* digestion rate: g/s*}
        maxgut=(0.05*77.77);               {* gut capacity: g  (3.89 Kg)*}
        vel=1.3;                                  {* const swim vel: m/s*}
        mbf=0.327;                         {* foraging metab cost: KJ/s *}
        rmr=0.0888;                           {* basal metab cost: KJ/s *}

        tsrf=79.4;                          {* post dive recover time: s*}
        tdive=221;                      {* duration of dive, incl tsf: s*}
{**********************}
type    boxref  = record        w,z:integer;    end;
        coord   = record        x,y:double;     end;
        tlog    = record        t,e:double;     end;
        corners  = array [1..4] of coord;
        fslist = array [1..3] of double;            {* [1=sl,2=st,3=hg] *}
        asquare = record        occu:boolean;           {*occupied=>true*}
                                crnr:corners;            {*corners of sq*}
```

```
                                cent:coord;           {*centre of square*}
                                dpth:double;           {*water depth: m *}
                                fsl:double;            {*no of prey in sq*}
                                fst:double;            {*no of prey in sq*}
                                fhg:double;            {*no of prey in sq*}
                                log:double;          {*time spent in box*}
                                hts:double          {*no. of fish caught*}
        end;
        fsprop  = record        wgt:fslist;       {*wgt of indiv fish: g*}
                                hnt:fslist;           {*handling time: s*}
                                eval:fslist;      {*E density fish: Kj/g*}
                                neat:fslist;      {*# shoal eaten: fish *}
                                ing:fslist;     end;        {*ingest eff*}
        end;
        forager = record        p:coord;                      {*location*}
                                b:double;                      {*bearing*}
                                box:boxref;               {* current box*}
                                lastp:coord;             {*last location*}
                                lastd:double;         {*last dist. moved*}
                                home:coord;         {* haul-out location*}
                                dleg:double;       {* d left on this leg*}
                                eat:fslist;  {*no.f eaten:1=sl,2=st,3=hg*}
                                gut:fslist;{*f in gut[1=sl,2=st,3=hg]: g*}
                                log:tlog;           {*temp. log for t+e *}
                                eres:double;             {*E reserve: Kj*}
       end;
       coast   = record        f:coord;             {*straight line from*}
                                t:coord;            {* f -> t           *}
                                r:double            {*reflect: r+(0-180)*}
       end;
        hitlist = array [1..(2*xbox)] of boxref;
        distlist = array [1..(2*xbox)] of double;
        squarelist = array [1..xbox,1..ybox] of asquare;
{*********************}
var     theclock                : EXTERN double;
        arena                   : EXTERN WinRec;
        box                     : EXTERN squarelist;
        fs                      : EXTERN fsprop;
        seal                    : EXTERN forager;
        Ch,pm                   : EXTERN char;
        dummy,sqwdt,sqhgt       : EXTERN double;
        klinokinesis            : EXTERN boolean;

{**********************}
procedure WINDOW;                                               extern;
function  getplotp(arenap:double; which:integer):integer;       extern;
procedure DRAWARENA(win:WinRec);                                extern;
{*procedure DISARENA(win:WinRec); extern;*}
procedure DISTRACK(win:WinRec);                                 extern;
```

```
procedure DISEVENT(win:WinRec);                                   extern;
{**********************}
function  power(a,b: double): double;                             extern;
function distance(a,b:coord):double;                              extern;
function bearing(here,there:coord):double;                        extern;
function gradient(from:coord; traj:double):double;                extern;

function hitline(from:coord;dir:double;tgf,tgt:coord):boolean;  extern;
procedure MOVEDIST(from:coord; b,d:double; var new:coord);      extern;
procedure
  INTERSECT(from:coord;dir:double;edf,edt:coord;var int:coord); extern;
procedure
  GETINTERSECT(wh:boxref; var hit1,hit2:coord; var ang1,ang2:double);
                                                                  extern;
procedure SQRSEARCH(var nhit:integer; var sqhit:hitlist);        extern;
procedure WHICHSQUARE(xref,yref:double; var which:boxref);       extern;

{**********************}
procedure MAKESQUARES;                                            extern;
procedure  GETFISH;                                               extern;
procedure
  HITFISH(wh:boxref; int1,int2:coord; var dpred:double; var fsph:integer);
procedure TRAVELOG(wh:boxref; dtravel:double);                    extern;
procedure GENLOG(fspl:integer);                                   extern;
{**********************}
procedure raninit(num:integer);                                   extern;
function ran3:double;                                             extern;
function  intostring(digits:integer):string;                      extern;
{**********************}
{*procedure  MOVE; extern;*}

#ifdef MYRAND
function drand48:double;                                          extern;
#define random(x)       drand48
#endif
```

A.3 Main program file

```
{\small
{***}
{****  program to implement event driven foraging  ****}
{****        in a patchy environment               ****}
{***}
{****  A.Hind                   25.4.96   ****}
{***}

program edf(input,output);
```

```
#include "edf.h"

var     disp:char;
        more,duration,outstep,nextout:double;
        totdstep:double;
        fbase,rbase,runout,resname,tbase,tname,dbase:string;
        resultfile,allresfile,trackfile:text;
        infseed,fseed,runn:integer;

#ifdef __alpha
        {* Globals *}
        theclock                : GLOBAL double;
        arena                   : GLOBAL WinRec;
        box                     : GLOBAL squarelist;
        fs                      : GLOBAL fsprop;
        seal                    : GLOBAL forager;
        Ch,pm                   : GLOBAL char;
        dummy,sqwdt,sqhgt       : GLOBAL double;
        klinokinesis            : GLOBAL boolean;
#endif


{*********************}

{*********************}

procedure  MOVERAND;

var     nextb,reflect,refl1,refl2:double;
        dstep,dhit,dtrav:double;
        nextp,int1,int2:coord;
        i,nhits,fhit:integer;
        sqshit:hitlist;
        event,moresea:boolean;
temp:double;

begin   dstep:=seal.dleg;
        reflect:=360;
        i:=1;
        GETINTERSECT(seal.box,int1,int2,refl1,refl2);
                                          {* near:int1, far:int2 *}
        dtrav:=distance(int1,int2);
        HITFISH(seal.box,int1,int2,dhit,fhit);  {*fhit: 1=sl,2=st,3=hg*}
        if (fhit>0) then
        begin   if (dhit>=dtrav) OR (dhit>=dstep) then  fhit:=0
                else
                begin   MOVEDIST(seal.p,seal.b,dhit,nextp);
                        TRAVELOG(seal.box,dhit);
```

```
        end
end;
if (fhit=0) AND (dstep<dtrav) then
begin   MOVEDIST(seal.p,seal.b,seal.dleg,nextp);
        TRAVELOG(seal.box,dstep);
end
else if (fhit=0) then
begin   TRAVELOG(seal.box,dtrav);
        SQRSEARCH(nhits,sqshit);
        if (nhits>0) then
                 moresea:=box[sqshit[i].w,sqshit[i].z].occu;
        if ((nhits=0) OR (moresea=false)) then  nextp:=int2
        else
        begin
        repeat  event:=FALSE;
                if i>1 then TRAVELOG(sqshit[i-1],dtrav);
                dstep:=dstep-dtrav;
                GETINTERSECT(sqshit[i],int1,int2,refl1,refl2);
                dtrav:=distance(int1,int2);
                HITFISH(sqshit[i],int1,int2,dhit,fhit);
                                         {*fhit:1=sl,2=st,3=hg*}
                if (fhit>0) then
                begin   if (dhit>=dtrav) OR (dhit>=dstep) then
                               fhit:=0
                      else
                      begin  event:=TRUE;
                             TRAVELOG(sqshit[i],dhit);
                             dhit:=dhit+distance(seal.p,int1);
                             MOVEDIST(seal.p,seal.b,dhit,nextp);
                      end;
                end;
                if (fhit=0) AND (dstep<dtrav) then
                begin   event:=TRUE;
                        MOVEDIST(seal.p,seal.b,totdstep,nextp);
                        TRAVELOG(sqshit[i],dstep);
                end;
                if i<nhits then
                   moresea:=box[sqshit[i+1].w,sqshit[i+1].z].occu;
                i:=i+1;
        until (event=true) or (i>nhits) or (moresea=false);

                if (i>nhits) then
                begin   nextp:=int2;
                        reflect:=refl2;
                        TRAVELOG(sqshit[nhits],dtrav);
                end;
                seal.box:=sqshit[i-1];
        end;
end;
```

```
        if (fhit>0) then
        begin   nextb:=seal.b;
                seal.dleg:=dstep;
        end
        else
        begin   if (reflect=360) then
                begin   if (klinokinesis=true) then
                                nextb:=nextb*(1-(seal.lastd/dmax))
                         else   nextb:=ran3*360;
                end
                else
                begin
if (reflect=0) OR (reflect=90) OR (reflect=180) OR (reflect=270)
{*if ((trunc(reflect) MOD 90)=0)*}
                                then nextb:=(ran3*180)+reflect
                        else    nextb:=((ran3*2-1)*90);
                end;
                seal.dleg:=totdstep;
        end;
        seal.lastp:=seal.p;
        seal.p:=nextp;
        if (nextb<360) then seal.b:=nextb else seal.b:=nextb-360;
        GENLOG(fhit);
end;
{**********************}

procedure SETUP;

var     num:double;
        ans:char;
        i,j:integer;

begin   MAKESQUARES;
        write('use klinokinesis y/n: ');  readln(ans);
        if ans="y" then klinokinesis:=true
        else klinokinesis:=false;
        write(' random walk step =  ');   readln(num);
        totdstep:=num;
        fs.wgt[1]:=fwgtsl;
        fs.hnt[1]:=handt;
        fs.eval[1]:=evalsl;
        fs.ing[1]:=ing;
        fs.neat[1]:=wgtsheat/fwgtsl;
        fs.wgt[2]:=fwgtst;
        fs.hnt[2]:=handt;
        fs.eval[2]:=evalhg;
        fs.ing[2]:=ing;
        fs.neat[2]:=wgtsheat/fwgtst;
        fs.wgt[3]:=fwgthg;
```

```
        fs.hnt[3]:=handt;
        fs.eval[3]:=evalhg;
        fs.ing[3]:=ing;
        fs.neat[3]:=wgtsheat/fwgthg;
        for i:=1 to xbox do
                for j:=1 to ybox do
                begin   box[i,j].occu:=false;
                        box[i,j].log:=0;
                        box[i,j].hts:=0;
                        box[i,j].dpth:=unidepth;
                end;
        GETFISH;
        seal.home.x:=hox;  seal.home.y:=hoy; {*haul-out location*}
end;

{**********************}

procedure INITIALISE;
var     i:integer;

begin   raninit(fseed);
        theclock:=0;
        duration:=0;
        with seal do
        begin   dleg:=totdstep;
                b:=initb;
                p.x:=home.x;
                p.y:=home.y;
                lastp:=p;
                WHICHSQUARE(p.x,p.y,box);
                for i:=1 to 3 do
                begin   eat[i]:=0;
                        gut[i]:=0;
                end;
                eres:=0;
                log.t:=0;
                log.e:=0;
        end;
end;


{**********************}

procedure ENDOUT;
var     datafile:text;
        fname:string;
        i,j:integer;

begin
```

```
{* results to file *}
        write(allresfile,runn);  write(allresfile,' ');
        write(allresfile,seal.Eres:12:6);  write(allresfile,' ');
        write(allresfile,seal.eat[1]:6:2);  write(allresfile,' ');
        write(allresfile,seal.eat[2]:6:2);  write(allresfile,' ');
        write(allresfile,seal.eat[3]:6:2);  write(allresfile,' ');
        write(allresfile,seal.gut[1]:6:2);  write(allresfile,' ');
        write(allresfile,seal.gut[2]:6:2);  write(allresfile,' ');
        write(allresfile,seal.gut[3]:6:2);  write(allresfile,' ');
        writeln(allresfile,theclock:1:1);

{* results to screen *}
        writeln('time  ',theclock:1:1,' Eres ',seal.Eres:6:1);
        writeln('fish, sl: ',seal.eat[1]:6:1,
                   '   st: ',seal.eat[2]:6:1,
                   '   hg: ',seal.eat[3]:6:1);
        writeln('gut,  sl: ',seal.gut[1]:6:1,
                   '   st: ',seal.gut[2]:6:1,
                   '   hg: ',seal.gut[3]:6:1);
        writeln(' RUN  : ',runn);
        writeln;
        if (dbase<>'n') then
        begin   fname:=dbase + intostring(runn);
                rewrite(datafile,fname);
                for i:=1 to xbox do
                        for j:=1 to ybox do
                        if (box[i,j].occu=true) then

begin   write(datafile,box[i,j].cent.x:12:6); write(datafile,' ');
        write(datafile,box[i,j].cent.y:12:6); write(datafile,' ');
        write(datafile,box[i,j].fsl:12:6);    write(datafile,' ');
        write(datafile,box[i,j].fst:12:6);    write(datafile,' ');
        write(datafile,box[i,j].fhg:12:6);    write(datafile,' ');
        write(datafile,box[i,j].log:12:6);    write(datafile,' ');
        writeln(datafile,box[i,j].hts:12:6);
end;
                close(datafile);
        end;
end;

procedure SEALOUT;
var     i:integer;

begin   write(resultfile,theclock:12:6);   write(resultfile,' ');
        write(resultfile,seal.Eres:12:6);  write(resultfile,' ');
        for i:=1 to 3 do
        begin   write(resultfile,seal.eat[i]:12:6);
                write(resultfile,' ');
        end;
```

```
        for i:=1 to 2 do
        begin   write(resultfile,seal.gut[i]:12:6);
                write(resultfile,' ');
        end;
        writeln(resultfile,seal.gut[3]:12:6);
end;


procedure TRACKOUT(evnt:integer);

begin   write(trackfile,seal.p.x);      write(trackfile,' ');
        write(trackfile,seal.p.y);      write(trackfile,' ');
        writeln(trackfile,evnt);

end;

{*********************}
procedure MOVELOOP;
var     trk:char;
        e:integer;

begin   e:=0;
        if (tbase<>'n') then
        begin   tname:=tbase + intostring(runn);
                rewrite(trackfile,tname);
                TRACKOUT(e);
        end;
        repeat  e:=e+1;
                MOVERAND;
                if (tbase<>'n') then TRACKOUT(e);
#ifdef SOLVER
                if (disp<>'n') then
                        if (disp='t') then DISTRACK(arena)
                                else    DISEVENT(arena);
#endif
                if theclock>nextout then
                begin   if (runout='y') then SEALOUT;
                        nextout:=nextout+outstep;
                end;
        until theclock>duration;
        if (tbase<>'n') then
        begin   TRACKOUT(e+1);
                close(trackfile);
        end;
        ENDOUT;
end;
{*********************}
procedure  GETBASENAMES;
```

```
var     seedstr:string;

begin   seedstr:=intostring(infseed);
        rbase:=resdir+fbase+'-r-'+seedstr+'r';
        if (tbase='y') then
                tbase:=resdir+fbase+'-t-'+seedstr+'r'
        else tbase:='n';
        if (dbase='y') then
                dbase:=resdir+fbase+'-d-'+seedstr+'r'
        else dbase:='n';
end;

{**********************}

begin   SETUP;
#ifdef SOLVER
        write('display track or event: t/p or n '); readln(disp);
        if (disp<>'n') then
        begin   WINDOW;
                DRAWARENA(arena);
        end;
#endif
        write('seed: ');                readln(infseed);
        write('run till (hrs) ');       readln(more);
        write(' results file  ');       readln(fbase);
        write('run file (y/n) :  ');    readln(runout);
        write('track file (y/n) :  '); readln(tbase);
        write('arena-dump file (y/n) :  '); readln(dbase);
        GETBASENAMES;
        rewrite(allresfile,rbase + 'all');
        fseed:=0;
        for runn:=1 to nruns do
        begin   if (runout='y') then
                       resname:=rbase+intostring(runn);
                fseed:=infseed*runn;
                INITIALISE;
                if (runout='y') then
                begin   rewrite(resultfile,resname);
                        SEALOUT;
                end;
                outstep:=(more*3600-duration)/nouts;
                nextout:=duration+outstep;
                duration:=more*3600;
                MOVELOOP;
                if (runout='y') then
                begin   close(resultfile);
                        SEALOUT;
                end;
        end;
```

```
        close(allresfile);

#ifdef SOLVER
        if (disp<>'n') then
        begin   read(Ch);
                if (Ch=blank) then
        end;
#endif
end.
```

A.4 Modules file

```
{***}
{****  contains utilities for event driven foraging model  ****}
{***}
{***}
{****  A.Hind                    20-5-98   ****}
{***}
{***   changed DIGESTION STUFF - has to stop to digest     ****}
{***   procs DIGEST and GENLOG changed                     ****}
{***}

#ifdef __alpha
module edf_mod(input, output);
#endif

#include "edf.h"

{*********************}
GLOBAL procedure MAKESQUARES;

var     b:double;
        i,j:integer;

begin   b:=0;
        for i:=1 to xbox do
        begin   for j:=1 to ybox do
                begin   box[i,j].crnr[1].x:=b;
                        box[i,j].crnr[4].x:=b;
                        box[i,j].cent.x:=b+(xinc/2);
                end;
                b:=b+xinc;
                for j:=1 to ybox do
                begin   box[i,j].crnr[2].x:=b;
                        box[i,j].crnr[3].x:=b;
                end;
        end;
```

```
        b:=0;
        for j:=1 to ybox do
        begin   for i:=1 to xbox do
                begin   box[i,j].crnr[3].y:=b;
                        box[i,j].crnr[4].y:=b;
                        box[i,j].cent.y:=b+(yinc/2);
                end;
                b:=b+yinc;
                for i:=1 to xbox do
                begin   box[i,j].crnr[1].y:=b;
                        box[i,j].crnr[2].y:=b;
                end;
        end;
        for i:=1 to xbox do
                for j:=1 to ybox do
                begin   box[i,j].occu:=false;
                        box[i,j].log:=0;
                        box[i,j].hts:=0;
                        box[i,j].dpth:=0;
                end;
end;
{*********************}
GLOBAL procedure  GETFISH;
var     datafile:text;
        fname:string;
        long,lat,sprat,sandeel,herring:double;
        wh:boxref;

begin   write('Input datafile name:- '); readln(fname);
#ifdef __alpha
        open(datafile,fname,HISTORY:=UNKNOWN);
#else
        open(datafile,fname,'unknown');
#endif
        reset(datafile);
        while not(eof(datafile)) do
                begin   while not(eoln(datafile)) do
                        begin
                                read(datafile,lat);
                                read(datafile,long);
                                read(datafile,sandeel);
                                read(datafile,sprat);
                                read(datafile,herring);
                        end;
                        readln(datafile);
                        WHICHSQUARE(long,lat,wh);
                        box[wh.w,wh.z].occu:=true;
                                    {*fsp: 1=sl, 2=st, 3=hg *}
                        box[wh.w,wh.z].fsl:=sandeel/fs.wgt[1];
```

```
                        box[wh.w,wh.z].fst:=sprat/fs.wgt[2];
                        box[wh.w,wh.z].fhg:=herring/fs.wgt[3];
                end;
end;
{**********************}
GLOBAL procedure
 HITFISH(wh:boxref;int1,int2:coord;var dpred:double;var fsph:integer);
                        {*fsp: 1=sl, 2=st, 3=hg *}
var     dsl,dst,dhg,r1,r2,r3:double;

begin   dpred:=ymax*10;
        fsph:=0;
        r1:=ran3;
        r2:=ran3;
        r3:=ran3;
        if (box[wh.w,wh.z].fsl=0) or (r1=0) then dsl:=10*ymax
                else  dsl:=(-ln(r1))/(detectsl*box[wh.w,wh.z].fsl);
        if (box[wh.w,wh.z].fst=0) or (r2=0)  then dst:=10*ymax
                else  dst:=(-ln(r2))/(detectst*box[wh.w,wh.z].fst);
        if (box[wh.w,wh.z].fhg=0) or (r3=0)  then dhg:=10*ymax
                else  dhg:=(-ln(r3))/(detecthg*box[wh.w,wh.z].fhg);
        if ((dsl=dst) AND (dst=dhg) AND (dhg=dpred)) then fsph:=0
        else
        begin   if (dsl<dst) and (dsl<dhg) then
                begin   dpred:=dsl;
                        fsph:=1;
                end
                else
                if (dst<dhg) then
                        begin   dpred:=dst;
                                fsph:=2;
                        end
                else    begin   dpred:=dhg;
                                        fsph:=3;
                                end;
        end;
end;

{**********************}
procedure DIGEST(fspd:integer; nfspd:double; var tlapse:double);
                                        {*adds digestion to sumt*}
var     totgut:double;
        i:integer;

begin   if (fspd>0) then
            seal.gut[fspd]:=seal.gut[fspd]+(nfspd*fs.wgt[fspd]);
        totgut:=0;
        for i:=1 to 3 do totgut:=totgut + seal.gut[i];
        if (totgut>maxgut) then
```

```
        begin   tlapse:=totgut/digestr;
                for i:=1 to 3 do
                begin   seal.eres:=seal.eres
                               +(seal.gut[i]*fs.ing[i]*fs.eval[i]);
                        seal.gut[i]:=0;
                end;
        end
        else    tlapse:=0;
end;
{***********************}
GLOBAL procedure TRAVELOG(wh:boxref; dtravel:double);

var     tud,ndives:double;

begin   tud:=(2*box[wh.w,wh.z].dpth)/vel;
                                          {*time up/down surf->depth*}
        ndives:=(dtravel/vel)/(tdive-tud);            {* tdive =ADL *}
        with seal do
        begin   log.t:=log.t+ndives*(tdive+tsrf);
                                           {*tsrf=post dive recovery*}
                log.e:=log.e+ ndives*(tdive+tsrf)*Mbf;
        end;
end;
{***********************}
GLOBAL procedure GENLOG(fspl:integer);
                        {*fsp: 0=no-hit 1=sl, 2=st, 3=hg *}

var     tdummy,ddummy:double;
        nfspl:double;

begin   if (fspl>0) then
        begin   nfspl:=fs.neat[fspl];
                seal.eat[fspl]:=seal.eat[fspl]+ nfspl;
                box[seal.box.w,seal.box.z].hts
                        :=box[seal.box.w,seal.box.z].hts + nfspl;
                ddummy:=vel*(nfspl*fs.hnt[fspl]);
                                          {*passes xtra t as a dist.*}
                TRAVELOG(seal.box,ddummy);
        end
        else    nfspl:=0;
        tdummy:=seal.log.t;
        DIGEST(fspl,nfspl,tdummy);        {* returns stop to digest *}

        if (tdummy>0) then                     {* stopped to digest *}
        with seal do
        begin   log.t:=log.t+ tdummy;          {*add digestion stop *}
                log.e:=log.e+ tdummy*rmr;
                              {*add metabolic cost during digest *}
        end;
```

```
        seal.eres:=seal.eres - seal.log.e;
        box[seal.box.w,seal.box.z].log
                :=box[seal.box.w,seal.box.z].log + seal.log.t;
        theclock:=theclock + seal.log.t;
        seal.log.t:=0;
        seal.log.e:=0;
end;

{*********************}
#ifdef __alpha
END.
#endif
```

A.5 Utilities file

```
{***contains utilities for event driven foraging model ***}
{***}
{***   Alasdair Hind            last update 25-4-98 ***}

#ifdef __alpha
module edf_utils(input,output);
#endif

#include "edf.h"

var     Ran3Inext,Ran3Inextp:integer; {* generator variables *}
        Ran3Ma:array[1..55] of double;
        mseed:double;
        idum:integer; {* dummy for rand num gen *}
{*********************}
#ifdef SOLVER

GLOBAL procedure  WINDOW;

var     B:SysRec;       BlackID,WhiteID,GreyID:ColorID;

begin   StartDisplay;
        BlackID:=GetColorID('Black');
        WhiteID:=GetColorID('White');
        GreyID:=GetColorID('LightGrey');
        SaveDefaults(B);
                B.DefFgd:=BlackID;
                B.DefBgd:=WhiteID;
                B.DefBdr:=GreyID;
        RestoreDefaults(B);
        if MonoDisplay then B.DefBdr:=BlackID;
```

```
        CurWinName:='arena';
        OpenWindow(arena,OpWinLeft,OpWinTop,OpWinWidth,OpWinHeight);
end;
{*********************}
GLOBAL function  getplotp(arenap:double; which:integer):integer;
                                        {* which - 0:x, 1:y *}
var     scale:double;
        intp:integer;

begin   if which=0 then
        begin   scale:=OpWinWidth-2*WinBorder;
                intp:=round((arenap/xmax)*scale)+WinBorder;
        end
        else
        begin   scale:=OpWinHeight-2*WinBorder;
                intp:=OpWinHeight
                        -(round((arenap/ymax)*scale)+WinBorder);
        end;
        getplotp:=intp;
end;

GLOBAL procedure DRAWARENA(win:WinRec);
var     xo,xm,yo,ym,xaxis,yaxis:integer;

begin   xaxis:=0;
        yaxis:=1;
        xo:=getplotp(0,xaxis);
        xm:=getplotp(xmax,xaxis);
        yo:=getplotp(0,yaxis);
        ym:=getplotp(ymax,yaxis);
        Line(win,xo,ym,xm,ym);
        Line(win,xm,ym,xm,yo);
        Line(win,xm,yo,xo,yo);
        Line(win,xo,yo,xo,ym);
        FlushDisplay;
end;

GLOBAL procedure DISTRACK(win:WinRec);
var     x1,x2,y1,y2,xaxis,yaxis:integer;

begin   xaxis:=0;
        yaxis:=1;
        x1:=getplotp(seal.lastp.x,xaxis);
        y1:=getplotp(seal.lastp.y,yaxis);
        x2:=getplotp(seal.p.x,xaxis);
        y2:=getplotp(seal.p.y,yaxis);
        Line(win,x1,y1,x2,y2);
        FlushDisplay;
end;
```

```
GLOBAL procedure DISEVENT(win:WinRec);
var     x1,y1,xaxis,yaxis:integer;

begin   xaxis:=0;
        yaxis:=1;
        x1:=getplotp(seal.lastp.x,xaxis);
        y1:=getplotp(seal.lastp.y,yaxis);
        Point(win,x1,y1);
        FlushDisplay;
end;

#endif
{*********************}
GLOBAL function  power(a,b: double): double; {*  power = a^b  *}
var     c:integer;
begin
        if a<0 then
        begin   if trunc(b)=b then
                begin   c:=trunc(b);
                        if (c mod 2)=0 then
                              power:=exp(b*(ln(-1*a)))
                        else  if (c mod 2)=1 then
                                power:=-1*exp(b*(ln(-1*a)))
                              else
                                writeln('cant do power on -ve numbers');
                end
                else writeln('cant do power on -ve numbers');
        end
        else
        if a=0 then power:=0 else power:= exp(b*(ln(a)));
end;
{*********************}
GLOBAL function distance(a,b:coord):double;
var dx,dy:double;
begin   dx:=a.x-b.x;
        dy:=a.y-b.y;
        distance:=sqrt((dx*dx)+(dy*dy));
end;
{*********************}
GLOBAL function bearing(here,there:coord):double;
var dx,dy,angle:double;

begin   dx:=there.x-here.x;
        dy:=there.y-here.y;
        if (dx=0) then
        begin   if (dy=0) then bearing:=-1
                else    if (dy>0) then bearing:=0
                        else    if (dy<0) then bearing:=180;
```

```
        end
        else
        begin   angle:=arctan(dy/dx)*(180/pi);
                if (dx>=0) and (dy>=0) then bearing:=90-angle
                else
                if (dx>=0) and (dy<0) then bearing:=90-angle
                else
                if (dx<0) and (dy<=0) then bearing:=270-angle
                else
                if (dx<0) and (dy>0) then bearing:=270-angle;
        end;
end;
{*********************}
GLOBAL function gradient(from:coord; traj:double):double;
var     radian:double;

begin   if traj<180 then radian:=(90-traj)*(pi/180)
        else
        if traj<360 then radian:=(270-traj)*(pi/180)
        else
        write('bearing > 360');
        gradient:=sin(radian)/cos(radian);
end;
{*********************}
GLOBAL function hitline(from:coord;dir:double;tgf,tgt:coord):boolean;

var     b1,b2:double;
        dummy:boolean;

begin   dummy:=false;
        b1:=bearing(from,tgf);
        b2:=bearing(from,tgt);

{** get cases: seal at end, seal direction along the line **}
        if (b1=b2) and (dir=b1) then dummy:=true
        else
        if (b1=-1) and (dir=b2) then dummy:=true
        else
        if (b2=-1) and (dir=b1) then dummy:=true
        else
{** if niether of special cases then check if line hit **}
        begin   if ((abs(b1-b2))=180) then dummy:=false
                else
                if (b1<b2) then
                begin   if ((b2-b1)<180) then
                                begin   if (dir>=b1) and (dir<=b2)
                                                then dummy:=true;
                                end
                        else
```

```
                                begin   if (dir<=b1) or (dir>=b2)
                                                then dummy:=true;
                                end
                end
                else
                if ((b1-b2)<180) then
                        begin   if (dir>=b2) and (dir<=b1)
                                     then dummy:=true;
                        end
                else
                        begin   if (dir<=b2) or (dir>=b1)
                                     then dummy:=true;
                        end;
        end;
        hitline:=dummy;
end;
{**********************}
function hitsquare(from:coord;crs:corners;dir:double):boolean;

var     bmax,bmin,b,b1,b2:double;
        dummy:boolean;
        i:integer;

begin   dummy:=false;  bmax:=0;  bmin:=360;  b1:=0;  b2:=0;
        for i:=1 to 4 do
        begin   b:=bearing(from,crs[i]);
                if (b>-1) and (b<bmin) then bmin:=b;
                if (b>-1) and (b>bmax) then bmax:=b;
        end;

{*case: sq. is north of seal-> min & max aren't outside angles*}
        if ((bmax-bmin)>180) then
        begin   if ((bmax-bmin)>270) then
                begin   for i:=1 to 4 do
                        begin   b:=bearing(from,crs[i]);
                                if (b>-1) and (b<>bmin) and (b<180)
                                    then b1:=b;
                                if (b>-1) and (b<>bmax) and (b>180)
                                    then b2:=b;
                        end;
                        if b1<b2 then
                        begin   bmin:=b1;
                                bmax:=b2;
                        end
                        else    begin   bmin:=b2;
                                        bmax:=b1;
                                end;
                end;
                if (dir<=bmin) or (dir>=bmax) then dummy:=true;
```

```
        end
        else

{** check for case seal is on east  edge **}
        begin   if (bmin=0) and ((bmax-bmin)=180) then
                begin   for i:=1 to 4 do
                        begin   b:=bearing(from,crs[i]);
                                if (b>-1)and (b<>bmin)and (b<>bmax)
                                     then b1:=b;
                        end;
                        if b1>180 then
                        begin   bmin:=bmax;
                                bmax:=360;
                        end;
                end;
                if (dir>=bmin) and (dir<=bmax) then dummy:=true;
        end;
        hitsquare:=dummy;
end;
{*********************}
GLOBAL procedure MOVEDIST(from:coord; b,d:double; var new:coord);

begin   new.x:=from.x + (sin((pi/180)*b)*d);
        new.y:=from.y + (cos((pi/180)*b)*d);
end;
{*********************}
GLOBAL procedure
   INTERSECT(from:coord;dir:double;edf,edt:coord;var int:coord);
var     dy,dx,me,ms:double;

begin   ms:=gradient(from,dir);
        dy:=edf.y-edt.y;
        dx:=edf.x-edt.x;
        if dx=0 then
        begin   int.x:=edf.x;
                int.y:=ms*(edf.x-from.x)+from.y;
        end
        else
        if dy=0 then
        begin   int.x:=((edf.y-from.y)/ms)+from.x;
                int.y:=edf.y;
        end
        else
        begin   me:=dy/dx;
                int.x:=(edf.y-from.y-(me*edf.x)+(ms*from.x))/(ms-me);
                int.y:=ms*(int.x-from.x)+from.y;
        end;
end;
{*********************}
```

```
GLOBAL procedure
   GETINTERSECT(wh:boxref; var hit1,hit2:coord; var ang1,ang2:double);
                              {* gets intersections with box edges *}
                                          {* + angles for reflecting*}
                        {* returns nearest as 1 and farthest as 2 *}

type    anglist = array[1..2] of double;
        intlist = array[1..2] of coord;

var     i,h:integer;
        tcrnr:corners;
        ang:anglist;
        hits:intlist;

begin   tcrnr:=box[wh.w,wh.z].crnr;
        for h:=1 to 2 do
        begin   hits[h]:=seal.p;
                ang[h]:=360;
        end;
        h:=1;
        for i:=1 to 3 do
        begin   if hitline(seal.p,seal.b,tcrnr[i],tcrnr[i+1]) then
                begin
                INTERSECT(seal.p,seal.b,tcrnr[i],tcrnr[i+1],hits[h]);
                        ang[h]:=bearing(tcrnr[i],tcrnr[i+1]);
                        h:=h+1;
                end;
        end;
        if hitline(seal.p,seal.b,tcrnr[4],tcrnr[1]) then
        begin   INTERSECT(seal.p,seal.b,tcrnr[4],tcrnr[1],hits[h]);
                ang[h]:=bearing(tcrnr[4],tcrnr[1]);
                h:=h+1;
        end;
        if (h=2) then
        begin   hit1:=seal.p;
                hit2:=hits[1];
                ang1:=360;
                ang2:=ang[1];
        end
        else if (distance(seal.p,hits[1])<distance(seal.p,hits[2]))
        then    begin   hit1:=hits[1];
                        hit2:=hits[2];
                        ang1:=ang[1];
                        ang2:=ang[2];
                end
                else    begin   hit1:=hits[2];
                                hit2:=hits[1];
                                ang1:=ang[2];
                                ang2:=ang[1];
```

```
                        end;
end;
{*********************}
procedure  SORTHITS(n:integer; var sqr:hitlist; var dis:distlist);

var     i, j, gap, top, switches:integer;
        tmpd:double;
        tmps:boxref;

begin   gap := n;
        repeat
                gap := trunc(gap/1.3);
                case gap of
                        0: gap := 1;
                        9,10: gap := 11;
                        otherwise;
                end;
                switches := 0;
                top := n - gap;
                for i:=1 to top do
                begin
                        j := i+gap;
                        if (dis[i] > dis[j]) then
                        begin
                                tmpd := dis[i];
                                dis[i] := dis[j];
                                dis[j] := tmpd;
                                tmps := sqr[i];
                                sqr[i] := sqr[j];
                                sqr[j] := tmps;

                                switches := 1;
                        end
                end
        until ((switches = 0) and (gap <= 1));
end;
{*********************}
GLOBAL procedure SQRSEARCH(var nhit:integer; var sqhit:hitlist);

var     i,j,c:integer;
        hitdist:distlist;

begin   c:=0;
        for i:=1 to xbox do
                for j:=1 to ybox do
                  if (i<>seal.box.w) or (j<>seal.box.z) then
                  if hitsquare(seal.p,box[i,j].crnr,seal.b) then
                  begin   c:=c+1;
                          sqhit[c].w:=i;
```

```
                        sqhit[c].z:=j;
                        hitdist[c]:=distance(seal.p,box[i,j].cent);
                end;
        nhit:=c;
        if (nhit>0) then SORTHITS(nhit,sqhit,hitdist);
end;
{**********************}
GLOBAL procedure  WHICHSQUARE(xref,yref:double; var which:boxref);
const   small=0.000001;

var     tempx,tempy:double;

begin   if (xref<0) then
        begin   tempx:=(xref-longmin)*(60/5)*xinc;
                tempy:=(yref-latmin)*(60/5)*yinc;
        end
        else
        begin   tempx:=xref;
                tempy:=yref;
        end;
        which.w:=trunc((tempx-small)/xinc)+1;
        which.z:=trunc((tempy-small)/yinc)+1;
end;
{**********************}
GLOBAL  procedure raninit(num:integer);

begin   mseed:=num;
        idum:=-10;
end;

GLOBAL  function ran3:double;
{* generates a uniform random variable *}

const   mbig=4.0e6;
        mz=0.0;         fac=2.5e-7;

var     i,ii,k:integer;
        mj,mk:double;

begin   if idum<0 then
        begin   mj:=mseed+idum;
                if mj>0 then  mj:=mj-mbig*trunc(mj/mbig)
                else    mj:=mbig-abs(mj)+mbig*trunc(abs(mj)/mbig);
                Ran3Ma[55]:=mj;
                mk:=1;
                for i:=1 to 54 do
                begin   ii:=21*i mod 55;
                        Ran3Ma[ii]:=mk;
                        mk:=mj-mk;
```

```
                        if mk<mz then   mk:=mk+mbig;
                        mj:=Ran3Ma[ii]
                end;
                for k:=1 to 4 do
                begin
                  for i:=1 to 55 do
                  begin  Ran3Ma[i]:=Ran3Ma[i]-Ran3Ma[1+((i+30) mod 55)];
                         if Ran3Ma[i]< mz then
                              Ran3Ma[i]:=Ran3Ma[i]+mbig
                  end
                end;
                Ran3Inext:=0;
                Ran3Inextp:=31;
                idum:=1
        end;
        Ran3Inext:=Ran3Inext+1;
        if Ran3Inext=56 then    Ran3Inext:=1;
        Ran3Inextp:=Ran3Inextp+1;
        if Ran3Inextp=56 then   Ran3Inextp:=1;
        mj:=Ran3Ma[Ran3Inext]-Ran3Ma[Ran3Inextp];
        if mj<mz then   mj:=mj+mbig;
        Ran3Ma[Ran3Inext]:=mj;
        ran3:=mj*fac
end;
{*********************}
GLOBAL  function  intostring(digits:integer):string;

var     dg,i:integer;
        rack: array[1..10] of char;
        letters:string;

begin   if (digits<10) then intostring:= chr(ord(’0’) + digits)
        else
        begin   letters:=’’;
                i:=0;
                repeat
                        i:=i+1;
                        dg:=digits MOD 10;
                        rack[i]:=chr(ord(’0’) + dg);
                        digits:=digits DIV 10;
                until digits=0;
                repeat
                        letters:=letters+rack[i];
                        i:=i-1;
                until   i=0;
                intostring:=letters;
        end;
end;
{*********************}
```

```
#ifdef __alpha
END.
#endif
```

A.6 Makefile

```
MXPATH = /home/alasdair/solver-5.04/modules

PC = pc

EDFPROG = edf
EDFINCL = edf.h
EDFSOURCES = edf.p  edf_mod.p edf_utils.p
EDFOBJ = edf.o edf_mod.o edf_utils.o

DECLIBS = -L/opt/local/lib -lsolv -lX11 -lm
SUNLIBS = -L/usr/openwin/lib -L/opt/local/lib -lsolv -lX11 -lm

catch:
	@echo Choose between 'make sun' and 'make dec'.
sun:
	@$(MAKE) LIBS="$(SUNLIBS)" all
dec:
	@$(MAKE) LIBS="$(DECLIBS)" all

COMMON  = -DSOLVER -DMYRAND -I$(MXPATH)
DEFINES = -C all -g
PFLAGS  = $(EPFLAGS) $(DEFINES) $(COMMON)
all: $(EDFPROG)
debug: clean all

$(EDFPROG): $(EDFOBJ) $(EDFINCL)
	$(PC) -o $@  $(EDFOBJ) $(LIBS)
distclean: clean
	$(RM) -f $(EDFPROG)
clean:
	$(RM) -f core $(EDFOBJ)

BAKDIR=`date +"%Y.%m.%d-%H.%M"`

backup:
	mkdir -p sbak/$(BAKDIR)
	cp Makefile $(EDFINCL) $(EDFSOURCES) sbak/$(BAKDIR)
```