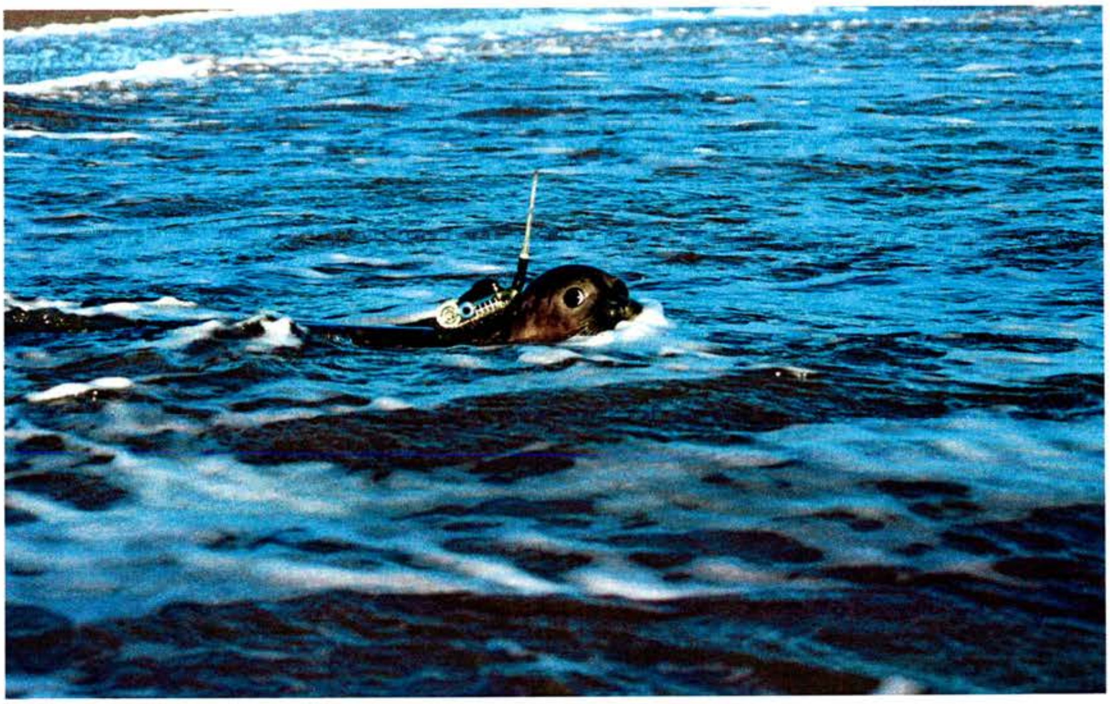
Ecology of harbour seals in southeastern Scotland.

Ruth J. Sharples

A thesis submitted to the University of St. Andrews for the degree of Doctor of Philosophy.

Division of Environmental and Evolutionary Biology

February 2005



CONTENTS

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ABSTRACT

The main aims of this study were to better understand the ecology of this species in this area as well as the species as a whole. Individual activity patterns of harbour seals recorded via satellite relay data loggers (SRDLs) were modelled to estimate the proportion of the population hauled-out and thus population size by extrapolating from counts made at haul-out sites throughout the year.

Seasonal variation in harbour seal diet in the east coast of Scotland was investigated through the analysis of faeces. Overall the diet was found to be dominated by sandeels (45%) and whiting (22%). There were significant seasonal trends in the consumption of sandeels, peaking in winter months. Fewer sandeels were consumed in the summer months when flat fish were more dominant, primarily flounder, as well as salmonids.

This study was the first time that satellite telemetry had been used on harbour seals in Britain and animals were found to be foraging further from haul-outs than previously thought. Foraging activity was densely aggregated into 'hot-spots' of localised foraging activity between 10 and 70 km from the haul-outs. Harbour seals selected sandy substrates with higher percentages of gravel than available, the habitat used by sandeels.

Endogenous characteristics of individuals were found to explain some of the observed variation in foraging activity. The distance travelled was significantly shorter for females and both the proportion of time at sea and foraging trip duration were positively related to body length for both sexes. The results presented here are valuable in improving our understanding of the ecology of this species and provides information that can be used to help inform conservation and management decisions.

ACKNOWLEDGEMENTS

For giving me the opportunity to carry out this project and for his support and encouragement I would like to thank my supervisor Dr Phil Hammond. I'd also like to thank him for finding the finances to make this project work. I'd like to thank the Natural Environment Research Centre for supporting this project financially, in providing my stipend (award reference NER/S/A/2000/03635).

I would like to thank all those that helped me on fieldwork of whom there are far too many to mention but without whom the work wouldn't have been possible. In particular I would like to thank Kate Grellier and Martin Cox for helping with counts and Simon Moss for all his help with catching and persevering to device new and ingenious ways to catch seals when our success rate was looking bleak.

I would like to thank Monique Mackenzie, Mike Lonergan and Jason Matthiopolous for their statistical advice at various stages throughout my PhD. Thanks to John Watkins and Stuart Middlemas for their help in aspects of determining seal diet.

I'm grateful to everyone at SMRU for their advice and enthusiasm over the past four years. I would especially like to thank all my office mates past and present for all the support and light relief they have provided over the years. In particular I'd like to thank Alice, Carol, Kate, Kelly and Kimberley for their support and friendship. My utmost thanks have to go to Catriona not only for her friendship, but for reading every word of this thesis at least once, for never complaining about the consultation service she has provided me with on R and ArcView and who is always able to find some positive words to keep me going.

Finally, thanks to my family for their support throughout my education. In particular thanks to my mum for her financial and emotional support throughout.

CHAPTER ONE:

General Introduction

1.1 Significance of studying harbour seal ecology

Ecology is the study of the interaction of organisms with one another and with their physical environment. Harbour seals are major marine predators and therefore influence, and are influenced by, the marine ecosystem in which they live. They are thus potential indicators of the health of the ecosystem providing managerially and scientifically useful evidence of environmental and ecosystem quality or trends in quality.

Harbour and grey seals coexist in many places, especially around Britain, and are therefore competing for the same resources, both being generalist predators of fish and cephalopods (Hammond and Harwood, 1985; Brown and Pierce, 1998). It is therefore interesting to study the ecology of the species to gain a better understanding of how they partition the environment into different niches. In British waters, grey seal ecology is relatively well-studied (Hammond and Harwood, 1985; Hiby and Harwood, 1985; McConnell *et al.,* 1999), harbour seal ecology is not, except for in the Moray Firth (Thompson and Rothery, 1987; Thompson *et al.*, 1989; Thompson and Harwood, 1990; Tollit, 1996; Thompson *et al.*, 1997).

Harbour seal ecology brings them into conflict with a number of anthropogenic activities. There are inevitable interactions with fisheries; such as the effects their predation has on fish stocks, as well as the effects fisheries can have on harbour seal populations through the removal of prey species. Harbour seals can also be killed through bycatch in some fisheries. Coastal developments such as the exploration and production of oil and gas as well as the development of renewable energy sources could also cause disturbance to the population. There is therefore a need to better understand the ecology to better inform the conservation of populations and management of human activities.

1.2 The Harbour Seal, *Phoca vitulina*

The harbour, or common seal, *Phoca vitulina* and the grey seal, *Halichoerus grypus* are the two species of seal that are commonly found around Britain (*Figure 1.1*). Harbour seals are the smaller of these two marine predators. They are species in the order Pinnipedia and the superfamily Phocoidea, otherwise known as the true seals. *Phoca vitulina vitulina* is the European sub-species of harbour seal. It is also found in Irish, Icelandic, Norwegian, Danish, German and Dutch waters. An estimated 50 to 60 thousand animals are found around Britain, which is thought to represent approximately 40 percent of the sub-species' overall population (Anon, 2004). The distribution of harbour seals in Britain when hauled out during the moulting season is illustrated in *Figure 1.2*.

Thus, there is a need to understand harbour seal ecology to inform conservation efforts and to assess the level of interaction and impact on commercially important fish stocks. This information also helps to determine the impact of disease on the population such as the 1988 and 2002 phocine distemper virus (PDV) epizootics (Harwood and Reijnders, 1988; Harding *et al*., 2002).

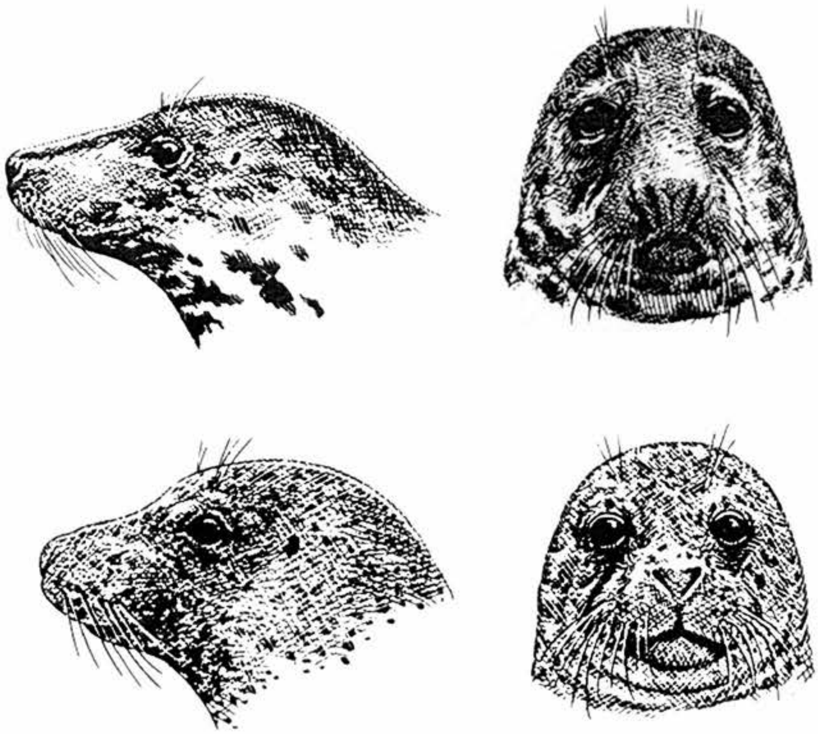

Figure 1.1: Grey seal (*Halichoerus grypus*) top and harbour seal (*Phoca vitulina*) bottom (Anderson, 1990).

Harbour seals haul-out on intertidal mud and sand banks as well as in rocky areas to rest, moult, give birth and suckle young. They give birth to their pups in June and July (Venables and Venables, 1955; Bigg, 1981; Thompson, 1988; Härkönen and Heide-Jørgensen, 1990) and parturition is followed by a 3-5 week lactation period. Pups are precocious and can swim from birth. Females come into estrus towards the end of the lactation period and copulation takes place in the water (Fisher, 1954). The fertilised zygote remains dormant for 2 to 2.5 months until implantation when development resumes at a normal rate; this reproductive delay is called embryonic diapause or delayed implantation (Fisher, 1954; Bigg, 1969). Given the degree of sexual dimorphism (Härkönen and Heide-Jørgensen, 1990) and male-male competition (Sullivan, 1981; Slater and Markowitz, 1983; Thompson, 1988) it is thought that harbour seals are likely to be polygynous (Thompson *et al.,* 1994). Harbour seals moult annually, peak moulting occurs between mid July and mid September, females completing their moult earlier than males (Thompson and Rothery, 1987).

Harbour seals are considered generalist predators, they are non-migratory and usually occur in close proximity to the coast in sheltered bays, estuaries and rocky shores and are fairly site faithful to haul-out areas (Bigg, 1981; Brown and Mate, 1983; Payne and Selzer, 1989; Olesiuk *et al*., 1990). Haul-outs tend to be used throughout the year, although abundance has been found to vary in relation to season (e.g. Slater and Markowitz, 1983; Thompson, 1989), tidal cycle (e.g. Schneider and Payne, 1983; Thompson and Miller, 1990), time of day (e.g. Stewart, 1984; Yochem *et al*., 1987; Thompson *et al.*, 1989) and weather conditions (e.g. Kreiber and Barette, 1984; Watts, 1992; Grellier *et al*., 1996).

1.3 Legal status of harbour seals in Britain.

Like many pinniped species, harbour seals feed on a wide variety of prey, which includes commercially important species of fish (Pierce *et al*., 1991; Brown and Pierce, 1997; Hall, Watkins and Hammond, 1998). In many areas there is ongoing debate about the impact of seal populations on fish stocks, and therefore fisheries, as well as the impact that fisheries may be having on seal populations (Beverton, 1985; Harwood and Croxall, 1988; Rae, 1960). Under the U.K. Conservation of Seals Act 1970, the Natural Environment Research Council (NERC) has a duty to provide scientific advice to government on matters related to the management of seal populations in Britain and surrounding territorial waters. EU member states have conservation obligations under the

Habitats Directive (Council Directive 92/43/EEC on the Conservation of Natural Habitats and Wild Fauna and Flora). Under the Habitats Directive, member states are required to consider Special Areas of Conservation (SACs) to protect the habitat of harbour seals as a means of maintaining populations at a 'favourable conservation status'. Harbour seals are widespread around the west coast of Scotland and throughout the Hebrides and Northern Isles. On the east coast of Britain, their distribution is more restricted with concentrations in East Anglia, Firth of Tay and the Moray Firth.

1.4 St Andrews Bay

St Andrews Bay is an open bay on the south east coast of Scotland with the Eden and Tay estuaries feeding into it. The sea-bed slopes gently, reaching 50 m in depth approximately 30 km offshore, and the sediment is largely sand with gravel. St Andrews Bay has one of the relatively isolated populations of harbour seals on the east coast of Britain. The population is thought to be stable in this area (Anon, 2004). Grey seals (*Halichoerus grypus*), harbour porpoises (*Phocoena phocoena*) and bottlenose dolphins (*Tursiops truncatus*) are the other species of marine mammal common to this area. There are numerous fisheries in the area but of most interest are the interactions between salmon and seals. The River Tay is an SAC for Atlantic salmon (*Salmo salar*) and the Tay Estuary is also a candidate SAC for harbour seals. Salmon stocks are decreasing and there are objections to this area being designated as an SAC for harbour seals whose population is considered stable (Salmon Fisheries Board, 2002; Anon., 2004).

1.5 Estimating population size

The most fundamental information required to inform the conservation of harbour seals and the management of activities affecting them is the size and status of their populations. Without this information it is impossible to assess the interactions between fisheries and pinniped populations or to assess whether or not the populations' conservation status is favourable. In Britain, harbour seal populations are monitored by making counts at haul-outs in the moult (details in *Chapter 3*), the results of which can be seen in *Figure 1.2*. The population of harbour seals in St Andrews Bay is relatively small and fairly isolated, with the nearest large haul-outs in the Moray Firth to the north and The Wash and Blakeney Point to the south.

Counts at haul-outs give an index of abundance. They provide a means to monitor changes in abundance across years but only give a minimum estimate of population size. At any time a count is made, a proportion of the population will be at sea and therefore absent from the haul-out. When counts are used to compare abundance between regions or between years it is necessary to assume that the proportion of animals that are absent at the time of the counts is constant. The validity of this assumption is considered in *Chapter 3*. Counts provide an index of abundance that will identify large-scale trends in population size. To be able to ascertain whether changes in local abundances observed at haul-outs are indicative of changes at a population level it is necessary to have a means of determining absolute abundance. To quantify fish consumption by a population of seals, estimates of absolute abundance are also required.

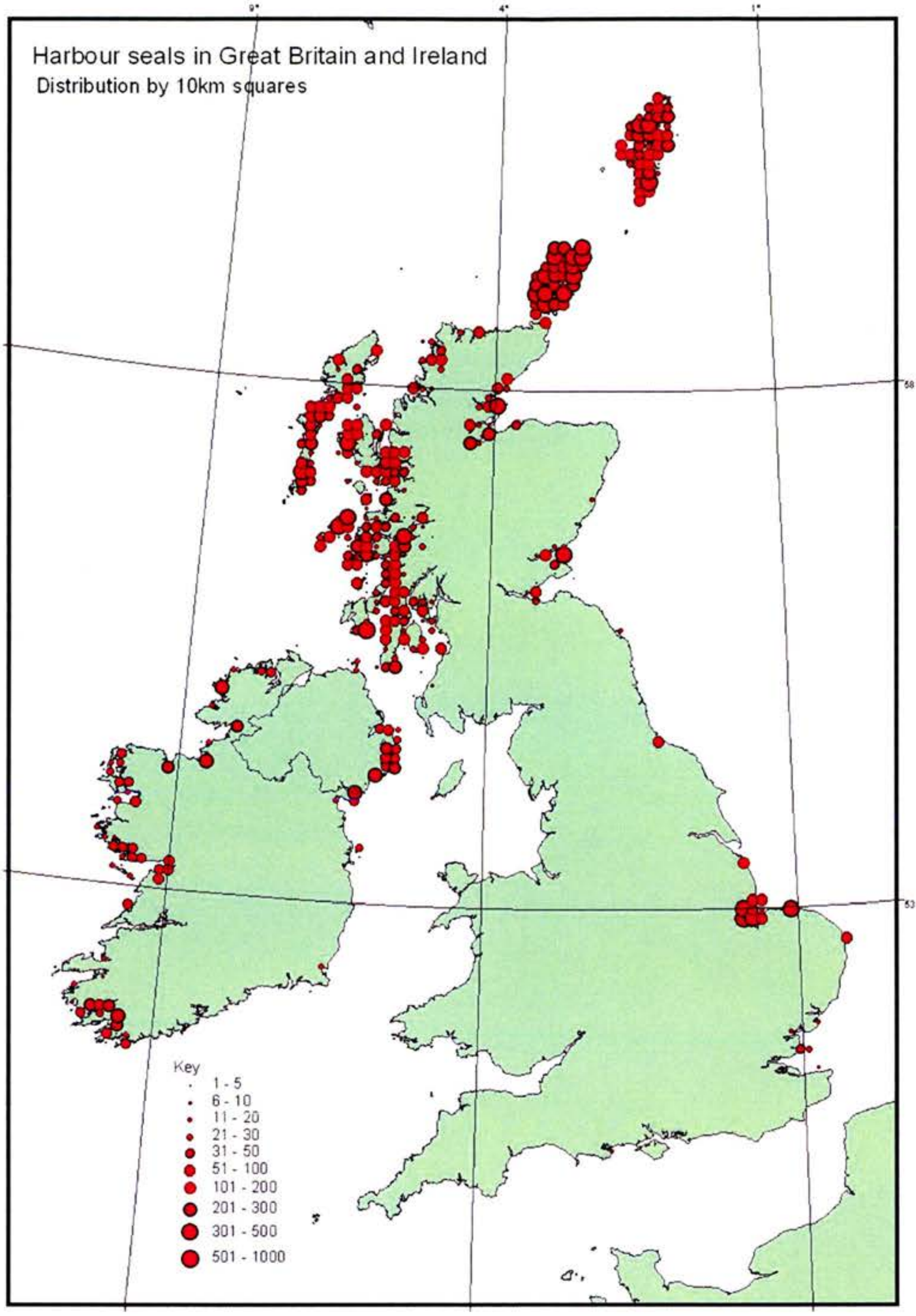

Figure 1.2: The August distribution of harbour seals in Great Britain and Ireland, by 10km squares. These data are from surveys carried out between 1996 and 2003 (Anon, 2004).

Estimating harbour seal population size is made difficult because there is no component of the population that can be reliably counted ashore and extrapolated to the whole population, as is possible for grey seals (Hiby and Harwood, 1985). In particular, pups are often born on intertidal shores and can swim within hours of birth so accurate pup counts are unobtainable. Information on the activity of seals, namely the amount of time individuals spend at sea, contributes to the estimation of total population size by allowing the extrapolation of counts made at haul-out sites.

Activity patterns can be determined through resightings of marked individuals, this can be in the form of branded animals (Härkönen and Harding, 2001) or the use of markings on the pelage to identify individuals (Mackey, 2004; Hiby and Lovell, 1990). The most commonly used technique has been to use telemetry to study the activity patterns of individual seals to determine the proportion of time animals are spending at sea allowing a correction factor for counts to be estimated (e.g. Eberhardt *et al.*, 1979; Pitcher and McAllister, 1981; Harvey 1987; Thompson *et al.*, 1987; Yochem *et al*, 1987; Thompson and Harwood, 1990; Mathews and Kelly, 1996; Thompson *et al.*, 1997; Ries *et al.*, 1998; Huber *et al.*, 2001; Simpkins *et al.*, 2003). Previous studies have used activity patterns, determined using telemetry, and counts throughout the breeding and moult period to estimate local harbour seal population size (Pitcher and McAllister, 1981; Yochem *et al.*, 1987; Thompson and Harwood, 1990; Thompson *et al.*, 1997; Härkönen *et al.*, 1999; Huber *et al.,* 2001; Simpkins *et al.*, 2003). This is because the greatest, most consistent, numbers of seals are assumed hauled-out at this time.

1.6 Diet

Studies of diet composition are important in understanding the ecology of the species. When information on diet composition are combined with information on the energetic requirements of a population, predictions of the total prey consumption can be made to enable their impact on prey stocks to be quantified in areas where there is potential for competition and/or conflict with fisheries. It is rarely possible to make direct observations of what seals are preying upon as they are free ranging and catch and feed on their prey at sea, largely underwater. There have been observations of larger fish species being brought to the surface to be eaten (Rae, 1968; Moore, 2003). Feeding can be observed by attaching a camera to the seal (e.g. Marshall, 1998; Bowen *et al.*, 2002; Littnan, Davis *et al.*, 2003; Baker and Parrish, 2004), however this relies on being able to retrieve the device, which is not always possible. Indirect methods for studying prey include using stable isotopes (e.g. Hobson and Montevecchi, 1991; Hobson and Welch, 1992), fatty acid analysis (e.g. Iverson, 1988; Iverson, 1993; Iverson *et al.*, 2004; Kirsch *et al.*, 2000) and the analysis of hard parts found in either stomachs (e.g. Rae, 1960, 1968, 1973; Frost and Lowry, 1980; Stewart and Murie, 1986; Bowen, Lawson and Beck, 1993) or scats (e.g. Pierce and Boyle, 1991; Laake *et al.*, 2002).

All methods for estimating seal diet are subject to some kind of bias (Pierce and Boyle, 1991). The sources of bias associated with determining diet through scat analysis are well known (*e.g.* da Silva and Nielson, 1985; Prime and Hammond, 1987; Harvey 1989; Bowen, 2000). Analysing the hard parts found in scats has the advantage of being non-invasive with large sample sizes attainable, prey can be identified to genus and often species and the size of prey can be determined. Otoliths are partially or fully digested during the passage through the gut; the degree of digestion varies among prey species. Captive feeding experiments have been used to determine species-specific digestion coefficients and numerical correction factors to account for this (Harvey, 1989; Prime and Hammond, 1987; Tollit *et al.*, 1997; Bowen 2000; Orr and Harvey 2001; Grellier and Hammond, *in press*). Estimating fish weights from the corrected otolith size introduces measurement error that also needs to be accounted for (Hammond *et al.*, 1994 a & b, Hammond and Rothery, 1996).

Harbour seals are considered to be generalist predators with their diet reflecting, to some extent, the local abundances of prey (*e.g.* Pierce, Boyle and Thompson, 1990; Härkönen and Heide-Jørgensen, 1991; Tollit *et al.*, 1997; Brown and Pierce, 1998). For example a study by Tollit *et al.* (1997) in the Moray Firth compared the diet composition of harbour seals with the estimated abundance of fish prey as determined through dedicated fisheries surveys. This study showed that the most abundant fish species contributed most to the diet, however less abundant species showed little similarity to their contribution to the diet.

The diet of harbour seals has been described for several areas of Britain, including the Wash (Hall *et al.*, 1998), the Moray Firth (Pierce *et al.*, 1991; Tollit and Thompson, 1996), Orkney (Pierce *et al.*, 1990), Shetland (Brown and Pierce, 1998), the west coast of Scotland (Pierce and Santos, 2003) and Northern Ireland (Wilson *et al.*, 2002). Predominant prey in these studies included sandeels, gadids, herring, sprat and flatfish (e.g. Pierce *et al.*, 1991; Tollit and Thompson, 1996; Hall, Watkins and Hammond, 1998; Pierce and Santos, 2003). The diet was found to vary between regions, seasonally and between years. It has been proposed that the observed variation is a result of changes in locally abundant prey species (Härkönen, 1987; Thompson 1989; Pierce *et al.*, 1990; Tollit *et al.*, 1997).

Information on the diet of the population of harbour seals in St Andrews Bay has not previously been available. Therefore, it is of interest to determine whether the diet of this population differs from the diet of harbour seals in different environments to the north and south of this area. The area has been designated as a candidate Special Area of Conservation for harbour seals. Concerns have been raised about the effects that commercial exploitation of local sandeel populations may be having on predators such as seals and seabirds that feed in the area (FRS, 2003).

1.7 Foraging Behaviour

Studying foraging behaviour, in particular where animals are foraging, provides an understanding of the habitats being used to obtain prey. This information is valuable for informing conservation and management strategies for marine mammals, for determining the overlap between foraging areas and fisheries, for designating protected areas, or for assessing the potential impacts of offshore developments such as oil and gas exploration and production.

Studying the distribution of seals at sea directly is largely impractical as seals spend the majority of their time under water and have a tendency to dive in response to disturbance, although line and strip transects have been conducted on a few occasions to provide information on distribution and abundance (e.g. Buckland and Cattach, 1993; McLaren, 1961). Telemetry provides more detailed information on the at-sea distribution of tagged individuals and is the more commonly used method (e.g. Boyd, 1989; McConnell *et al.,* 1992; Folkow, Martensson, and Blix, 1996; Campagna, Fedak & McConnell, 1999; Le Boeuf *et al.,* 2000; Field *et al.,* 2001; Lowry, *et al*., 2001; McConnell *et al.,* 2002; Harcourt *et al.,* 2002; Hindell *et al.,* 2003; Bradshaw *et al*., 2004).

Many studies of seals have aimed to characterise the habitat used for foraging with respect to environmental variables (e.g. Boyd, and Arnbom, 1991; Guinet *et al.,* 1994; Tollit *et al*., 1998; McConnell *et al*., 1999; Sjöberg and Ball, 2000; Field *et al*., 2001; Burns *et al*., 2004) and prey distributions (e.g. Costa, *et al*., 1989; Boyd, *et al.,* 1994;). Harbour seal foraging has been studied in a number of geographical areas and these studies have described the range and distribution of the species (Pitcher and McAllister, 1981; Brown and Mate, 1983; Stewart *et al*., 1989; Thompson and Miller, 1990; Thompson, 1993; Thompson *et al*., 1998; Suryan and Harvey, 1998; Lowry *et al*., 2001) as well as characterising feeding habitats with respect to bathymetry and sediment type (Bjørge *et al.,* 1995; Tollit *et al*., 1998).

The distances travelled to forage by harbour seals vary considerably between different areas, however the majority of foraging seems to occur within

50 km of haul-outs (Pitcher and McAllister, 1981; Brown and Mate, 1983; Stewart *et al.*, 1989; Thompson and Miller, 1990; Thompson, 1993; Bjørge *et al.*, 1995; Suryan and Harvey, 1998; Thompson *et al.*, 1998; Tollit *et al.*, 1998; Lowry *et al.*, 2001) with further ranging movements being recorded when animals are observed moving between haul-outs (Lowry *et al.*, 2001). Harbour seals have been found to use a number of different foraging habitats. In the Moray Firth, animals were found to be diving in depths of 10 to 50 m on mainly sandy substrates (Tollit *et al.,* 1998), whereas animals in Norway used both shallow kelp areas as well as 150 to 200 m deep basins with a muddy sea bed (Bjørge *et al.,* 1995). It is likely that harbour seals favour particular sediment types and water depths depending on local geographical variations in available habitat and prey (Harkonen,1987).

Prior to this study there was no information on foraging behaviour of harbour seals in south east Scotland. There has been a study of the movements and foraging areas of grey seals in this area (*n*=2) as well as the Farnes in north-east England (*n*=12) where foraging was found to be associated largely with gravelly sand (McConnell *et al.*, 1999). Harbour seal foraging behaviour has been studied to the north of this study site in the Moray Firth using VHF telemetry. These tagging studies tend to have been focused on the breeding season with tagging occurring in May (Thompson *et al.*, 1989; Thompson and Miller, 1990; Thompson *et al.*, 1996), where foraging was found to occur within 60 km of their haul-outs. The number of animals tagged out with this time is relatively low, *n*=2 in Thompson *et al.* 1991 and *n*=5 in Thompson *et al.*, (1996*a*). These two studies showed conflicting results. The earlier study suggested that seals were restricting their range in winter months feeding on dense aggregations of over wintering clupeids. The later study found animals to be travelling slightly further offshore than in the summer months and there was a noticeable absence of clupeids found in the diet (Thompson *et al.,* 1996*b*). This study increases the sample of animals that have been tracked throughout the winter months and builds on this existing knowledge of harbour seal distribution.

1.8 Activity Budgets

To further understand the ecology of a species it is necessary to know how individuals allocate time to different activities. The proportion of time spent at-sea and the characteristics of foraging trips in particular provide details of how the population gains enough energy to survive. There have been few studies of activity budgets outwith the breeding season and moult (Thompson *et al*., 1997). Year round information on activity budgets can be used to help paramatise energetics models to determine the energetic requirement of different components of the population and hence the amount of prey the population is likely to be consuming, providing more reliable estimates of prey consumption.

1.9 Outline and aims of the study

The aims of this study were to develop a better understanding of the ecology of harbour seals in St Andrews Bay, by estimating the size of the population, by determining their diet, by locating foraging areas and investigating factors affecting foraging characteristics, and by studying their activity budgets.

Chapter 3 introduces a methodology to utilise activity pattern data collected through most of the year combined with haul-out counts made throughout most of the year to estimate total population size. Previous knowledge of the size of the population of harbour seals using St Andrews Bay has been restricted to annual counts made during the moult by aerial survey. In this study, abundance estimates are made from November through to June providing information on the numbers of animals using of this area throughout most of the year.

Chapter 4 describes and quantifies the diet of harbour seals hauling out in St Andrews Bay through identifying hard parts recovered from scats collected monthly for more than two years. Published digestion correction factors and allometric equations were used to estimate undigested otolith size and fish length and weight. A bioenergetics model was used to estimate annual prey consumption, in part parameterised by the population estimates made in *Chapter 3* as well as from published data.

Chapter 5 describes the at-sea distribution of harbour seals using data collected through satellite telemetry. It explores whether animals randomly disperse from the haul-out to forage or whether there are localised areas of dense foraging activity. At-sea distribution is related to environmental variables to determine whether particular habitats are being actively selected to forage in.

In *Chapter 6* the variation in the activity of harbour seals in south east Scotland and the degree to which this variation can be explained by endogenous characteristics such as sex and body size is investigated. Findings are compared with those for harbour seals in the Moray Firth.

St Andrews Bay is one of ten areas in Britain that has been designated as a candidate SAC for harbour seals. As such there is a need to improve our understanding of the basic ecology of the population in this area to understand how best to ensure it remains a healthy, viable, population and to assess the level of interaction and impact on commercially important fish stocks as well as the effect fisheries may have on this predator. Prior to this study there was little information on this population of harbour seals. This study aimed to fill some important information gaps on the population of harbour seals using St Andrews Bay.

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CHAPTER TWO:

Materials and Methods

2.1 Study Site

There were 14 discrete areas used by harbour seals for hauling out in this area, as shown in *Figure 2.1*. The main areas used by harbour seals to haul-out were in the Firth of Tay, Eden Estuary and Abertay Sands. All sites are intertidal sand banks. The Eden Estuary sites can be accessed by foot and were therefore most prone to disturbance.

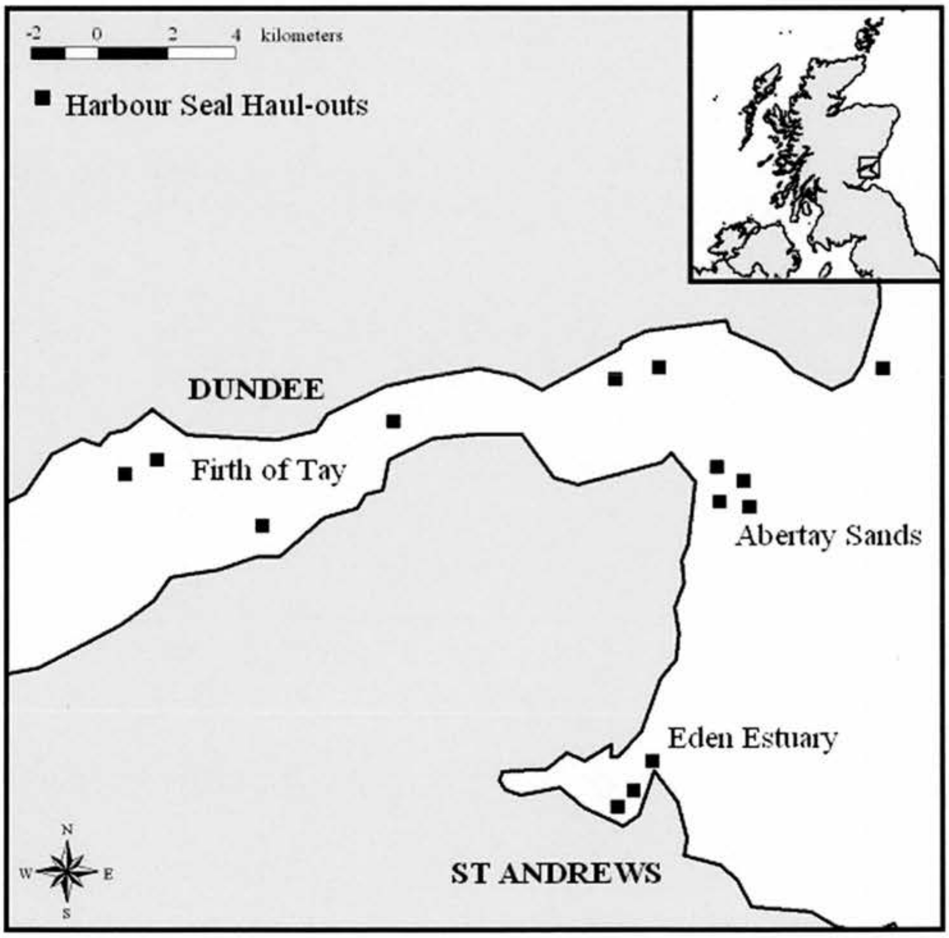

***Figure 2.1*:** Harbour seal haul-outs in St Andrews Bay.

2.2 Counts

Recognisance of the St Andrews Bay area was made by boat using prior knowledge of haul-out sites of harbour seals from aerial surveys as well as local knowledge. All haul-out areas used by harbour seals in the area were identified and an at sea route designed so that all haul-out sites could be visited within approximately plus or minus two hours of low tide. Counts were made from a 6 m rigid inflatable boat (RIB). The nature of the route prevented seals that were disturbed at one haul-out from hauling-out at a subsequent haul-out prior to it being counted, reducing the risk of individuals being counted more than once.

Counts of seals at all haul-out areas were attempted at least monthly, although logistical considerations, such as weather constraints, meant this was not possible throughout the entire study period. On such occasions a count was made at the next available opportunity.

During every count, a minimum of three persons were on board the boat, one person at the helm and the two remaining personnel available to make counts using 7x50 binoculars. Because the presence of a boat at close proximity might scare some individuals into the water jeopardising an accurate count, prior to approach initial counts were made at a distance of approximately 500 m to ensure a count was obtained when all individuals were present. Counts were repeated whilst slowly approaching the haul-out until confident with the number of seals counted. After the count was complete, it was necessary to disturb seals hauled-out as counting trips were combined with collecting faecal samples used in dietary analyses (C*hapter 4*).

2.3 Capturing and handling seals to deploy SRDLs.

Two techniques were used and adapted for catching seals. If seals were hauled out away from the water's edge and remained undisturbed until the boat was within range, the 'rush and grab' technique was used. The boat was rapidly driven towards the haul-out site and beaches and hoop nets were used to capture seals on land. The nets consist of a hoop of approximately 1 m diameter, made of 20 mm diameter plastic hosing, with a funnel of netting (10 mm mesh) attached to it.

The other technique employed was similar to that described in Jefferies, (1993). A 120 m net was set from a boat at speed around a haul-out site as animals fled to the water. The aim was for the net to form a barrier within which seals were trapped or entangled. A second boat assisted by bringing the loose end of the net to shore and then moved along the length of the net to discourage seals from getting over the float line. As the net was hauled ashore animals were untangled from the net and either released or transferred to hoop nets until ready to be drugged.

Once seals were captured, they were weighed and anaesthetised using 0.05 mg kg $^{-1}$ zoletil^{100} (Virbac, France), delivered intravenously to the extradural vein using a 19-gauge needle. Body mass was measured using a 100 kg (accuracy = ±0.5kg) Salter spring balance. Body length was measured, while the seal was anaesthetised, as the straight length distance from the tip of the nose to the end of the tail (to the nearest 0.5 cm). Axial girth was measured at the base of the fore flippers. The tape measure was pulled tightly then relaxed as the animal exhaled for this measurement, again while the seal was anaesthetised.

Prior to tag attachment, the fur was dried using paper towels and menthylated spirit, degreased using acetone and then the tag was secured using fast setting epoxy resin (Fedak, *et al.*, 1983). All capture and handling procedures were performed under Home Office project licence 60/2589 and conformed to the Animals (Scientific Procedures) Act 1986.

***Figure 2.2*:** SRDL attached to the neck of a harbour seal.

The tags were attached to the neck of the animal at the base of the skull; the position is shown in *Figure 2.2*. The antenna was positioned to face forward so that if the seal's head only surfaced partially whilst at sea, an uplink with satellites was still possible. The tags detached from the seals during the annual moult in August if not before.

Four out of 25 seals captured were caught using the rush and grab technique, all of which were males. The remaining 21 were caught using the seine net method. Males were consistently easier to catch throughout the study.

2.4 Details of Seals Caught

Table 2.1 shows the details of seals that were captured and tagged; there were 13 males and 12 females tagged and a range of weights from 50 to 92 kg. No seals below the weight of 50 kilograms were tagged due to the size of the tags.

Table 2.1: Details of seals captured and duration of tagging.

Seal	Sex	Weight (kg)	Girth (cm)	Length (cm)	Date of Capture	Date of Last Transmission	Duration of Tracking (days)
A	M	68	90	138	02 Nov 01	17 Apr 02	166
B	M	69	87	144	02 Nov 01	27 Jan 02	86
C	M	76	112	142	19 Nov 01	23 Mar 02	124
* D	M	51	94	125	20 Nov 01	26 Apr 02	157
E	F	66	102	137	16 Jan 02	21 Jun 02	156
F	M	58.5	99	125	16 Jan 02	19 May 02	123
G	F	82	106	144	16 Jan 02	02 May 02	106
H	F	76	108	145	16 Jan 02	01 May 02	105
I	F	75	108	137	16 Jan 02	26 May 02	129
J	F	72	101	142	16 Jan 02	06 Aug 02	202
K	F	50	85	121	24 Oct 02	26 Apr 03	184
L	M	64	97	136	24 Oct 02	20 Feb 03	119
M	M	88	109.5	143	24 Oct 02	04 Mar 03	131
N	M	71	102	141	24 Oct 02	07 Mar 03	134
O	M	78	101	143	24 Oct 02	23 Mar 03	150
P	M	77	96	132	24 Jan 03	01 Jul 03	158
Q	M	87	104	126	24 Jan 03	04 Jun 03	158
R	F	51.5	90	123	11 Mar 03	22 Jul 03	133
S	F	67	96	135	11 Mar 03	22 Jul 03	133
T	M	52	91	120	11 Mar 03	8 Jun 03	89
U	F	75	109	127	11 Mar 03	18 Jul 03	129
V	M	82	106	138	11 Mar 03	14 Jun 03	95
W	F	92	111	134	25 Mar 03	27 Jul 03	124
X	F	72	110	131	25 Mar 03	07 Jul 03	104
Y	F	63.5	96	139	25 Mar 03	21 Jun 03	87

* D was not included in further analysis as behaviour was considered non-representative of a healthy harbour seal.

2.5 Duration of tagging.

The tags remained on the seals and continued transmitting for between 86 to 202 days (*Table 2.1*). The average duration of data received from seals was

131 days, just over four months. Some tags were lost in the summer months in July and August in the onset of the moult. When tags stopped transmitting prior to the moult this was believed to be due to the tags falling off the animals rather than tag failure. This was primarily because the end of transmissions was abrupt, indicating it was not due to wear on the antenna and secondly, all tagged animals sighted during counts could be explained by tagged animals known to be in the area.

Ten animals were tracked in 2001-2002 and 15 in 2002-2003 (*Figure 2.3*). In the first study period (November 2001 to July 2002) very few of the tags deployed in November and January were still transmitting by the months of June and July. As a result, the tagging period was staggered for the second study period with deployments in November, January and March. This greatly increased the sample of animals tracked in June and July as shown in *Figure 2.3*.

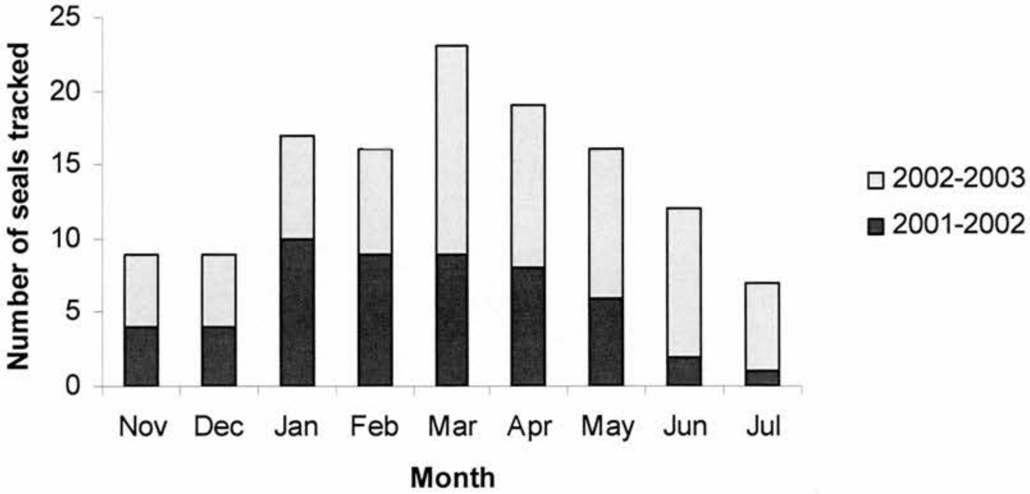

***Figure 2.3*:** Number of seals tracked per month of study period.

*Five weeks of tracking data for October are not presented here.

2.6 Description and Programming of Satellite Relay Data Loggers.

The transmitters deployed used the Argos satellite system (Argos, 1989), which consists of UHF (ultra high frequency) receivers on board two polar orbiting satellites that pick up signals (uplinks) from Argos transmitters within their field of view. The location of the transmitter was determined from the frequency of the Doppler shift of the signal (McConnell *et al.,* 1999). Up to 256 bits of data could be encoded in a single uplink and this was relayed via ground stations and made available on line. The accuracy of a location was calculated at the ground stations and each location assigned an index of accuracy, termed location quality (LQ), 3 being the highest accuracy and zero, minus one and two of unguaranteed accuracy (see *table 2.2*). The accuracy primarily depended upon the number of uplinks to the satellites within a pass (McConnell *et al*., 1992). 33873 locations were received in total; *table 2.2* shows the percentage of locations of each location quality. Both the predicted level of accuracy provided by Argos (1989) as well as the level of accuracy found experimentally from tagged captive grey seals (Vincent *et al.,* 2002)

Table 2.2: Accuracy of locations associated with different Argos location qualities expressed as the 68th percentile. The figures taken from Vincent *et al.* (2002) are the average of the 68th percentiles of latitude and longitude (there was more error found to be associated with the longitude that the latitude).

Location Quality	Predicted accuracy of locations (Argos, 1989)	Accuracy of locations found by Vincent *et al.*, 2002.	Percentage of LQ received
3	150 m	226 m	4.7
2	350 m	372 m	5.9
1	1000 m	757 m	8.6
0	not guaranteed	27896 m	6.4
-1	not guaranteed	1003 m	25.1
-2	not guaranteed	5905 m	49.3

Argos satellites are polar orbiting and therefore the closer the transmitter is to the North or South Pole the more times a satellite passes over it. Due to the latitude of this study site there are times of the day with poor satellite coverage. The tags are programmed not to transmit in these periods of poor coverage between 2200 hrs and 0200 hrs in order to conserve battery power. The temporal distribution of locations received is illustrated in *figure 2.4*. As a result of the satellite coverage, information on movements of the animals that occurred between these times can only be inferred.

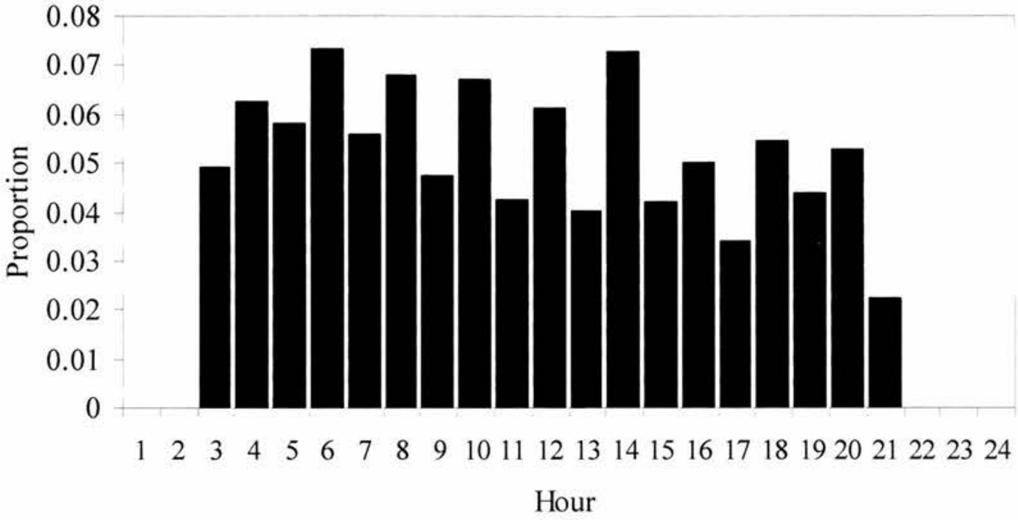

***Figure 2.4*:** Temporal distribution of uplinks.

The number of locations received per animal per day varies considerably largely due to the behaviour of the animal. The mean number of locations received per day, per animal was 10.5, with individual averages ranging from as much as 15 locations per day to as few as 6 locations per day (see *figure 2.5*).

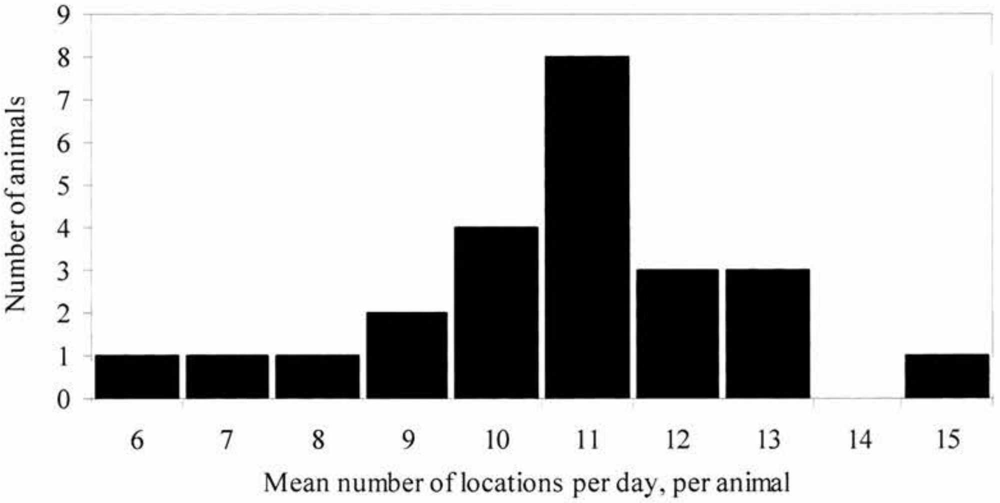

Figure 2.5: Mean number of locations received per day.

The Argos Satellite Relay Data Logger (SRDL) (Sea Mammal Research Unit, University of St Andrews, Scotland) measured 100 x 70 x 45 mm (excluding the 150 mm antenna) and weighed 305g. It consisted of a data logger interfaced to an Argos transmitter unit, a depth sensor and submergence sensor, which were used to determine the seals' activity (Sea Mammal Research Unit, http://www.smru.st-and.ac.uk/protected/technical.html).

The seals behaviour is classified into three different categories using the following rules: if the tag was dry for more than 10 minutes it was classified as hauled out; a haul-out was determined to have ended when the tag became wet or submersed for a minimum of 16 seconds and below two meters. Below a depth of two meters the seal was classified as diving and above a depth of two metres it was classified as at the surface. SRDLs were programmed to store data and select data randomly to transmit at times when there was good satellite coverage; this prevented any temporal bias in the coverage of data received.

The information received on haul-out behaviour was in the form of a start and end time of each haul-out period and an interpolated location from the locations received. Each haul-out event was also numbered so those that fail to be transmitted can be taken into account. Information was also received for the times spent at the surface when the animal was above 2 metres depth. This also takes the form of a start and end time and an interpolated location. Information on dive behaviour includes not only the start and end time of each dive but also the duration of the following surface interval. Information on the depth and shape of each dive was also recorded. The maximum depth of the dive was received as well as information to best represent the profile of the dive. Four time-depth points of inflection of the dive are selected before storage and transmission where the depth versus time trajectory change most significantly (Fedak *et al.*, 2001). Summary data were recorded by the SRDLs providing information on whether an animal was at the surface, diving or hauled-out throughout any given two hour time period (00:00-02:00, 02:00-04:00, etc.). This data set has the advantage of representing all three types of behaviour equally and although information on all two hour periods will not be received, what is received will not be biased to particular activities. The percentage of summary data received from each seal ranged between 63 and 98 percent with a mean of 84.3% and a standard error of 1.8%.

Data were viewed using MAMVIS (Fedak *et al.*, 1996). The data were managed using a Microsoft Access database and largely analysed using the R statistical environment (R Development Core Team, 2004), the details of which are described within each chapter.

2.5 Smoothing of Argos locations

An empirical approach (Lonergan, unpublished) was taken to reduce the effect of positional inacurracies in the locations provided by the Argos satellite tags. Changes in lattitude and longitude were treated independently, and movement in each dimension represented by a cubic spline. The splines were fitted as Generalised Additive Models using the mgcv library (Wood and Augustin, 2002) within the R statistical environment (R Development Core Team, 2004) and with the points weighted according to published estimates (Vincent *et al.*, 2002) of the precisions of their locational qualities.

There are a number of potential problems associated with this smoothing method. However it appeared to be the most realistic filter available at the time of the study. Because the 'actual' path of the animals were unknown, deciding which filter is performing best can only be made arbitrarily. This method of smoothing is not based on an underlying model of animal movement, and the level of smoothing and curvature used are arbitrary. Also the technique is anisotropic to reduce the computational power required. This may cause movements in a diagonal direction to be treated differently than movements between east and west or north and south. As the smoothing technique is based on smoothing splines, a curve is being fitted to the data and therefore directed travel in a straight line is likely to be underrepresented. Another artefact of this technique is that loops can appear in the predicted track that would appear not to be supported by the locations received.

Raw locations, as well as filtered locations can be seen in *appendix 1* and *2*. Movements of animals are hard to discern through the degree of noise apparent in the maps of raw locations. The maps of movements once filtered allow a much clearer image of type of movement undertaken, for example repeated directed travel to the same area at sea.

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CHAPTER THREE:

Estimating harbour seal abundance using an analytical framework incorporating telemetry and count data.

3.1 ABSTRACT

Estimating harbour seal population size is difficult because there is no component of the population that can be reliably counted ashore and extrapolated to the whole population. With one exception, harbour seals in Britain have been counted ashore annually during the August moult and population sizes are reported as minima because there are no robust estimates of the proportion of animals ashore when counts are made. Here, individual activity patterns of harbour seals recorded via satellite relay data loggers (SRDLs) are modelled to estimate the proportion of the population hauled-out and thus population size by extrapolating from counts made at haul-out sites.

Counts of seals at each haul-out site within St Andrews Bay were carried out by boat at least once a month between October 2001 and June 2003. All counts were made within two hours of low tide. SRDLs were deployed on 25 animals during this period, collecting data for 86-200 days per animal.

Behaviour of seals when outwith and within 10 km of haul-outs were treated separately in a two-stage model to distinguish between the processes involved in foraging and hauling out respectively. The proportion of time spent within 10 km of the haul-out was modelled using a generalized linear model with month as the explanatory variable. To model the proportion of time hauled out (when within 10 km of haul-out), a generalized linear mixed model with a first order autoregressive process was used to account for temporal autocorrelation across repeated measures on the same individuals. Explanatory variables used were height of tide, month and hour. Estimated population size varied among months from 1062 to 2375 seals, averaging 1746 seals (95 % confidence interval

1238 to 2301). It had been assumed, based on previous studies, that approximately two-thirds of the population was hauled-out during the moult when the population has been surveyed. The results presented here indicate that only 40 percent are hauled out at this time, and that estimates of absolute abundance are considerably greater than previously believed.

3.2 INTRODUCTION

3.2.1 Importance of estimating population size

In many areas harbour seal (*Phoca vitulina*) numbers are believed to be increasing and the species is considered a threat to local fisheries (Beddington *et al.*, 1985; Harwood and Croxall, 1988). In other areas declines in abundance at haul-outs have been observed and concern expressed over the status of populations (Pitcher, 1990; Simmonds, 1991; Thompson *et al.*, 2001). Of particular concern are the impacts that disease epidemics, such as the phocine distemper virus (PDV) epizootics in 1988 and 2002 (Harwood and Reijnders, 1988; Harding *et al.*, 2002), and pollution events, such as the Exxon Valdez oil spill in Alaska (Frost *et al.*, 1999), may have on populations. To be able to ascertain whether changes in local abundances observed at haul-outs are indicative of changes at a population level it is necessary to have a means of determining absolute abundance.

Under the U.K. Conservation of Seals Act 1970, the Natural Environment Research Council (NERC) has a duty to provide scientific advice to government on matters related to the management of seal populations in Britain and surrounding terrestrial waters. NERC has appointed the Special Committee on Seals (SCOS) to formulate this advice and supports the Sea Mammal Research Unit (SMRU) to provide scientific information to SCOS. In addition, conservation obligations under the European Community Habitats Directive (Council Directive (92/43/EEC) on the Conservation of Natural Habitats and Wild Fauna and Flora) require member states to designate special areas of conservation (SACs) to protect the habitats of species listed in Annex II, which includes both harbour (*Phoca vitulina*) and grey seals (*Halichoerus grypus*). Of key importance to the management and conservation of a population is the ability to measure and detect changes in its status (i.e. whether the population is stable, increasing or decreasing) and it's size.

3.2.2 Value of minimum estimates of population size as an index of abundance.

Historically, counts made at haul-out sites in the moult have been used as estimates of the total population, assuming all animals are hauled out at these times (Van Bemmel, 1956; Reijnders, 1976). However, data on individual activity patterns indicate that this is not the case (Harvey, 1987; Yochem *et al.*, 1987; Thompson *et al.*, 1989; Härkönen *et al.*, 1999). Haul-out counts thus provide only minimum estimates of population size.

To monitor harbour seal population trends around Britain, the SMRU makes a minimum of one count of seals at each haul-out site around Scotland and along the east coast of England. Seals on sandbanks are photographed using large format aerial photography (Duck and Thompson, 2003). Where seals haul out on rocky shores and are camouflaged, a thermal imaging camera from a helicopter is used (Duck and Thompson, 2003). These counts are made during the annual moult because seals are assumed to spend longer at haul-out sites at this time of year so the greatest, most consistent numbers of seals will be ashore. In addition to this, while the animals are moulting their skin is warmer and therefore more visible on the thermal imagery. For consistency among surveys, counts are made in the first three weeks of August within two hours of low tide whenever this occurs between 13:00 and 19:00 hours, and in restricted weather (the cloud base needs to be higher than 1200 feet with good visibility).

During a survey, a number of seals are at sea and therefore not counted. Thus these counts underestimate total population size and are used only as an index of the population to detect trends. Further information is required to convert these counts into absolute population estimates. In addition, to use these counts as an index of population to assess population trends, it is necessary to assume that there are no confounding trends in the proportion of seals in the water (over time and among sites) (Thompson and Harwood, 1990a). In comparing studies conducted in several different areas it seems unlikely that these assumptions are valid.

The numbers of seals hauled-out at any site varies considerably throughout the year. During the moult there are peaks in haul-out numbers (Simpkins *et al.,* 2003; Thompson, 1989; Slater and Markowitz, 1983). Mathews and Kelly (1996) found that in the last weeks of the moult, the number of seals hauled out decreased by as much as 85 percent and that the timing of this decrease varied by as much as two weeks among years. If there is only one count made each year, inconsistent timing of the count, in relation to the peak in numbers, will greatly affect the value of the population index used to assess population trends. A study by Härkönen e*t al.* (1999) on harbour seals in Sweden found that different age groups and sexes haul-out at different times over the moult. At no point during the summer months was the proportion on land representative of the entire population, so the timing of a survey may affect the component of the population that is counted.

The assumption that the proportion of seals in the water at a given time of year is constant among sites is also likely to be violated. A study of six haul-out sites on the coast of Washington and Oregon found that the proportion of animals hauled out among sites varied from 0.54 to 0.73 and concluded that regional correction factors were needed (Huber *et al.*, 2001).

Minimum population estimates that make the above assumptions may be useful in determining large-scale trends in population size. However, for conservation and management issues such as in the estimation of prey consumption by a population or in the designation of SACs at a local and regional scale absolute abundance estimates are required. To determine absolute abundance for such purposes, haul-out counts must be corrected for the proportion of animals that are in the water when a count is made.

3.2.3 Using information on individual activity patterns to estimate total population size.

Information on the activity of seals, namely the amount of time individuals spend at sea, contributes to the estimation of total population size by allowing the extrapolation of counts made at haul-out sites. One way to estimate the proportion of seals in the water is through mark-recapture studies. Long-term freeze-branding programmes have been used as a means of identifying individuals. When counts are made, the number of marked animals ashore is noted, allowing the proportion of marked animals absent from the haul-out to be calculated, giving the proportion of animals at sea (Härkönen and Harding, 2001).

The most commonly used technique has been to use telemetry to study the activity patterns of individual seals to determine the proportion of time animals are spending at sea allowing a correction factor for counts to be estimated (Eberhardt *et al.*, 1979; Pitcher and McAllister, 1981; Harvey 1987; Yochem *et al*, 1987; Ries *et al.*, 1998; Thompson and Harwood, 1990; Mathews and Kelly, 1996; Thompson *et al.*, 1997; Huber *et al.*, 2001; Simpkins *et al.*, 2003). Ries *et al.* (1998) used a combination of VHF radio telemetry and aerial surveys in a mark recapture technique to estimate population size. This technique uses the presence of tagged seals at haul-outs during the seven aerial surveys made to determine a correction factor. This technique requires a large number of tagged seals to ensure that the behaviour recorded in one discrete time period represents the behaviour of the population as a whole. The technique also required the rate of tag loss to be estimated to prevent false absences from the haul-out being recorded.

Using individual activity budgets has been found to considerably alter estimates of population size; one example of a study in Orkney is presented here (Thompson and Harwood, 1990*a*). VHF telemetry was used to monitor harbour seal activity in Orkney and estimate a correction factor for the proportion of time animals spent hauled out. It was found that seals spent, on average, 0.59 of their time hauled out (95% confidence interval 0.42-0.75) in the first two weeks in August (Thompson and Harwood, 1990a). The population estimate for Orkney, derived by this method, was approximately three times the previous estimates of the harbour seal population in the area (Vaughan, 1975; McConnell, 1985). This was in part due to the technique used to estimate population size as well as the timing of the counts, counts made previously were in the breeding season and were half those made in the moult in this study.

This proportion of seals hauled out can vary according to a number of extrinsic factors including: the tidal cycle (Schneider and Payne, 1983; Thompson and Miller, 1990*b*), weather conditions (Watts, 1992; Grellier *et al*., 1996; Kreiber and Barette, 1984), time of day (Stewart, 1984; Yochem *et al*., 1987; Thompson *et al.*, 1989), season (Slater and Markowitz, 1983; Thompson, 1989) the nature of haul-out sites (Thompson *et al*., 1997) and prey abundance. There are also a number of intrinsic factors such as age and sex that have been found to effect when seals haul-out (Thompson and Rothery, 1987; Thompson *et al*., 1989; Thompson *et al*., 1997; Kovacs *et al*., 1990; Thompson and Miller, 1990; Härkönen *et al.,* 1999).

Previous studies have used activity patterns, studied using telemetry and counts throughout the breeding and moult period, to estimate local harbour seal population size (Pitcher and McAllister, 1981; Yochem *et al.*, 1987; Thompson and Harwood, 1990; Thompson *et al*., 1997; Härkönen *et al*., 1999; Huber *et al.,* 2001; Simpkins *et al*., 2003). This is because the greatest, most consistent, numbers of seals are assumed hauled-out at this time. One problem with studying activity throughout the moult using telemetry is tag loss, because tags are usually attached to the fur and are therefore shed during the moult. Hence, these studies either require tags that are deployed near to the time of the moult when data will be collected for only a short period before the tags are shed in the moult or tags designed to be attached by other means, such as to the flipper (Simpkins *et al*., 2003; Huber *et al*., 2001).

3.2.4 Estimating the total population of harbour seals using St Andrews Bay.

This study introduces a methodology to utilise activity pattern data collected through most of the year combined with haul-out counts made throughout most of the year to estimate total population size. Previous knowledge of the size of the population of harbour seals using St Andrews Bay has been restricted to annual counts made during the moult by aerial survey. In this study, abundance estimates are made from November through to June providing information on the usage of this area throughout the year.

Behaviour of seals when near (<10km) of haul-outs was modelled separately from their behaviour when further away in order to separate the processes involved in foraging and hauling-out and to reduce variability in estimated haul-out proportions. Due to the longitudinal nature of the telemetry data, a generalized linear mixed model was used to account for temporal autocorrelation across repeated measures on the same individuals. Explanatory variables used were height of tide, state of tide, hour and month.

3.3 METHODOLOGY

3.3.1 Data Collection

Information on the study site, details of counts and the animals that were captured to deploy SRDLs as well as a description and programming of the SRDLs can be found in *Chapter 2*: Materials and Methods.

3.3.2 Framework for Analysis

The behaviour of tagged animals suggests that there are two different processes with two different time scales affecting haul-out behaviour. Animals in St Andrews Bay tend to make prolonged foraging trips of one to two weeks, followed by a period of a few days on or near a haul-out site. The covariates that may be expected to explain haul-out behaviour such as the tidal cycle and the time of day are unlikely to explain why an animal remains at sea for an average of 6 days (SE = 0.39 days, n = 24), as this behaviour is on a different temporal scale to the afore-mentioned covariates. These differences in the processes likely to be affecting the at-sea behaviour (when the animal is no longer in close proximity to the haul-out) and the near haul-out behaviour, lead logically to a two-stage model in which the processes are treated separately. The first stage models the proportion of time spent within range of the haul-out and the second stage models the proportion of time hauled-out when near the haul-out.

Calculating population estimates.

Population size was calculated as:

$$\hat{P} = \frac{c}{\hat{n} \times \hat{h}}$$ ***Equation 3.1***

Where:

$\hat{P}$ = population size

c = the number of seals counted at haul-outs

$\hat{n}$ = the probability of being within 10km of haul-out

$\hat{h}$ = probability of being hauled out given being within 10 km of haul-out

3.3.3 Separating Near Haul-out Behaviour.

Near haul-out behaviour was classified as within 10 km of a haul-out. A distance of 10 km was chosen because visual inspection of the data showed that it separated those movements around haul-outs from those made to areas to forage at sea. Due to the varying qualities of location fixes, a seal was deemed to be within 10 km of haul-out if: a location fix that fell within 10 km was of a location quality of one or greater (see *Chapter 2*), or if three consecutive poor quality locations (LQ < 1) occurred within 10 km. In this instance, the time of the first of the three poor quality locations was taken to represent the start of a period near the haul-out. The same classification rules were used to record the departure of an animal from the 10 km radius.

Figure 3.1 illustrates the selection of the 10 km separation between near haul-out behaviour and offshore 'foraging' behaviour. Only the locations with travel speeds slower than 0.5 m s^{-1} and not associated with haul-outs are shown as a density per kilometre squared. This highlights where likely foraging activity is occurring (see *Chapter 5*). 10 km was chosen in order to include the haul-outs and surrounding areas while excluding the dense foraging areas that appear to begin between 15 and 20 km from the haul-out.

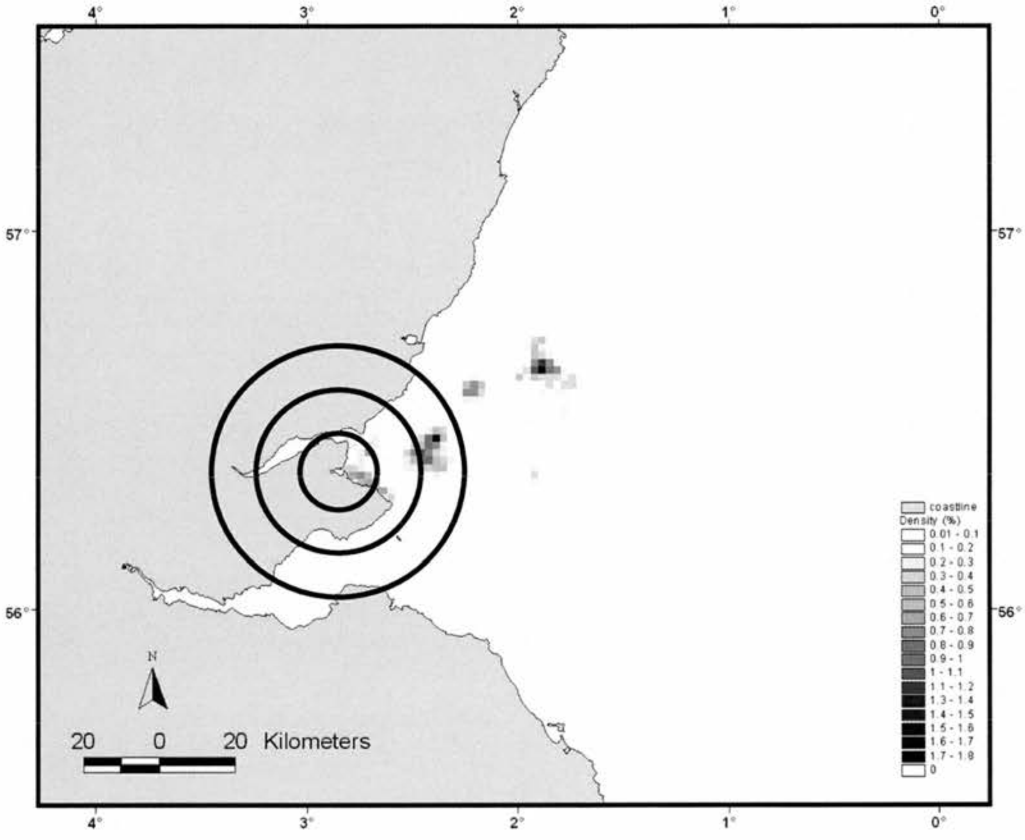

Figure 3.1: Mean percentage density of SAS locations per 1 km^2 for all seals, with concentric circles at 10, 20 and 30 km from the haul-out.

3.3.4 Modelling the proportion of time spent within 10km of haul-out.

A generalized linear model (GLM) was used to model the proportion of time spent within 10 km of haul-out. The correlation structure in the data was best fitted by a first order autoregressive process (AR(1)) as identified from a correlogram and this was incorporated into the model (Mackenzie pers comm.).

The AR(1) error structure takes account of the temporal non-independence of the data; without this, standard errors would be underestimated.

Response Variable

The response was modelled as a binomial variable. For each two-hour period animals were classified as within a 10 km radius of haul-out (1) or outwith this area (0). From this, the proportion of time spent near haul-out was estimated for each animal for each month of the study period.

Explanatory Variable

The only explanatory variable in the model was month. There was only one value per seal for each month of the proportion of time near haul-out, so there are no random effects and a mixed effects model (see below) was not needed.

3.3.5 Modelling the proportion of time hauled-out.

A generalized linear mixed model (GLMM) was used to model the proportion of time that seals were hauled-out given that they were within 10 km of a haul-out site. This model structure was chosen because of the longitudinal nature of the data, which contains many repeated measures of relatively few individuals (Crawley, 2002). As for the model of the proportion of time spent within 10 km of haul-out, the correlation structure was that of a first order autoregressive process (AR(1)), as identified from a correlogram. This GLMM thus allowed for temporal autocorrelation across repeated measures on the same individuals and should therefore give reliable standard errors rather than underestimating them due to the observations being correlated.

Response Variable

The modelled response was again a binomial variable, whether the animal was hauled-out or not. Each two-hour block was treated as a binomial trial. If an animal was hauled out for greater than 50 % of the time the trial was considered positive (1) and if hauled out for less than 50 % the trial was considered negative (0). How well these proportions could be changed into binomial data was examined by plotting a frequency histogram (*figure 3.2)*. A very large majority of values fell close to 0 or 1, giving confidence that this transformation would not bias the results.

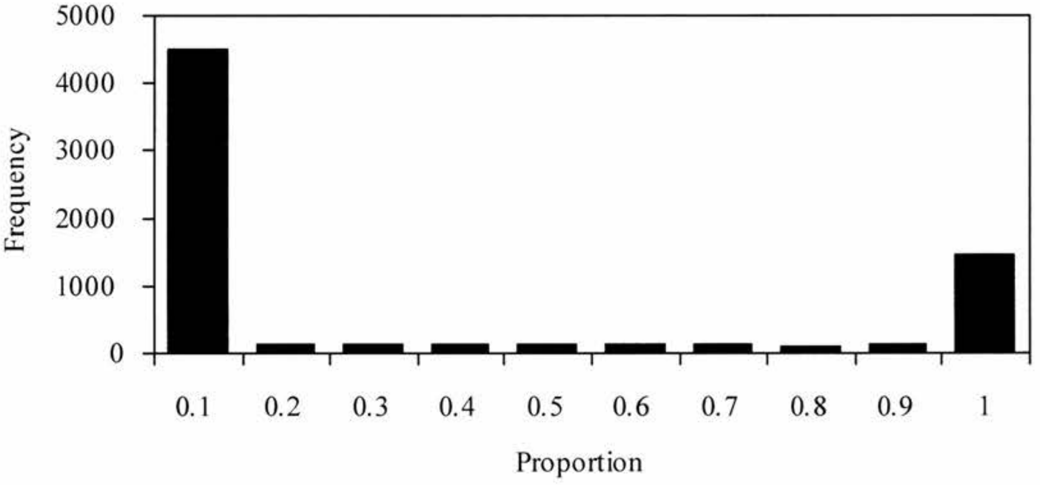

Figure 3.2: Frequency histogram of proportion of time hauled out in two hour blocks when within 10 km of a haul-out site.

Explanatory Variables.

The explanatory variables included in the model were month, time of day, tide height, state of tide and year. As time of day is a circular statistic, hour (h) was transformed to the cosine and sine of Greenwich Mean Time (GMT) (cos[(*h*/24)x360] and sin[(*h*/24)x360]). Tide height was measured in meters. State of tide was treated as binomial, 1 for a rising tide and 0 for a falling tide.

Month was included as a factor rather than as a circular statistic as the data considered here were only for eight months of the year and there are considerably different numbers of animals hauled out in July when tags fall off compared to November where tagging begins. Also in the remaining months of the year, where there was no data collected due to the moult, the behaviour is known to differ significantly due to the breeding season and moult and it would therefore be inappropriate to interpolate across this period. Individual seal was included in the model as a random effect allowing the intercept or baseline value for haul-out activity to vary with seal.

The GLMMs were fitted to the data with a binomial error distribution using the penalized quasi-likelihood method with a logit link function and an AR(1) error structure using the modelling software 'Statistical Application Systems' (SAS) (SAS version 8).

3.3.6 Model Selection

The most parsimonious model was found using backwards-stepwise selection, with altering starting points, from a fully saturated model with interaction terms up to second order. The Akaike information criterion (AIC) value was used in model selection; however some discretion was used to determine those variables and interaction terms that were included in the final model. Despite two interaction terms and state of tide being slightly significant and remaining in the model using backwards selection, these were later removed as they provided no improvement to the fit of the model and gave considerably more complexity to the model making results difficult to interpret. Predictions were made from both models by incorporating appropriate values for the explanatory variables at the time a count was made.

3.3.7 Calculating confidence intervals.

Estimates of precision for each model (that took account of the dependence in the data) were combined in a parametric simulation approach to estimate confidence intervals around estimates of population size. Parameter estimates and standard errors from the fitted models on the scale of the link function were sampled at random to generate slope co-efficients. Then the predicted coefficient values were generated as above to calculate predictions on the scale of the link function. The inverse link function was then used to obtain predictions on the scale of the response. This was performed for both models and then the probabilities for each model were multiplied together. The central 95 percent of values for 100 000 simulations were used to find the upper and lower confidence limits (Mackenzie pers comm.).

3.3.8 Effect of error in counts

The counts made at haul-outs used in estimating the population size are assumed to be 100% accurate, i.e. if an animal is hauled-out the probability of it being counted is one. As there is likely to be some error associated with the counts, what was considered to be a worst-case scenario was tested by calculating population estimates with counts that were 20 percent higher and 20 percent lower than the observed counts.

3.4 RESULTS

3.4.1 Numbers of harbour seals hauled-out.

Figure 3.3 shows the seasonal variation in numbers of seals counted at haul-out sites in St Andrews Bay. Numbers were low in winter months and steadily increased through spring and remained stable through to the moult in August-September, across all study years. Numbers then decreased sharply between September and October. In 2001 and 2003 there was a decline in numbers in June and July in the breeding season. At this time seals were more likely to be disturbed by walkers and joggers in the area.

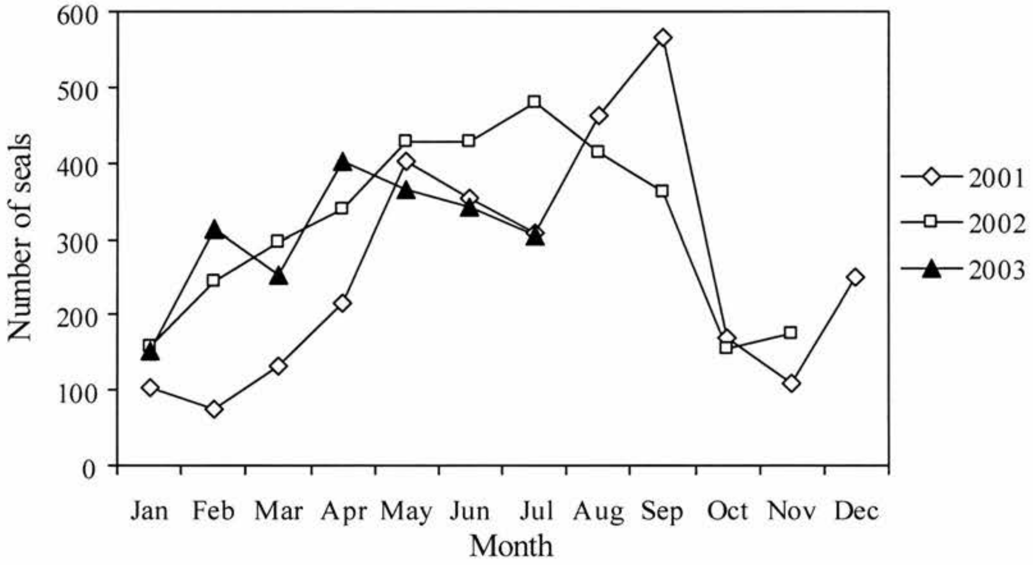

Figure 3.3: Counts made at harbour seal haul-outs from January 2001 to July 2003.

3.4.2 Separation of time near haul-out and at sea.

Figure 3.4 shows the observed proportion of time animals spent near haul-out (within 10km of haul-out) and at sea (outwith 10km of haul-out). On average, a higher proportion of time was spent near the haul-out in the summer months, with a steady increase from the winter months. Percentage time spent near the haul-out ranged from 30% in December to 50% in June.

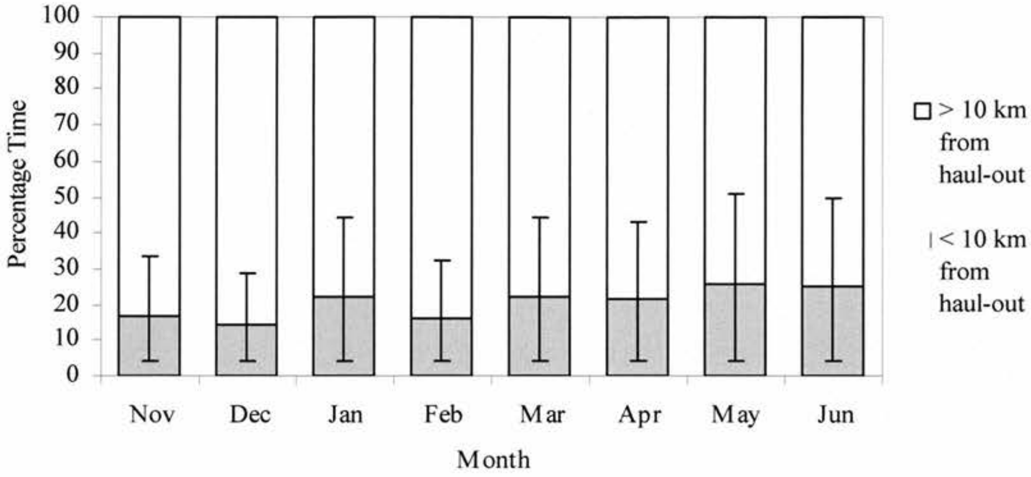

Figure 3.4: Percentage time spent within and outwith 10 km of haul-out per month with 95 % confidence interval.

* Data for July are not presented as only females were tagged at this time.

3.4.3 Modelling the proportion of time spent near the haul-out.

Month was the only explanatory variable included in this model and was highly significant and explained over 15 percent of the deviance. *Figure 3.5* shows the predicted values from the GLM for the proportion of time animals are spending within 10 km of haul-out for each month. The proportion of time spent near the haul-out steadily increased from the winter through to the summer months with a slight decrease in June, although the 95% confidence intervals are wide compared to the variation across months.

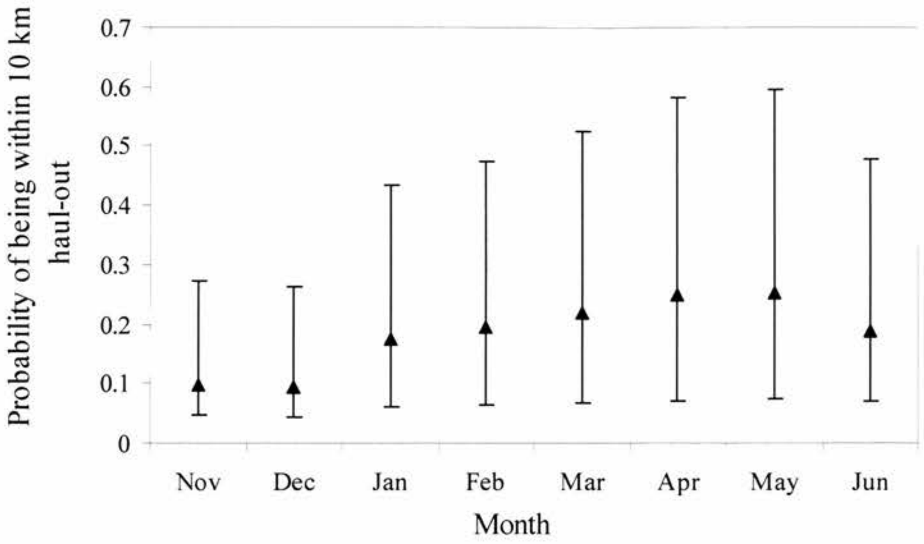

***Figure 3.5*:** Predictions from GLM for the proportion of time animals spend within 10 km of haul-out per month with 95 % confidence intervals.

3.4.4 Modelling haul-out behaviour

From a saturated model with second order interactions, only height of tide (in metres), cosine of hour and month were retained in the model, all as highly significant at the 0.1% level (*Table 3.1*). State of tide (whether rising or falling) was dropped from the model using backwards-stepwise selection. Interactions with height of tide and month as well as cosine of hour and month were significant at the 5% level but were dropped from the model because the increased complexity did not change the results. Year was not significant nor did it improve the fit of the model therefore both years of the study period were pooled in the final analysis shown in *Table 3.1*.

Table 3.1: Coefficients, standard errors and significance of those variables included in the final GLMM to model the proportion of time hauled out within 10 km of haul-outs.

Explanatory Variable	Coefficient	Standard Error	Significance
Height of tide	-1.064	0.022	P<0.01
Cosine of hour	-0.233	0.040	P<0.01
Nov	-1.893	0.337	P<0.01
Dec	-1.023	0.330	.
Jan	-0.732	0.304	.
Feb	0.008	0.303	.
Mar	-0.277	0.290	.
Apr	-0.001	0.283	.
May	-0.305	0.284	.
Jun	-0.004	0.286	.

Figure 3.6 shows how the variability in haul-out probabilities is explained by the height of tide in this model for each month. Time of day is held at midday for presentation purposes in this figure. It shows that the probability of hauling out decreases with increasing height of tide. The probability of hauling out is also much lower in winter months.

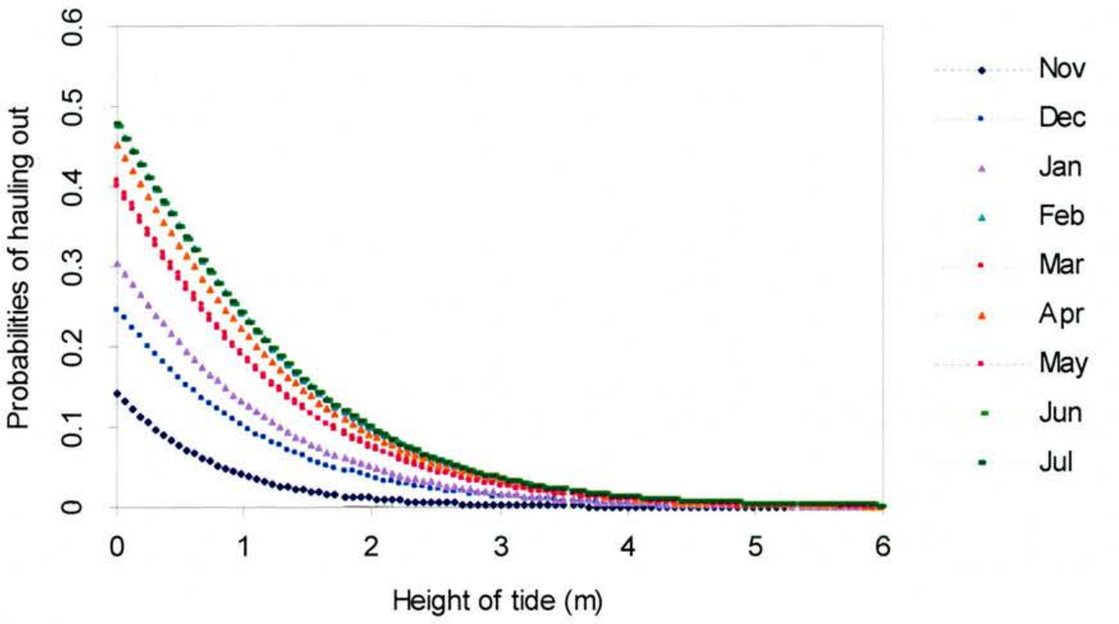

Figure 3.6: Estimated probability of hauling out as a function of tide height, by month.

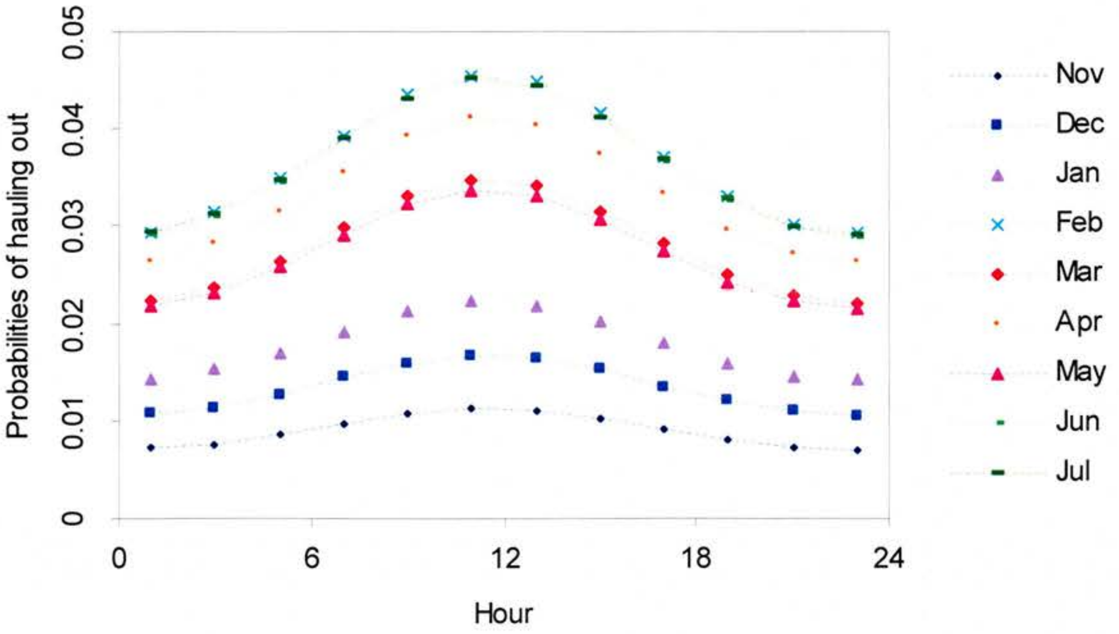

Figure 3.7: Estimated probability of hauling out as a function of time of day by month.

In *Figure 3.7* the height of tide is held at the mean of the data set to visualise the fitted probability of hauling out against time of day. The probability of hauling out is greatest at midday in all months. The probability of hauling out is again lower in winter months for all times in the day.

3.4.5 Population estimates

Table 3.2 gives the count data for each month as well as the predicted probability of being within 10 km and of being hauled-out along with the population estimate derived at from these values.

The probability of being near the haul-out varied minimally, ranging from 0.09 in some of the winter months to 0.25 in spring (*Table 3.2*). The probability of being hauled-out when within this area ranged from 0.39 to 0.97 (*Table 3.2*). Despite the variation in the outputs from the two models and the seasonal variation in the counts shown previously (*Figure 3.3*), the population estimates are fairly consistent, ranging from 1062 to 2770 animals (*Table 3.2*).

***Table 3.2*:** Predicted probabilities and counts used in calculating population estimates. Confidence intervals are given in *Figure 3.8*.

Month	Count	Probability of being near haul-out	Probability of being hauled-out	Population Estimate
Nov-01	80	0.10	0.54	1540
Dec-01	151	0.09	0.76	2142
Jan-02	229	0.17	0.83	1585
Mar-02	244	0.22	0.93	1200
Mar-02	297	0.22	0.80	1687
Apr-02	340	0.25	0.95	1450
May-02	429	0.25	0.93	1827
Jun-02	429	0.19	0.95	2375
Nov-02	105	0.10	0.39	2770
Jan-03	149	0.09	0.69	2172
Jan-03	152	0.17	0.82	1062
Feb-03	313	0.17	0.92	2049
Mar-03	253	0.22	0.93	1236
Apr-03	402	0.25	0.88	1837
May-03	366	0.25	0.94	1547
Jun-03	343	0.19	0.97	1870

The population estimates for each count made are shown in *Figure 3.8*. The population estimates range between 1062 and 2770 seals with a mean of all the times at which counts were made of 1746. All population estimates lie within the 95 percent confidence intervals of all the other estimates. The most recent population estimate was that for June 2003: 1870 seals (95 % CI: 1121 to 2148). *Figure 3.8* also highlights the seasonal variation in counts made at haul-outs and the ability of the model to correct these to consistent population estimates.

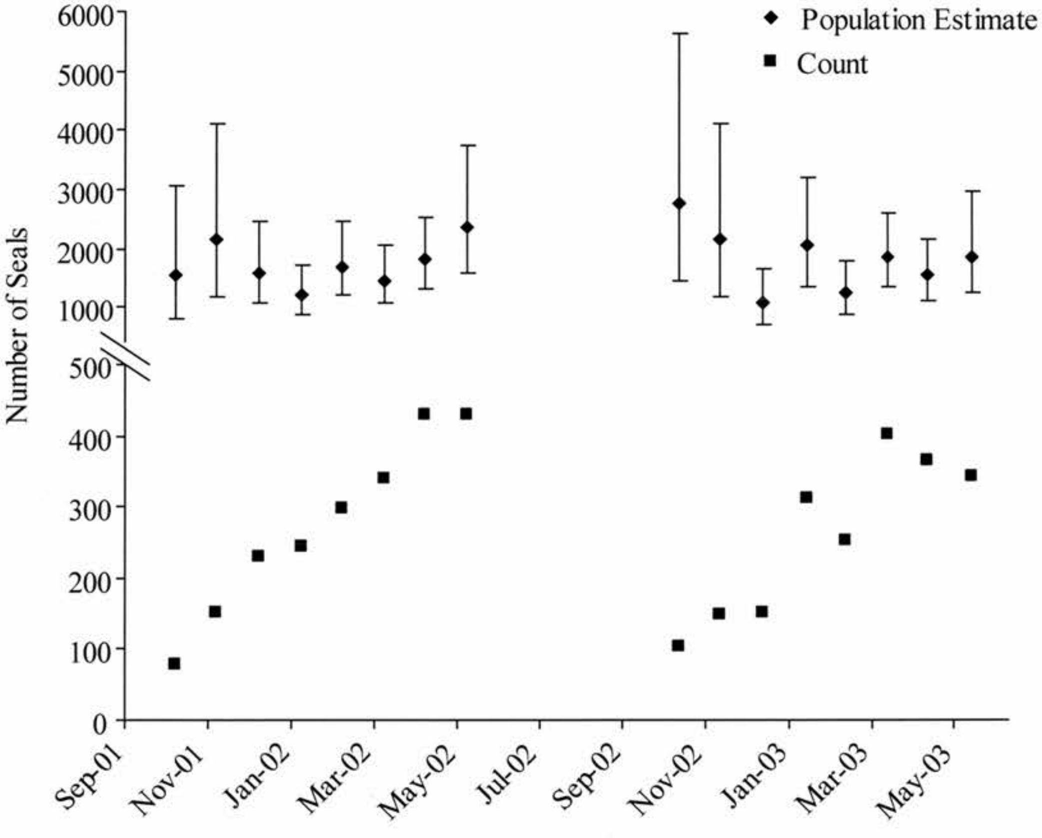

Figure 3.8: Population estimates with 95 percent confidence intervals and counts made at haul-outs.

*For presentation purposes only, the counts made in early March 2002 and early January 2003 are presented as the February 2002 and December 2002 count and population estimate.

Confidence intervals are particularly high for November as there were fewer animals tracked and also the behaviour of the seals tracked was noticeably more variable in this month for both models.

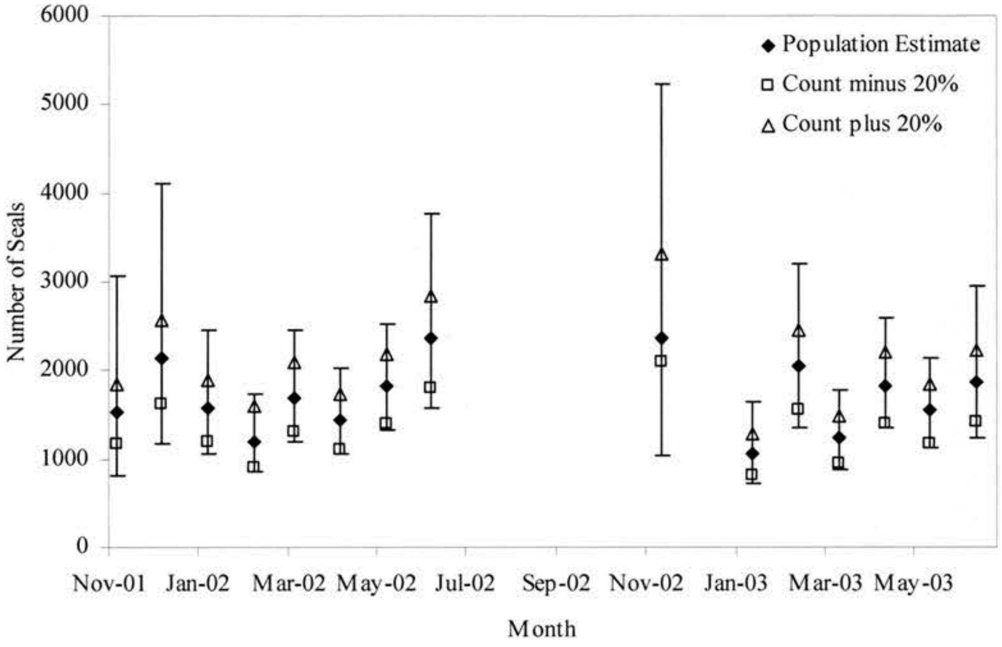

Figure 3.9: Population estimates (95% confidence intervals) with counts altered by +/- 20 percent.

Adjusting the counts to incorporate a maximum 20 percent error gave population estimates that fall within the 95 percent confidence intervals of the population estimates predicted from the observed data (*Figure 3.9*). Estimation of population size was thus judged to be robust to errors in count data.

3.5 DISCUSSION

3.5.1 Estimates of Abundance

This study has vastly improved our knowledge of seal populations in the St Andrews Bay area. Previously, the population has only been monitored through single aerial surveys every other year. The usefulness of such surveys has been discussed in the introduction. This is the first attempt to estimate absolute abundance of harbour seals in the area and the first to estimate abundance throughout most of the year.

A total of 668 harbour seals were counted during the moult at haul out sites in St Andrews Bay in the 2002 aerial survey (Duck and Thompson, 2003). This gives a minimum population estimate for the area. This number was not corrected to account for the proportion of animals in the water at the time of the aerial surveys. Previous telemetry studies collected during the breeding season in the Moray Firth (Thompson *et al.*, 1997) and in the Wadden Sea (Ries *et al.*, 1998) found the proportion of the population hauled out to be approximately two thirds of the total population size (61 and 64 % respectively). In St Andrews Bay, the size of the population estimate relative to the size of the count suggests that at the time of the survey in the moult only 36% of the population is hauled-out. This is considerably lower than the studies conducted in the Moray Firth and the Wadden Sea. However these were conducted in the breeding season rather than in the moult when numbers hauled-out may well be greater due to different components of the populations moulting at different times. Also there isn't data in this time period due to the tags having been shed by the start of the moult, there is no valid way of estimating the variation around this extrapolated value. However, from the average level of variation observed at other times of year the

95% confidence interval could be from 24% to 63%. From these wide confidence intervals the apparent difference in haul-out behaviour between regions in this time period may not be as extreme as initial impressions. Data would be required within this time period to make direct comparisons between studies.

This study has provided considerably more information than single abundance estimates made in the moult or breeding season because information was collected on how the animals were using the area throughout most of the year. The seasonal variation in the number of seals hauled out was shown to result from the changing proportion of time animals spend at sea, rather than any major change in the number of animals using the area to haul-out and forage. In other areas where there are a number of large haul-out sites in relatively close proximity, such as in Orkney, Shetland and the west coast of Scotland, changes in the local abundance of seals hauled out in an area may reflect animals moving between haul-out sites to gain better access to different foraging areas. Other studies estimating absolute abundance have concentrated on one time of year, usually the pupping season or moult (Pitcher and McAllister, 1981; Harvey 1987; Yochem *et al*, 1987; Thompson and Harwood, 1990; Mathews and Kelly, 1996; Thompson *et al.*, 1997; Ries *et al.*, 1998). They have not provided information on the number of animals using an area throughout the year, which could be important information for the designation of conservation areas such as SACs.

3.5.2 Ecological implications

One implication of these findings is that the population of harbour seals in St Andrews Bay has greater energetic requirements than might previously have been assumed. Not only because estimates of abundance are higher, but also because of the high proportion of time animals are spending at sea, presumably reflecting foraging effort. If animals are indeed spending a greater proportion of time at sea than has been recorded in other areas, we can speculate that this may reflect the energetic compromise the seals are undergoing in this area. The density of prey may be more diffuse, or of a lower nutritional quality, placing greater energetic constraints on the population, requiring a greater proportion of time to be spent travelling and in pursuit of prey. The data presented here are insufficient to reliably confirm this hypothesis and the greater proportion of time spent at sea may be due to foraging being more profitable at greater distances from haul-outs making it more economical to rest at sea near the foraging areas rather than always returning to the haul-out to rest (see *Chapter 6*).

Higher population estimates equate to greater estimates of fish consumption. If the predation pressure of harbour seals in this area is greater, the potential impact on fish stocks, and interactions between this marine predator and fisheries are also greater. *Chapter 4* estimates the species composition of the diet of harbour seals from St Andrews Bay highlighting the degree of overlap with commercially exploited species of fish.

Consistent population estimates throughout the year (*Figure 3.8*) gives information on the integrity of the population. The implication is that low numbers of seals counted at haul-out sites in the winter months are not due to emigration of seals from the area. Instead the population appears to be discrete and the variation in numbers counted was a result of seasonal changes in the time spent near the haul-out site and time spent hauled out. There is however, evidence that there is a degree of mixing between populations of harbour seals, and although large numbers of animals don't appear to be migrating as such, some individuals do move large distances and are found in different populations (Bonner and Whitthames, 1974; Thompson *et al*., 1994). The lack of genetic variation found between the population of harbour seals in the Wash in Britain and the Dutch Wadden Sea also supports a degree of mixing between populations (Swart, Reijjnders and Van Delden, 1996).

3.5.3 Advantages of Methodology

Information on individual activity patterns was used to correct for those animals in the water when counts of seals at haul-outs were made. Variations on this basic concept have been used in many studies; modelling haul-out behaviour with variables such as state of tide, time of day and weather conditions (e.g. Watts, 1996; Frost *et al*., 1999; Sjoberg *et al*., 1999; Simpkins *et al*., 2003). Previous studies have concentrated on the times of year when the largest proportions of animals are hauled-out, in the breeding season or in the moult (e.g. Thompson *et al*., 1997; Simpkins *et al*., 2003); here the validity of estimating population size throughout the year is assessed. One of the benefits of this approach is that it permits telemetry data, which is collected throughout the year to study other aspects of harbour seal ecology, to be used in determining abundance. Satellite telemetry would not be a cost effective technique if it was only being used to estimate abundance but, as demonstrated here, it can be utilised for this purpose when studying a number of aspects of harbour seal ecology simultaneously. If tagging is conducted in the breeding season or moult then tags are quickly shed if attached to the fur (Thompson *et al*., 1997). If tags are attached to hind flippers (Simpkins *et al*., 2003) data collection is limited to haul-out behaviour, as the tag is always submersed and therefore no transmissions are made while at sea. In addition it is expected that the most extreme differences in haul-out behaviour by different sex and age groups will occur throughout the breeding and moult period. Therefore information on the activity budgets of each component of a population are needed to calculate reliable population estimates at these times (Thompson *et al.*, 1989; Thompson and Miller, 1990; Härkönen *et al.*, 1999).

Outwith the breeding and moult period animals spend a greater proportion of time at sea. Conventional modelling approaches have been unable to find relationships between haul-out behaviour and the explanatory variables, as such data sets are flooded with zeros for the long periods when the animals are at sea. The two-stage model used here accounted for the variability at the two different temporal and spatial scales, separating the processes involved in foraging and hauling out. This methodology proved very successful as highlighted in *Figure 3.8*, where counts made at haul-outs are shown to vary considerably throughout the year and yet estimates of abundance using this model framework consistently correct for this seasonal variation in haul-out behaviour. The methodology was also found to be robust to changes in the number of animals hauled-out that could either result from observer error or human disturbance at some haul-outs (*Figure 3.9*).

3.5.4 Wider applications of methodology

The model framework developed here could be applied to any haul-out site used by harbour seals to advance the knowledge of the species' usage of the area. However, telemetry data from each site would be required, as the behaviour between sites cannot be assumed to be consistent. The distance of a haul-out site from foraging areas is likely to greatly affect the proportion of time spent at sea. If animals are found to be making daily coastal foraging trips, it may be more appropriate to use only the haul-out behaviour model. However, where animals are travelling further to forage it is likely that they will spend longer periods at sea making this two-stage model framework more appropriate. Also in studying long-term changes in the population within an area, there is still a need for new telemetry and count data because if, for example, prey availability changes, the proportion of time animals haul-out is also likely to change (Thompson *et al.*, 2001).

In this study 10 km was chosen as the point of separation in the two stages of the model. This was partly due to the inaccuracies in locations received, which prevent it being appropriate to use any finer resolution, as well as being close enough to the haul-out to prevent hot-spots of foraging activity being included in the stage of the model analysing near shore behaviour. The choice however is still fairly arbitrary, and therefore the effect of using other cut offs was experimented for, testing both 5, 10, 15 and 20 km as well as using a one stage model. The amount of variance explained in the near-shore haul-out behaviour model was lower for all other distances from the haul-out. A one-stage model not separating offshore and near haul-out behaviour found no significant relationships with the explanatory variables.

This is a technique that can readily be applied to other species of seal. However the degree of movement of the species will define the area in which the population abundance can be assessed. Where seals remain at sea for long periods, haul-out behaviour is likely to be more effectively modelled using the two-stage technique described here. It is also a useful tool in estimating seasonal abundance within an area.

3.5.5 Methodological improvements

Abundance estimates for some months have large confidence intervals due to the small number of seals tracked and their varied behaviour. Confidence intervals could be improved by tracking a larger number of seals. The fit of the model may be improved by the inclusion of other variables, for example, the weather. Weather conditions, such as rainfall, temperature and wind, have been found to have a weak effect on numbers of harbour seals hauled-out in the Moray Firth (Grellier *et al.,* 1996). That study was only conducted over the summer months; in winter when weather conditions are more extreme there may be a more significant effect on haul-out behaviour. Including weather conditions in the model would not be straightforward, as haul-outs have different aspects and therefore will be affected by different prevailing weather conditions. Photoperiod may also help capture haul-out behaviour better than month or time of day, which is likely to be arbitrary to a seal (Watts, 1996). Intrinsic factors such as the age, sex and body composition of the seals may also help refine the model. However information on the population structure of harbour seals in St Andrews Bay would also be required to accomplish this.

Information on the availability and distribution of prey stocks are likely to explain more of the variability in where animals are at sea, however the temporal and spatial resolution of information on the abundance of prey stocks is not currently known in the study area.

The main assumptions made in this study were that the counts were accurate and that the tagged animals in this study were representative of the population as a whole. The validity of these assumptions is discussed here.

Monthly population estimates are based on single counts assuming no variability. The accuracy of counts made at haul-outs was considered by testing a worst-case scenario. It was shown that when counts were inaccurate by 20 percent, predictions of population estimates were still within the 95 percent confidence intervals of the actual population estimates. So the modelling process is relatively robust to inaccuracies in counts of seals (see *figure 1.9*).

A number of studies in different locations have found that there are seasonal changes in attendance of various age classes of both sexes (Thompson and Rothery, 1987; Thompson *et al*., 1989; Kovacs, Jonas and Welke, 1990; Thompson and Miller, 1990; Härkönen, Hårding and Lunneryd, 1999), which may invalidate the assumption that tagged animals are representative of the population. Both males and females of varying sizes were represented in the sample, although the numbers of each sex are not even in each month of tracking (see *Table 2.1*), and no seals weighing less than 50 kg were tagged due to the size of the SRDLs. The smallest animal tagged was 120 cm in length. This length corresponds to animals in the year two age class, as estimated from growth curves produced by Corpe (1996) who aged teeth taken from live caught seals in the Moray Firth, and by Härkönen and Heide-Jørgensen (1990) who aged teeth from dead animals retrieved during the 1988 epizootic in the Kattegat-Skagerrak area. There is little data on the population structure of harbour seals in St Andrews Bay. The population structure of harbour seals prior to the 1988 epizootic in the Kattegat-Skagerrak was simulated and from this study 33 percent of the population were estimated to be of age class two and below (Heide-Jørgensen, Härkönen and Åberg, 1992). Therefore, if the St Andrews Bay population structure is assumed to be comparable to that in the Kattegat-Skagerrak, the behaviour of one third of the population is not represented in these abundance estimates. A freeze-branding study in the Kattegat-Skagerrak found that pups haul-out behaviour is highly variable in the summer months, ranging from 85 percent in June to as little as 10 percent in September (Härkönen *et al.,* 1999). If these differences persist throughout the year the skewed sample of tagged seals could have a considerable effect, generating a bias in the population estimates.

In this study, all tagged animals were captured in the area of the Eden Estuary and Abertay Sands yet the telemetry results from these areas are also applied to the animals in the mouth of the Tay Estuary (*Chapter 2, Figure 2.1*). From the 25 seals tagged, all of those captured in the Eden Estuary used only the Eden Estuary to haul-out throughout the study period. Similarly, of those seals captured at Abertay Sands only one was seen to move to a haul-out in the Tay Estuary. There would appear to be little mixing of seals between haul-outs so there could be differences in the behaviour of animals in the Tay Estuary despite the close proximity to the other haul-outs in this area (*Chapter 2, Figure 2.1*). The foraging behaviour of Tay Estuary animals may be different; they could be foraging more within the estuary (*Chapter 4*). There is currently no information available on the movements of seals in the Tay Estuary to validate this. Regional variation in attendance of haul-outs has been illustrated in other studies.

However, these haul-out sites are not in as close proximity as those studied here (see *Figure 2.1*).

One further way in which the tagged sample of seals may not be representative of the population is that the addition of a tag on an animal may alter its behaviour. The SRDLs will create some additional drag to the animal that may be enough to alter the seal's behaviour. All tags weighed less than 0.5 % of body weight in this instance but transmitters have been seen to affect behaviour of pinnipeds when larger data recorders have been deployed (Gentry and Kooyman, 1986). The proportion of time that a tagged seal spends hauled-out may be reduced due to the increased pressure to forage caused by higher energetic costs of travelling with the additional drag from the tag. This could only be determined by studying the additional cost of drag created by tags theoretically, experimentally, or by attaching larger devices to seals with satellite tags to see if proportion of time hauled-out differed significantly compared to seals without the extra drag. However, this might be questionable ethically. If the tags were affecting the proportion of time animals were hauling out this would result in an overestimation of the population size using the methods in this study. This is due to the proportion of time animals are spending in the water being overestimated from the telemetry data so that counts on land are inferred to represent a smaller proportion of the population than they actually do.

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CHAPTER FOUR:

Estimated diet and annual prey consumption of harbour seals from St Andrews Bay.

4.1 ABSTRACT

Seasonal variation in harbour seal diet in the east coast of Scotland was investigated from faeces collected monthly during 40 trips over a two and a half year period. A total of 33051 otoliths from 31 species were recovered from 323 faeces. Data on fish otoliths were corrected for partial and complete digestion and used to estimate the proportion by weight, of each species in the diet.

Six prey species made up more than 85 percent of the total prey consumed by weight. Overall the diet was dominated by sandeels (45%) and whiting (22%). There were significant seasonal trends in the consumption of sandeels, peaking in winter months when sandeels are dormant in the sand or spawning. Few sandeels were consumed in the summer months and the diet was then dominated by flat fish, primarily flounder.

4.2 INTRODUCTION

Studies of diet composition of pinnipeds are important not only for ecological studies of a species but also to enable their impact on prey stocks to be quantified. There is no method for analysing the prey eaten by seals that is not subject to some kind of bias (Pierce and Boyle, 1991) and there are several practical difficulties in determining the diet of pinnipeds. These are mainly because they are free ranging and catch and feed on their prey at sea, largely underwater.

4.2.1 Techniques for determining the diet of harbour seals

Historically the diet of pinnipeds has been determined through examining stomach contents of dead animals (e.g. Rae, 1960, 1968, 1973; Frost and Lowry, 1980; Stewart and Murie, 1986; Bowen, Lawson and Beck, 1993). Animals tend to be shot on land where a large proportion of stomachs were found to be empty (Rae, 1960; Bowen and Harrison, 1996) or around fishing operations where stomach contents are likely to be biased towards the target species of the particular fishery (Tollit, 1996). Actively sampling animals has the obvious ethical and conservation disadvantage associated with it and is often not compatible with other ecological studies. However one advantage is that the age and sex of the individual seal sampled is known, and therefore diet can be determined for each component of the population (Bowen and Harrison, 1996).

Fatty acid and stable isotope analysis are two indirect methods of studying diet based on the principle that characteristics of the prey are reflected in different tissues of the predator. In stable isotope analysis, the occurrence of naturally occurring isotopes of carbon ($^{13}C/^{12}C$), nitrogen ($^{15}N/^{14}N$) and sulphur ($^{34}S/^{32}S$) can be measured and used to establish trophic relationships and sources of nutrients in marine food webs (e.g. Hobson and Montevecchi, 1991; Hobson and Welch, 1992). This technique does not provide information on the species composition of the diet that is often of interest in conservation and management decisions.

The fatty acids from prey are deposited largely unaltered into the blood, milk and blubber of marine mammals (Iverson, 1988; Iverson, 1993; Kirsch *et al.*, 2000). Fatty acid analysis can provide qualitative information on the diet, and quantitative estimation is possible (Iverson *et al.*, 2004), however a comprehensive library of the fatty acid composition of prey species in each region, of all size groups and in different seasons is ideally required. The relationship of fatty acids in the prey to those in the marine mammal is not straightforward; the marine mammal produces it's own fatty acids and has the capacity to alter others before they are deposited. The way fatty acids are deposited and mobilised is not fully understood and further information is required to be confident in utilising the method (Iverson, 1993).

The diet of pinnipeds is more typically studied by identifying hard parts recovered from scats, including bones, fish otoliths (sagittae) and cephalopod beaks (Pierce and Boyle, 1991; Laake *et al.*, 2002). Collecting scats is non invasive and provides larger sample sizes. The prey can generally be identified to species level using this technique although some prey remains may only be identifiable to higher taxonomic levels. The size of otoliths and beaks is related to the size of prey permitting estimation of the proportion by weight of each prey species in a sample. However, otoliths are digested as they pass through the gut and otoliths from different species are selectively digested to different degrees. Captive feeding experiments can determine species-specific digestion coefficients to help account for this (Harvey, 1989; Prime and Hammond, 1987; Tollit *et al.*, 1997; Bowen 2000; Orr and Harvey 2001; Grellier and Hammond, *in press*). Estimating fish weights from the corrected otolith size introduces measurement error that needs to be taken account of (Hammond *et al.*, 1994 *a* & *b*, Hammond and Rothery, 1996). The effect of digestion on some species' otoliths may mean that they are completely digested and not represented in data at all, numerical correction factors derived from feeding experiments can help correct for this source of bias (Bowen, 2000). An additional consideration is that cephalopod beaks have been found to be retained in the stomachs of pinnipeds for long periods and therefore may not represent consumption on the same time scale as fish otoliths retrieved from faeces (Pitcher, 1980; Bigg and Fawcett, 1985).

4.2.2 Harbour seal diet in Britain

The analysis of hard parts found in scats is the one technique that has routinely been used to study the diet of seals around Britain. Harbour seal diet has been described in the Wash (Hall *et al.*, 1998), the Moray Firth (Tollit and Thompson, 1996; Pierce *et al.*, 1991), Orkney (Pierce *et al.*, 1990), Shetland (Brown and Pierce, 1998), the west coast of Scotland (Pierce and Santos, 2003) and Northern Ireland (Wilson *et al.*, 2002).

The dominant species in the diet of harbour seals in the Wash, between October 1990 and September 1992, was whiting (24%) followed by sole (15%), dragonet (13%) and goby (11%) with other species of flatfish, gadoids and sandeels making lesser contributions. Seasonal changes in the diet were apparent, for example whiting showed a distinct peak in late autumn through to spring whereas sole peaked in spring (Hall, Watkins and Hammond, 1998).

In the Moray Firth, between February 1989 and February 1996, Tollit and Thompson (1996) found that the dominant species was sandeels (47%) followed by lesser octopus (27%), whiting (6%) and flounder (5%). Again there was seasonal variation with sandeels being of little importance in the summer months and whiting being more frequent in the diet in winter. Another study in the same area found that clupeids (herring and sprat) dominated the diet in winter and that sandeels were dominant in spring and summer (Pierce *et al*., 1991). Harbour seals in the Inner Hebrides consumed few sandeels, the most important prey species were scad, herring and whiting (Pierce and Santos, 2003).

From these, and other studies throughout Britain it is clear that harbour seals are feeding on a wide variety of prey but that the diet is often dominated by a few key species. The diet was found to vary between regions, seasonally as well as between years. It has been proposed that the observed variation is a result of changes in locally abundant prey species (Härkönen, 1987; Thompson 1989; Pierce *et al*., 1990; Tollit *et al*., 1997). Given this variation is it clear that diet studies should ideally not be extrapolated across regions or between years and seasons.

The diet of harbour seals is likely to be effected by how the available habitat is partitioned between other top predators such as grey seals, cetaceans and sea birds. In the Moray Firth comparative diet studies have been conducted on both grey and harbour seals. The diet showed considerable overlap with sandeels, gadoids, flatfish and cephalopods forming over 95 percent of the diet of both species (Thompson *et al.*, 1996). In the study area of the North Sea, sandeels form the base 'food-fish' for many predators including a number of predatory fish such as gadoids. The food web is very complex but sandeels provide a significant component in the majority of the top marine predators diet (Furness and Tasker, 2000; Lewis *et al.*, 2001; Pierce *et al.*, 2004; Smith, 1997). Identifying impacts from fisheries is complex as increases in predatory fish cause a reduction in the availability of 'food-fish' such as sandeels to other top predators. Bioenergetics modelling shows that the impact of changes in predatory fish populations are likely to have a far more substantial impact on sandeel stocks than the sandeel industrial fishery and other top predators combined (Furness, 2002). This may not be the case where local populations of sandeels are exploited having a greater impact on top predators with a limited foraging range in the area (Fisheries Research Services, 2003; Furness and Tasker, 2000).

4.2.3 Quantifying diet using bioenergetic models

Several bioenergetic models have been developed to quantify the energetic requirements of a population and to assess the contribution each prey species makes to the diet (Härkönen and Heide-Jørgensen, 1991; Olesiuk, 1993; Laake *et al.*, 2002; Winship *et al.*, 2002). The models contain the following basic elements: pinniped individual energetic requirements, diet composition and population size. There are a number of sources of variation in these elements of the models, for example the energetic requirements of a pinniped will depend on its age and sex, as well as its status, whether moulting, pregnant or lactating, although models can be expanded to take account of this if data are available (Hiby and Duck, 2001; Laake *et al*., 2002). Bioenergetic models vary in how each sample or scat is treated. For example the ratio estimator method (Laake *et al*., 2002) treats the contents of each sample as a random sample of prey. Whereas the 'split sample model' works on the assumption that each scat represents a constant amount of energy intake so despite one scat containing more otoliths the scat sample will be given the same weighting as one containing very few otoliths in calculating the overall diet. Differences in the methodologies used to determine the diet of a population have been found to produce substantially different results (Laake *et al*., 2002; Middlemas, 2003).

4.2.4 Estimating the diet of harbour seals using St Andrews Bay

In this study, diet of the harbour seals using St Andrews Bay was investigated through identifying hard parts recovered from scats collected monthly for 32 months. Published digestion correction factors and allometric equations were used to estimate undigested otolith size and fish length and weight. A bioenergetics model was used to estimate annual prey consumption, in part parameterised by the results of population estimates made in *Chapter 3* as well as from published values.

4.3 METHODODOLOGY

4.3.1 Scat collection

Scat samples were collected between November 2000 and June 2003 from sand banks within St Andrews Bay (*Chapter 2, Figure 2.1*). Collections at all haul-out sites were made monthly, within two hours either side of low tide. Scats were collected, placed in individual plastic bags and stored at –20°C until processed.

To check that the samples collected were as representative as possible of all of the haul-outs within St Andrews Bay, the haul-outs were subdivided into regions and the number of samples collected in each region compared.

4.3.2 Sample processing

Scat samples were thawed and washed through a nest of sieves (5.0, 1.0, 0.l5, 0.25 mm) to collect the hard parts. Prey species were identified from sagittal otoliths and cephalopod beaks using published identification guides (Clarke 1986; Härkönen, 1986; Leopold *et al.* 2001) and an Intel Play QX3 computer microscope with either x10 or x60 magnification. Due to the level of erosion of otoliths it was not always possible to identify otoliths to species level, in which case they were identified to the lowest possible taxonomic grouping.

The length or width of each otolith was measured to the nearest 0.01 mm using digital callipers. Where large numbers of otoliths of a single species were found in a sample, a random sub-sample of 50 otoliths was measured. For cephalopod beaks the upper and lower hood lengths were measured, again to the nearest 0.01 mm using digital callipers.

4.3.3 Quantifying the proportion of the diet by weight and estimation of errors

The size of otoliths prior to digestion was estimated using digestion correction factors. Species-specific digestion coefficients were applied which were derived from captive feeding experiments (*Table 4.1*). Where digestion coefficients were not available for a species, the average value of 1.25 was used (Tollit *et al*., 1997).

Prey lengths were calculated from the undigested otolith lengths or widths using allometric equations (Leopold *et al.,* 2001). Published allometric equations were also used to estimate prey weight (*Table 4.2*), and as with length, the weights of fish consumed were calculated from the estimated undigested otolith dimensions. The estimated weights were then corrected for the number that had not been measured due to sub sampling. Numerical correction factors (NCF) were applied to each species to correct for the proportion of structures that were completely digested (Bowen, 2000). Where species-specific correction factors were not available an average value for the taxonomic group was taken.

A method developed by Hammond and Rothery (1996) was used to estimate the total variance and empirical 95 % confidence limits of the estimated proportion of prey species in the diet. This method uses resampling from a parametric distribution describing measurement error with bootstrap resampling of the observed data. An array is created from the weights of each species and samples are drawn with replacement at random from the array. Resampling was undertaken 1000 times; this was conducted in S-Plus (S-Plus 2000, release 3, Mathsoft Inc) with a programme adapted from Middlemas (2003).

For the bioenergetics model the weights of fish were transformed into energy values using energy densities (Hammond, Hall and Rothery, 1994*b*). A ratio estimator model was used to estimate the proportion of each prey species in the diet of this population of harbour seals. This method assumes that after correction for differential loss of hard parts between species that the contents of the scats are a random sample of those consumed. The model was applied to each quarter of the year separately to account for seasonal variation.

$$\widehat{\pi}_i = \frac{e_i}{\sum_{i=1}^{\omega} e_i}$$

$\widehat{\pi}_i$ = the proportion of prey species *i* in the diet in units energy

e_i = the total energy of prey *i*

ω = the total number of prey species in the sample

(Laake *et al.*, 2002)

Where e_i is :

$$e_{ij} = \sum_{j=1}^{n} w_{ij} d_j$$

w_{ij} = the weight of species i in sample j

d_j = the energy density of species i

n = the total number of otoliths/beaks of species i

To obtain the biomass consumption of each prey species or prey group the following equation is used:

$$B_i = \frac{\xi \pi_i}{e_i}$$

B_i = biomass consumption of prey i

π_i = the proportion of the energy requirement derived from prey i

ξ = total energy requirement of predator population

e_i = energy density of prey i

The corrected counts presented in *Chapter 3* were used to provide the number of seals in the population. The daily energy requirement per capita used was 4680 kcal, taken from Härkönen and Heide-Jørgensen (1991). This figure was calculated from the average daily energy requirement based on measurements of seasonal changes in mass and estimates of energy required for maintenance and growth. Hiby and Harwood (1985) found that in modelling the energetic requirement of the British grey seal population that changes in population size is insufficient for predicting changes in food consumption due to the changes in age structure significantly affecting the energetic demands. The age structure of the population was not taken into account in estimating consumption here because little is known about the population structure of harbour seals in St Andrews Bay. Härkönen and Heidejørgensen (1991) studied the energetic requirement of harbour seals in the Skagerrak based on the variable energetic requirements of different components of the population. This study found that, despite the considerable changes in the population structure pre- and post-phocine distemper virus, the total energetic requirement remained proportional to the total size of the population.

Table 4.1: Digestion coefficients, numerical correction factors and energy densities used in determining diet composition. Digestion coefficients were from Tollit *et al.*, (1997). Energetic densities were from Coull *et al.*, 1989. NCFs were taken from Bowen (2000), ^{1}: average for all non-gadid and non-flatfish species, ^{2}: average gadid, ^{3}: average flatfish, (as used by Middlemas, 2003).

Fish species	Digestion coefficient	Numerical correction factors (NCFs)	Energy densities (kCal)
Cod	1.3	1.26^2	739
Whiting	1.39	1.30	772
Haddock	1.25	1.10	728
Saithe	1.25	1.26^2	794
Pollock	1.25	1.26^2	794
Bib	1.25	1.26^2	1102
Poor cod	1.25	1.26^2	1102
Plaice	1.15	1.60	937
Mackerel	1.25	2.67^1	1587
Herring	1.165	3.00	1587
Sandeels	1.125	3.60	1367
Unid. flatfish	1.19	2.08^3	816
Lemon sole	1.23	2.08^3	772
Sprat	1.15	4.80	1587
Flounder	1.22	2.08^3	728
Dragonet	1.25	2.67^1	970
Bass	1.25	2.67^1	1036
Dab	1.16	2.20	717
Megrim	1.25	2.08^3	720
Brill	1.22	2.08^3	816
Butterfish	1.25	2.67^1	846
Smelt	1.25	2.67^1	880
Turbot	1.25	2.08^3	891
Witch	1.25	2.08^3	882
Eelpout	1.25	2.67^1	795
Goby	1.38	2.67^1	1367
Squid	1.25	1.20	860
Octopus	1.03	1.20	688
Sea trout	1.25	2.67^1	1000
Salmon	1.25	2.67^1	1000

Table 4.2: Species-specific allometric equations (Tollit, 1996*a*).

Fish species	Latin name	Fitted allometric relationship
Cod	*Gadus morhua*	$\ln FW = 5.049 + 4.434 (\ln OL - 2.262) + 0.094/2$
Whiting	*Merlangius merlangus*	$\ln FW = 5.505 + 4.501 (\ln OW - 1.535) + 0.069/2$
Haddock	*Melanogrammus aeglefinus*	$\ln FW = 4.817 + 4.554 (\ln OL - 2.354) + 0.033/2$
Saithe	*Pollachius virens*	$\ln FW = 4.714 + 4.500 (\ln OL - 2.141) + 0.191/2$
Pollock	*Pollachius pollachius*	$\ln FW = 4.195 + 4.204 (\ln OL - 2.051) + 0.024/2$
Bib	*Trisopterus luscus*	$\ln FW = 5.871 + 4.738 (\ln OL - 2.191) + 0.058/2$
Poor cod	*Tricopterus minutes*	$\ln FW = 4.068 + 4.564 (\ln OL - 2.125) + 0.034/2$
Plaice	*Pleuronectes platessa*	$\ln FW = 5.417 + 3.405 (\ln OL - 1.794) + 0.097/2$
Mackerel	*Scombrus scombrus*	$\ln FW = 5.102 + 4.039 (\ln OL - 1.241) + 0.082/2$
Herring	*Clupea harengus*	$\ln FW = 4.572 + 5.191 (\ln OW - 0.574) + 0.064/2$
Sandeels		$\ln FW = 1.122 + 2.710 (\ln OL - 0.595) + 0.038/2$
Unid. Flatfish		$\ln FW = 6.300 + 5.595 (\ln OL - 1.126) + 0.238/2$
Lemon sole	*Microstomus kitt*	$\ln FW = 5.486 + 3.804 (\ln OL - 1.133) + 0.186/2$
Sprat	*Sprattus sprattus*	$\ln FW = 2.539 + 4.695 (\ln OW - 0.056) + 0.058/2$
Flounder	*Platychthys flesus*	$\ln FW = 1.220 + 5.384 (\ln OL - 1.700) + 0.028/2$
Dragonet	*Callionymus lyra*	$\ln FW = 3.256 + 4.459 (\ln OL - 0.894) + 0.077/2$
Bass	*Dicentrarchus labrax*	$\ln FW = 5.706 + 2.362 (\ln OL - 2.331) + 0.021/2$
Dab	*Limanda limanda*	$\ln FW = 4.517 + 4.175 (\ln OL - 1.506) + 0.073/2$
Megrim	*Lepidorhombus whiffiagonis*	$\ln FW = 0.000 + 0.000 (\ln OL - 0.000) + 0.000/2$
Brill	*Scophthalamus rhombus*	$\ln FW = 4.179 + 3.227 (\ln OL - 1.191) + 0.050/2$
Butterfish	*Pholis gunnellus*	$\ln FW = 1.810 + 1.421 (\ln OW - 0.050) + 0.000/2$
Smelt	*Osmerus eperlanus*	$\ln FW = 1.709 + 3.719 (\ln OL - 1.161) + 0.006/2$
Turbot	*Psetta maxima*	$\ln FW = 5.377 + 2.999 (\ln OL - 1.363) + 0.062/2$
Witch	*Glyptocephalus cynoglossus*	$\ln FW = 5.407 + 3.264 (\ln OL - 1.768) + 0.095/2$
Eelpout		$\ln FW = 4.199 + 4.474 (\ln OW - 0.365) + 0.328/2$
Goby		$\ln FW = -0.486 + 5.369 (\ln OW - 0.242) + 0.108/2$
Squid	*Loligo sp.*	$\ln FW = 31.092 + 2.497 (\ln OL - 0.000) + 0.050/2$
Octopus	*Eledone cirrosa*	$\ln FW = 8.251 + 2.337 (\ln OL - 0.000) + 0.050/2$
Sea trout	*Salmo trutta*	$\ln FW = 5.933 + 4.121 (\ln OL - 1.438) + 0.048/2$
Salmon	*Salmo salar*	$\ln FW = 6.119 + 4.155 (\ln OL - 1.478) + 0.039/2$

The individual prey species were subdivided into prey groups for some of the analysis (*Table 4.3*).

Table 4.3: Groups of prey species found in the diet.

Group	Species
Salmonids	Salmon, Sea Trout
Gadids	Cod, Whiting, Haddock, Saithe, Pollock, Bib, Poor cod
Clupeids	Herring, Sprat
Flatfish	Plaice, Lemon sole, Dab, Flounder, Turbot, Witch, Brill
Sandeels	All sandeel species
Cephalopods	All octopus and squid species
Others	Mackerel, Dragonet, Bass, Butterfish, Eelpout, Goby

4.4 RESULTS

4.4.1 Numbers of faeces and otoliths

Nine harbour seal haul-outs in St Andrews Bay were visited 40 times between November 2000 and July 2003; 323 faecal samples were collected, 312 (97%) of those contained otoliths and/or beaks. A total of 33051 otoliths and beaks were recovered and 31 different species were identified from these samples.

Due to a number of months with limited samples sizes (*Figure 4.1*), the data were analysed quarterly. Quarters are taken to be December through to February, March through to May, June through to August and September through to November. The numbers of scats per quarter ranged from 19 to 54 (*Table 4.4).*

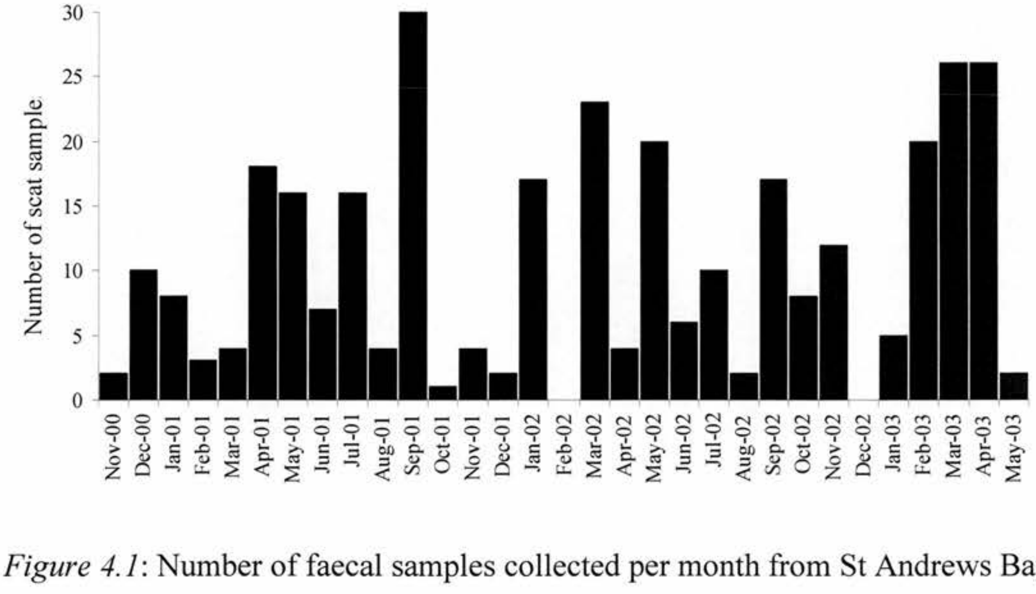

Figure 4.1: Number of faecal samples collected per month from St Andrews Bay.

Table 4.4: Number of faecal samples collected and those that were found to contain otoliths or cephalopod beaks distributed quarterly.

Quarter	Number of Samples	Number of samples containing otoliths
Dec-00 to Feb-01	21	19
Mar-01 to May-01	38	36
Jun-01 to Aug-01	27	26
Sep-01 to Nov-01	35	35
Dec-01 to Feb-02	19	18
Mar-02 to May-02	47	47
Jun-02 to Aug-02	20	20
Sep-02 to Nov-02	37	32
Dec-02 to Feb-03	25	25
Mar-03 to May-03	54	54
Total	**323**	**312**

The number of samples collected from each geographic region was comparable; 81 at haul-outs in the Tay Estuary; 127 in the Eden Estuary and 88 from Abertay Sands (*Chapter 2, Figure 2.1*). Samples were assumed to be representative of animals using all the haul-outs in the St Andrews Bay area. There was however variation in the seasonal representation of each region as can be seen in *figure 4.2*, with higher numbers of samples being collected in Abertay through winter months.

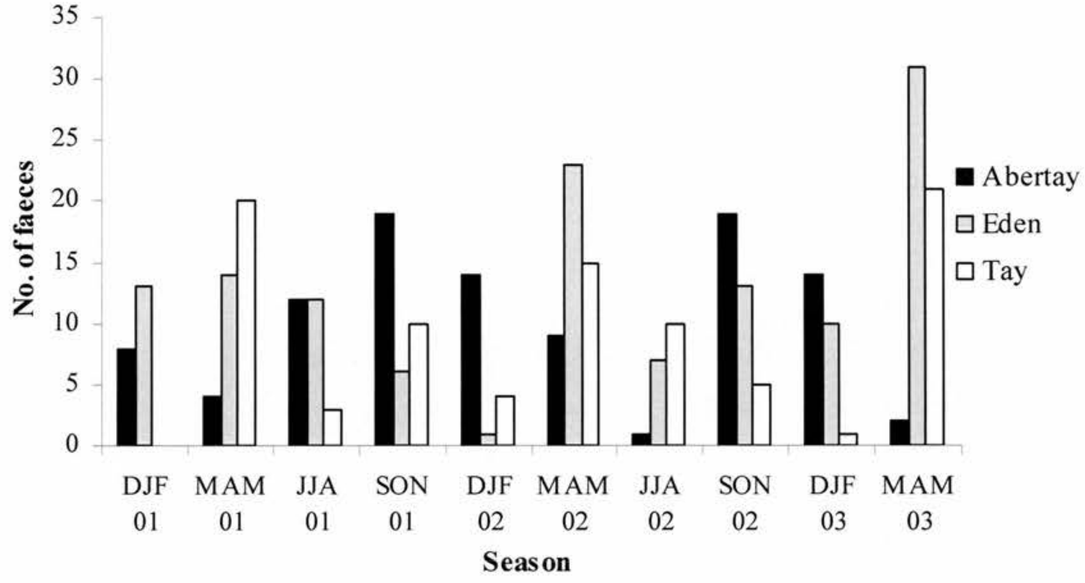

Figure 4.2: Regional and seasonal distribution of faecal samples collected.

Sandeel otoliths were by far the most numerous, 27,772 were recovered in total, followed by whiting (1,028) and otoliths from flatfish that were too small and too digested to identify to species (965) (*Table 4.5*). Cephalopod beaks were rare, with only two squid beaks and 12 octopus beaks being recovered.

Table 4.5: Number of samples, and number of otoliths recovered from each of prey species by quarter.

	2000-2001				2001-2002				2002-2003	
	DJF	**MAM**	**JJA**	**SON**	**DJF**	**MAM**	**JJA**	**SON**	**DJF**	**MAM**
No. of faeces	21	38	27	35	19	47	20	37	25	54
Cod	3	24	4	2	1	6	2	7	-	-
Whiting	427	292	14	5	3	170	2	46	11	58
Haddock	-	6	-	-	-	16	-	6	2	8
Saithe	-	1	-	21	-	1	1	4	-	25
Pollock	-	1	-	2	-	7	-	1	-	-
Bib	-	-	-	-	-	-	1	-	-	6
Poor cod	-	4	-	-	-	4	-	1	-	-
Plaice	19	7	27	22	1	26	3	18	9	34
Mackerel	-	8	-	-	-	-	-	-	-	-
Herring	-	2	2	21	1	10	222	-	-	-
Sandeels	2301	1981	1959	2113	2026	5288	349	1849	5652	4254
Unid. flatfish	25	33	47	46	-	673	3	104	5	29
Lemon sole	-	-	-	1	-	-	-	-	10	-
Sprat	-	-	-	-	-	-	-	1	5	-
Flounder	4	35	48	84	2	58	69	8	-	113
Dragonet	1	-	-	1	1	5	-	1	-	2
Bass	-	1	-	-	-	3	-	-	-	-
Dab	14	11	26	40	2	126	3	8	3	46
Megrim	-	-	-	-	-	-	2	-	6	-
Brill	-	1	-	-	-	-	-	-	-	1
Butterfish	30	9	-	4	-	2	-	27	-	121
Smelt	-	53	-	-	-	20	-	-	-	-
Turbot	-	-	1	-	-	-	-	4	-	-
Witch	-	1	-	11	-	4	-	4	1	6
Eelpout	-	-	-	-	-	-	-	15	-	-
Goby	-	16	15	45	-	33	15	2	2	92
Squid	-	1	-	-	-	-	-	1	-	-
Octopus	2	2	-	-	-	-	-	6	1	-
Sea trout	-	-	-	1	-	15	-	-	-	-
Salmon	-	1	-	1	-	-	7	-	-	39
Haddock/ Saithe	-	-	-	2	-	3	1	-	-	1
Plaice/ Flounder	4	5	2	5	-	-	2	2	-	4

The frequencies of occurrence as a percentage of a set of samples within a quarter are presented in *Table 4.6*. Sandeels were the most frequently observed species, found in 64 % of samples overall, and were present in a minimum of 35 % of samples within any one quarter. Whiting were the next most frequently observed species, found in 25 % of samples overall, and observed in a minimum of 10 % of samples in each quarter. Other species with a high overall frequency of occurrence were flounder (17 %), unidentified flatfish (12 %), plaice (10 %) and gobies (10 %).

Table 4.6: Percentage frequency of occurrence by quarter.

	2000-2001				**2001-2002**				**2002-2003**	
	DJF	**MAM**	**JJA**	**SON**	**DJF**	**MAM**	**JJA**	**SON**	**DJF**	**MAM**
No. of faeces	21	38	27	35	19	47	20	37	25	54
Cod	4.8	7.9	7.4	2.9	5.3	2.1	5.0	5.4	-	-
Whiting	42.9	50.0	14.8	11.4	15.8	34.0	10.0	21.6	24.0	25.9
Haddock	-	7.9	-	-	-	4.3	-	5.4	4.0	5.6
Saithe	4.8	2.6	-	5.7	-	2.1	5.0	2.7	-	1.9
Pollock	-	2.6	-	2.9	-	4.3	-	2.7	-	-
Bib	-	-	-	-	-	-	5.0	-	-	1.9
Poor cod	-	2.6	-	-	10.5	-	5.0	-	-	-
Plaice	14.3	5.3	18.5	8.6	5.3	19.1	5.0	8.1	8.0	11.1
Mackerel	-	2.6	-	-	-	-	-	-	-	-
Herring	-	2.6	3.7	5.7	5.3	8.5	10.0	-	-	-
Sandeels	90.5	73.7	63.0	51.4	94.7	44.7	35.0	54.1	68.0	61.1
Unid. flatfish	9.5	13.2	18.5	11.4	-	29.8	5.0	10.8	8.0	14.8
Lemon sole	-	-	-	2.9	-	-	-	-	4.0	-
Sprat	-	-	-	-	-	-	-	2.7	4.0	-
Flounder	9.5	21.1	33.3	20.0	5.3	17.0	20.0	13.5	-	27.8
Dragonet	9.5	-	-	2.9	5.3	6.4	-	2.7	-	1.9
Bass	-	2.6	-	-	-	2.1	-	-	-	-
Dab	9.5	7.9	25.9	20.0	5.3	12.8	10.0	8.1	4.0	18.5
Megrim	-	-	-	-	-	-	5.0	-	4.0	-
Brill	-	2.6	-	-	-	-	-	-	-	1.9
Butterfish	4.8	2.6	-	5.7	-	2.1	-	2.7	-	5.6
Smelt	-	5.3	-	-	-	4.3	-	-	-	-
Turbot	-	-	3.7	-	-	-	-	2.7	-	-
Witch	4.8	2.6	-	5.7	-	2.1	-	2.7	4.0	3.7
Eelpout	-	-	-	-	-	-	-	2.7	-	-
Goby	-	13.2	14.8	11.4	-	17.0	10.0	5.4	4.0	24.1
Squid		2.6						2.7		
Octopus	9.6	5.2						16.2	4.0	
Sea trout	-	-	-	2.9	-	2.1	-	-	-	-
Salmon	-	2.6	-	2.9	-	-	5.0	-	-	3.7
Haddock/ Saithe	-	-	-	2.9	-	4.3	5.0	-	-	1.9
Plaice/ Flounder	9.5	7.9	7.4	8.6	-	-	10.0	2.7	-	1.9

4.4.2 Prey Size

The size of prey taken by harbour seals found in St Andrews Bay tended to be small. The most abundant prey item was sandeels with a size range of 5 to 25 cm, 90 % falling below 15 cm in length (*Figure 4.3*). Given this size range, these sandeels are likely to be lesser sandeels, *Ammodytes marinus*, *Gymnammodytes semisquamatus* or the inshore species, *Ammodytes tobianus*.

Whiting were the next most abundant prey and although this species can reach lengths of over 70 cm, 90 % of whiting taken by harbour seals were less than 30 cm in length (*Figure 4.3*). The majority of flatfish consumed were between 10 and 30 cm. Gobies were also a frequent prey item and the majority of those consumed were estimated to be between 5 and 15 cm (*Figure 4.3*). The salmon consumed were largely between 10 and 60 cm with a few larger examples that were over 90 cm in length.

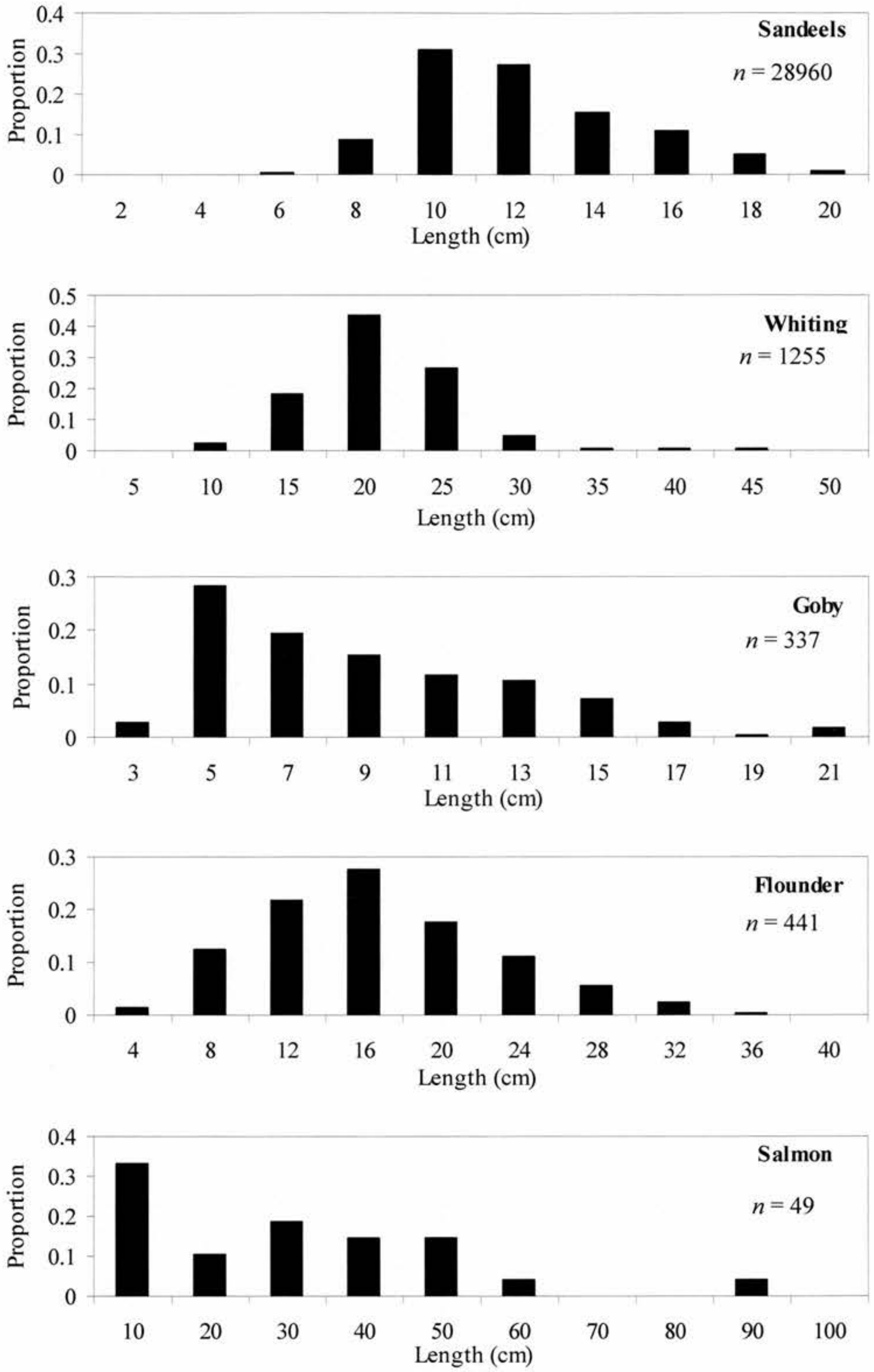

Figure 4.3: Length frequency distributions for the five dominant prey species by weight.

4.4.3 Seasonal trends

Sandeels were the only dominant prey species (by weight) that showed repeated, marked seasonal trends between years. Sandeels were most frequent in the winter months, particularly through December, January and February and less abundant in the summer months (June, July, August) and this pattern was consistent across years (*Figure 4.4*). To determine if this pattern was significant, the frequency of sandeels during the winter quarter (December, January and February) was compared with the frequency observed in the summer quarter (June, July, and August) using a 2-tailed Z test. Sample sizes were the number of scats as given in *Table 4.3*. The difference between these two quarters was found to be highly significant ($Z = -248$, $p < 0.001$).

Although whiting did not show a repeated seasonal trend there appeared to be more found in the diet in the first half of the study period compared to the second. To test this, the frequency of whiting in December 2001 to February 2002 was compared with March 2002 to May 2003, again using a 2-tailed Z test, and found a highly significant difference between the two time periods ($Z = -50$, $p<0.001$).

The percentage, by weight (with 95 % confidence intervals), of each of the 10 major species in the St Andrews Bay harbour seal diet, by quarter, are given in *Table 4.7*. Overall, sandeels were the most dominant prey species (41%), followed by whiting (22%). Despite seasonal variation, sandeels were the dominant species in each quarter. During the quarters when sandeel presence in the diet was relatively low there were higher levels of flatfish including flounder, plaice and dab consumed (*Table 4.7*). Salmon, although absent in most quarters and overall making up less than five percent by weight, had percentages as high as 15.06 % and 26.57 % in June, July, August (2002) and March, April, May (2003) respectively (*Table 4.7*).

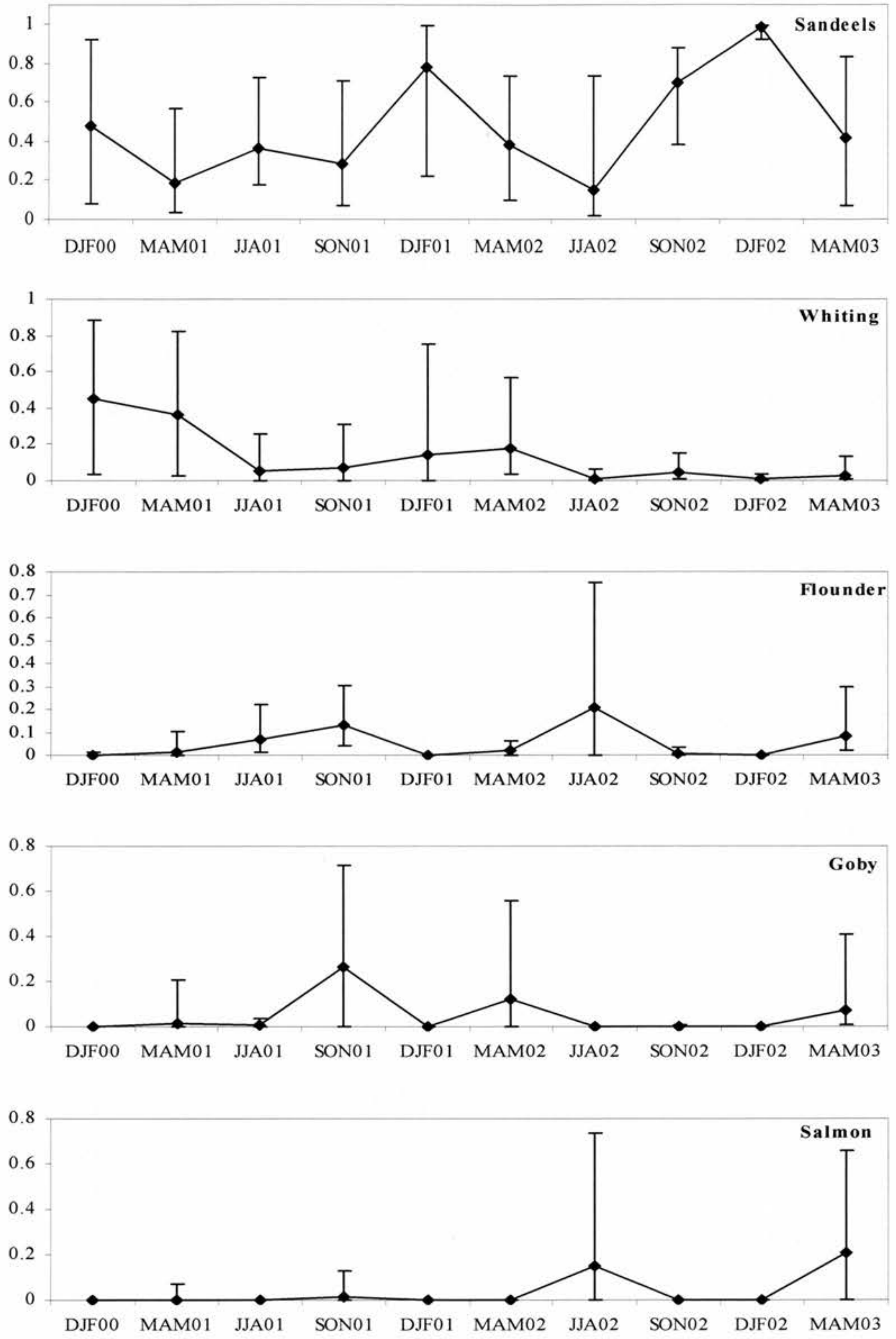

Figure 4.4: Quarterly proportions, by weight, using NCFs (*Table 4.1*), of the main prey species in the diet of harbour seals in the St Andrews Bay Area. The bars around the point estimates are 95 % confidence intervals estimated using the method described by Hammond and Rothery (1996).

Table 4.7: Percentage, by weight, using NCFs, and 95 % confidence intervals for the 10 major prey species items in the diet of St Andrews Bay harbour seals. 95 % confidence intervals are shown in parentheses.

	DJF00	**MAM01**	**JJA01**	**SON01**
Sandeels	48.17 (8.08-91.95)	38.91 (3.45-56.54)	36.02 (18.73-73.31)	28.40 (6.78-70.73)
Whiting	44.79 (3.17-88.89)	36.20 (2.26-81.98)	5.37 (0.10-25.35)	7.07 (0.16-30.98)
Flounder	0.25 (0-1.04)	1.43 (0.14-10.22)	6.75 (1.55-22.22)	13.33 (3.92-30.27)
Goby	0	1.19 (0.00-20.38)	0.39 (0.00-3.83)	26.53 (0.02-55.83)
Salmon	0	0	0.30 (0-13.14)	0
Plaice	0.21 (0-1.63)	0.28 (0-5.48)	5.13 (0.20-17.91)	2.55 (0-11.38)
Dab	1.02 (0-11.20)	0.30 (0-5.22)	5.75 (0.31-28.12)	1.24 (0.30-5.27)
Unidentified Flatfish	1.26 (0-11.30)	0.50 (0.02-4.87)	4.64 (0.23-16.03)	0.92 (0.10-4.10)
Butterfish	0.38 (0-4.48)	0	0	0.19 (0-0.94)
Cod	0.4 (0-7.31)	0.01 (0-0.05)	0.38 (0-3.58)	0.60 (0-7.46)
	DJF01	**MAM02**	**JJA02**	**SON02**
Sandeels	77.81 (22.18-99.42)	38.21 (9.43-73.85)	15.31 (2.19-73.57)	69.82 (38.15-87.39)
Whiting	14.21 (0-75.26)	17.57 (3.36-56.21)	0.51 (0-5.89)	4.76 (1.18-15.22)
Flounder	0.04 (0-0.24)	1.99 (0.26-6.31)	20.99 (0-75.18)	0.95 (0.05-3.61)
Goby	0	12.42 (0.34-55.83)	0.02 (0-0.21)	0.05 (0-0.54)
Salmon	1.25 (0-13.14)	0	15.06 (0-73.76)	0
Plaice	0.02 (0-0.17)	0.57 (0.06-2.55)	0	2.77 (0-10.98)
Dab	0.06 (0-0.52)	1.27 (0.13-4.58)	0.28 (0-2.40)	0.58 (0-4.24)
Unidentified Flatfish	0	10.82 (0.86-36.39)	0.28 (0-2.98)	2.62 (0.02-10.95)
Butterfish	0	0.02 (0-0.08)	0	0.21 (0-1.19)
Cod	0.26 (0-3.69)	0	0	2.98 (0-19.08)

Table 4.7 continued: Percentage, by weight, using NCFs, and 95 % confidence intervals for the 10 major prey species items in the diet of St Andrews Bay harbour seals. 95 % confidence intervals are shown in parentheses.

	DJF02	**MAM03**
Sandeels	98.05 (92.46-99.68)	41.92 (7.41-83.40)
Whiting	0.63 (0.05-3.84)	2.92 (0.64-13.04)
Flounder	0	8.21 (2.00-29.61)
Goby	0	7.04 (0.47-40.73)
Salmon	0	26.57 (0-65.92)
Plaice	0.10 (0-0.59)	0.68 (0.04-2.67)
Dab	0.01 (0-0.11)	1.47 (0.28-6.62)
Unidentified Flatfish	0.50 (0-3.52)	0.99 (0.12-6.09)
Butterfish	0	2.01 (0-6.16)
Cod	0	0

4.4.4 Effect of using numerical correction factors in estimating diet composition

The overall difference in diet composition with and without using NCFs is illustrated in *Figure 4.5*. The main difference is that without using NCFs, gadoids, which have large, robust otoliths, are the dominant prey group but when NCFs are used to correct for complete digestion of otoliths, sandeels become the dominant species by weight in the diet.

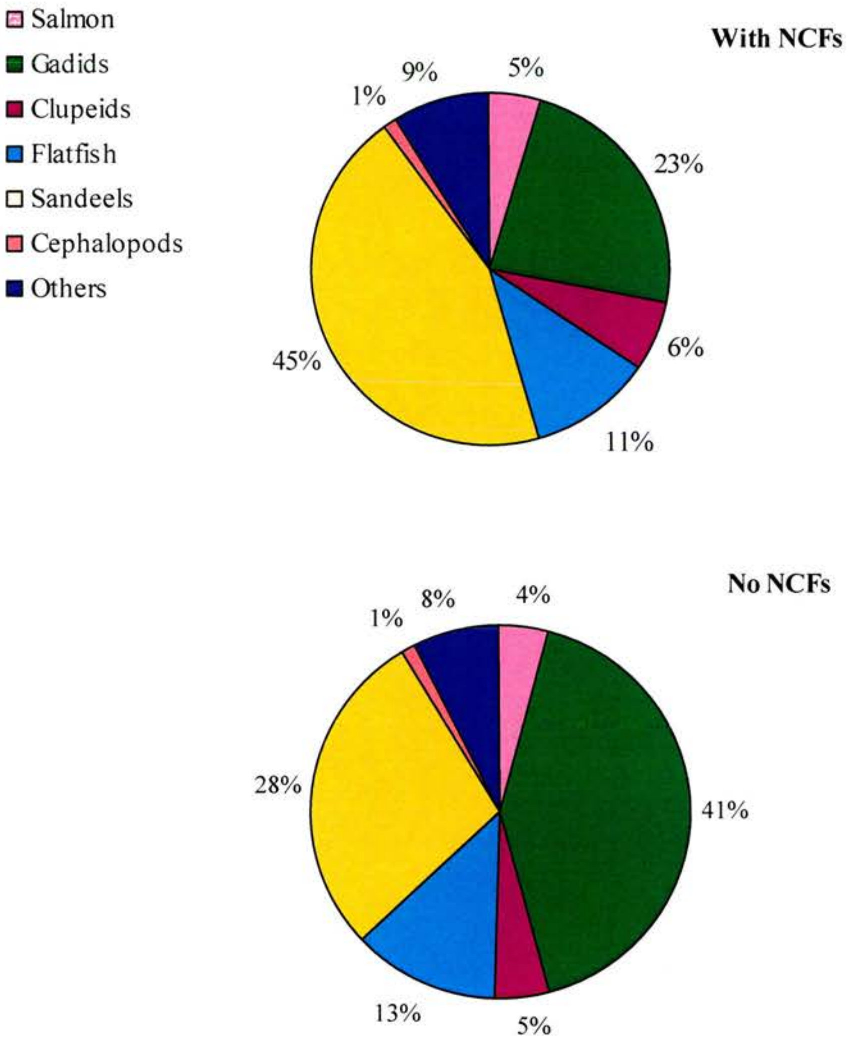

Figure 4.5: Proportion, by weight, that each prey group makes to the diet with and without including NCFs.

The inclusion of NCFs in estimating diet has the effect of increasing the proportion of sandeels and decreasing the proportion of whiting and other gadoids (*Figure 4.6*).

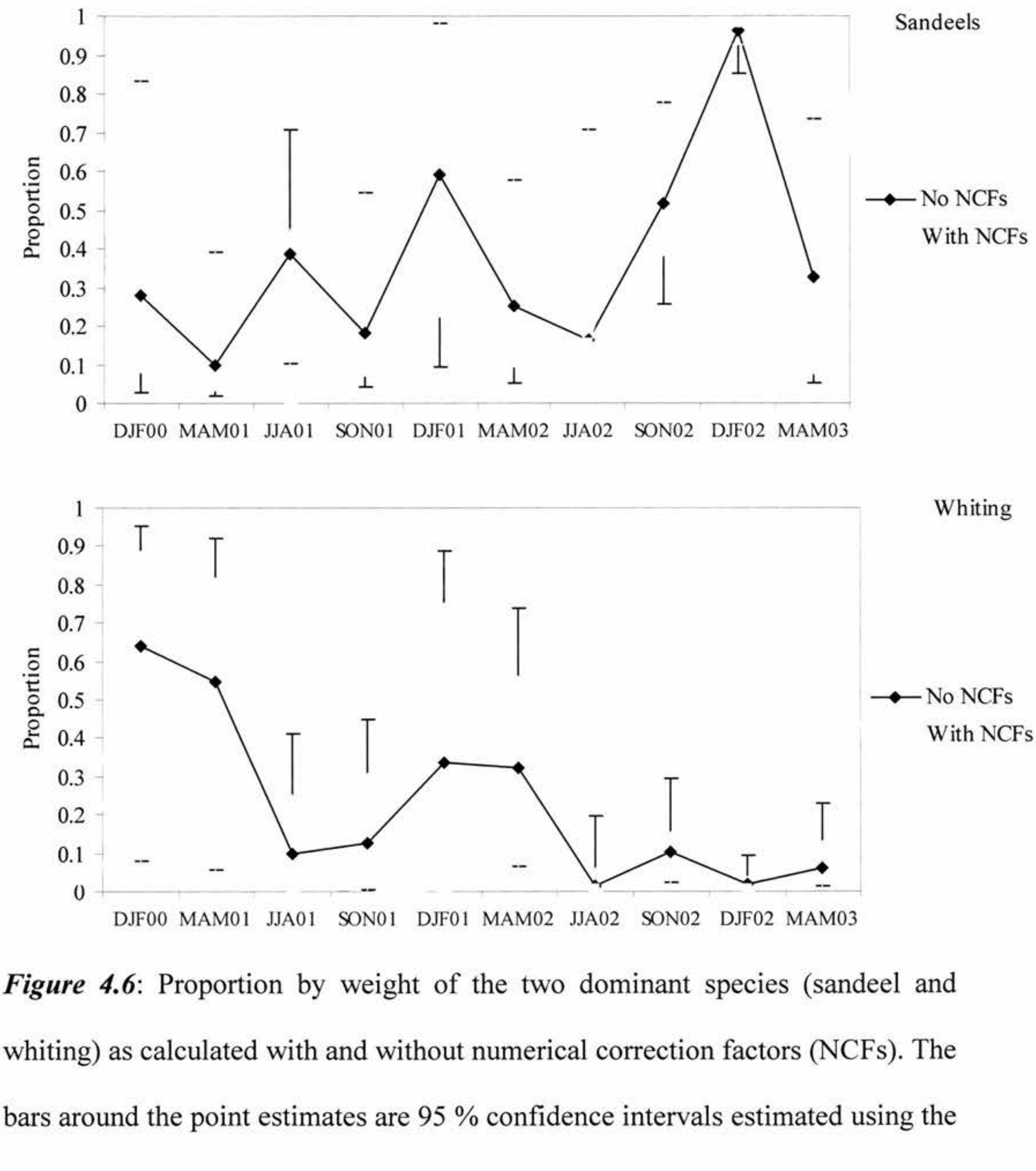

Figure 4.6: Proportion by weight of the two dominant species (sandeel and whiting) as calculated with and without numerical correction factors (NCFs). The bars around the point estimates are 95 % confidence intervals estimated using the Hammond and Rothery (1996) method.

4.4.5 Overall fish consumption estimate

The annual consumption of the 10 major prey species is presented in *Table 4.8*. Sandeels are by far the most dominant species by weight followed by whiting, flounder and goby.

***Table 4.8*:** Total annual consumption using NCFs.

Species	Mean Annual Consumption (tonnes) (95 % confidence intervals)
Sandeels	1521 (1136-2000)
Whiting	560 (263-709)
Flounder	242 (71-426)
Salmon	181 (0-275)
Goby	129 (33-214)
Unidentified flat fish	100 (36-174)
Plaice	65 (22-135)
Dab	41 (17-99)
Cod	15 (2-46)
Butter fish	13 (3-28)

4.5 DISCUSSION

4.5.1 Methodology

There are numerous advantages and disadvantages of using otoliths and cephalopod beaks collected from scats to determine diet and these have been discussed extensively in the literature (Jobing and Breiby, 1986; Jobling, 1987; Hammond and Prime, 1990; Pierce and Boyle, 1991; Cottrell *et al.*, 1996; Hall *et al.*, 1998; Browne *et al.*, 2002; Middelmas, 2003). Some of the main assumptions are summarised here.

1) The scats collected may not be representative of the population as a whole. For example, Härkönen *et al.*, (1999) found that different segments of the population haul-out with different frequencies throughout the summer which will have the effect of creating a bias in the segment of the population that is represented in scat samples in different months. In addition, *Chapter 6* shows that males are travelling significantly further than females, increasing the chance of them defecating at sea before reaching the sand banks. This may also have the effect of over representing the diet of seals foraging near shore and underestimating those foraging at greater distances from the haul-out, particularly males.

2) Not all species consumed are represented in the scat. There have been previous observations of seals not consuming the heads of large fish (Fu *et al.*, 2001; Rae, 1968; Moore, 2003), however these observations were closely linked to fisheries and may not be representative of feeding behaviour in the wild.

3) Otolith digestion rates vary among species. Here the partial digestion of otoliths is accounted for (Prime and Hammond, 1987) as well as estimating the

'measurement' error (Hammond and Rothery, 1996). Otoliths can also be completely digested and here numerical correction factors were used to account for this; however there are few experimental data and average values for fish groups were often used (Bowen, 2000). Digestion coefficeients have been found to vary considerably by species and therefore it is logical to assume that NCFs may well follow this pattern and if obtained could alter the results considerably.

4. Some otoliths recovered may be secondary prey, i.e. they could be from the stomach contents of the primary prey consumed. This could potentially increase the estimated number of sandeels consumed considerably. However, in this and other studies where sandeels have made up a significant part of the diet, it was common to find hundreds of sandeel otoliths in the absence of otoliths from larger species that may be feeding on sandeels (Hammond and Prime, 1990; Hammond *et al.*, 1994).

Despite the potential sources of bias in using this technique the benefits still outweigh those currently provided by other techniques for determining diet. Namely that the technique identifies prey, usually to species level, and provides a means to quantify consumption of different prey species and size in the diet throughout the year. However, there is considerable uncertainty surrounding the estimates of consumption of this population of seals using this technique and results should only be presented alongside an explanation of the various assumptions and sources of bias and error that are associated with them. The uncertainty around estimates of consumption is large in this study due to the relatively low sample sizes in each quarter. To reduce this uncertainty, more frequent visits to haul-outs would be required.

4.5.2 Harbour seal diet in the North Sea

Harbour seal diet has been studied throughout this species range within the North Sea. From this and other studies of the diet of harbour seals in the North Sea it is clear that there is substantial regional variation, although there are some dominant species common to the diet between areas, namely sandeels and whiting. In St Andrews Bay sandeels (41%) and whiting (22%) were the two dominant species in the diet of harbour seals. Further north of this study site in the Moray Firth the diet was also found to be dominated by sandeels (47%), followed by lesser octopus (26%) and whiting (6%), (Tollit and Thompson, 1996). In the southern North Sea in the Wash, whiting (24%) and sole (15%) were the main species, with sandeels being one of the minor components of the diet (Hall *et al.*, 1998). Across in the eastern North Sea, in the Skagerrak, herring, blue whiting and whiting were the primary species in the diet (Härkönen and Heide-Jørgensen, 1991). These studies were conducted across a range of years and some of the differences observed could be attributed to temporal differences rather than regional ones. Its assumed that these prey choices reflect the abundance of locally available prey species (Härkönen, 1987; Thompson 1989; Pierce *et al.*, 1990; Tollit *et al.*, 1997).

4.5.3 Seasonal and between year variation

Seasonal and between year variation has been observed in many studies of harbour seal diet and inferences have been made to explain these findings through prey availability (Härkönen, 1987; Pierce *et al.*, 1991; Tollit and Thompson, 1996; Hall *et al.*, 1998; Brown and Pierce, 1988; Middlemas, 2003). Sandeels were the dominant prey species throughout the year in St Andrews Bay, however significantly more were consumed in winter months. These findings are in contrast to those reported in the Moray Firth (Pierce *et al.*, 1991*a*), where sandeels dominated in the summer and clupeids dominated in winter months. It was suggested that when sandeels hibernate in the sediment over winter they are decreased in availability and at this time clupeids migrate inshore in the winter and are increased in availability and hence the prey switch. The results presented from St Andrews Bay suggest that sandeels are more available in winter months and this could be due to sandeels being more available in December and January when they are spawning (there are sandeel spawning grounds throughout St Andrews Bay) (Holland *et al.*, 2002). Another possibility is that when sandeels are dormant in the sediment they are more available to seals, possibly requiring less energy to capture than in the summer months when they are mid water. The prey switch observed in the Moray Firth could be explained by the greater availability of clupeids when they migrate inshore and their slightly higher calorific value compared to sandeels (*Table 4.2*).

Whiting were consumed in significantly lower numbers throughout the second half of the study period in 2002 and 2003. Commercial whiting landings have been steadily declining since the 1980s; 2002 saw the lowest catches of whiting ever recorded (FRS, 2004). The drop in landings between 2001 and 2002 is insufficient to explain the differences observed in seal diet and the majority of the commercial whiting catch occurs to the east of Shetland (FRS, 2004) outwith the St Andrews Bay study area. There are whiting spawning grounds throughout St Andrews Bay (FRS, 2004) and high numbers of immature fish are found around the Scottish coast which would support the small fish sizes observed in the diet (*Figure 4.2*).

4.5.4 Seal consumption in relation to commercial fish catches.

Sandeels are an important forage species for numerous marine predators, gadoids and sea birds consuming far more than seals (Fisheries Research Services, 2003). Sandeels also support the largest fishery in the North Sea with landings in the order of a million tonnes (Holland *et al*., 2002). The population of harbour seals in St Andrews Bay is estimated to be consuming 1521 (95% CI = 1136-2000) tonnes of sandeels annually. There is little concern expressed over seals depleting these stocks, however concern has been expressed about the effects of local concentrated fishing effort on the predators in areas where they congregate (Fisheries Research Services, 2003; Furness and Tasker, 2000). Due to concern over poor breeding success in kittiwake populations, the sandeel fishery off the east coast of Scotland was closed in 2002-2003 and is being monitored annually to assess whether it could be re-opened (Fisheries Research Services, 2003). Sandeels were found to be the most important prey item in the harbour seals diet in St Andrews Bay and if fisheries have depleted local sandeel aggregations in this area there may be adverse effects on the population of harbour seals in this area. Results on seal movement presented in *Chapter 5* indicate that seals are foraging in areas used by the sandeel fishery, a large sand bank complex known to have high concentrations of lesser sandeels.

Whiting is ranked the forth most important demersal fish to the Scottish fishing fleet. In the North Sea whiting is also one of the most important predators of commercially important fish (Fisheries Research Services, 2004). Norway pout, sandeels, haddock, cod and whiting themselves are frequently preyed upon. It has been estimated that each year the whiting population consumes several hundred thousand tonnes of these species in the North Sea. Commercial landing of whiting in the North Sea are approximately 200 thousand tonnes (Fisheries Research Services, 2004). The consumption of 560 (95 % CI = 263-709) tonnes annually consumed by the harbour seal population in St Andrews Bay would seem relatively minor.

Harbour seals in this area were not found to be consuming large quantities of other commercially important prey species such as cod (15, 95 % CI = 2 - 46 tonnes) or haddock (4, 95 % CI = 0 - 13 tonnes) and their consumption of whiting may actually help to improve the stocks of such species through reducing whiting numbers. Increasing importance is being placed on an ecosystem approach in fisheries management to understand the effects of multi-species interactions.

There has been concern expressed over the impacts of pinniped predation on stocks of salmonids (Harwood and Croxall, 1988). In St Andrews Bay the importance of salmon to the overall diet of harbour seals appears to be relatively minor, contributing 5% by weight. Salmonid otoliths were largely found in those scats collected at haul-outs in the Tay Estuary in spring and summer months but not consistently across years, possibly due to the scarcity of samples. The estimated biomass of salmonids consumed per year by the population of harbour seals in St Andrews Bay was 198 tonnes (95 % CI = 0 - 295). The recorded rod and line catches of salmonids in the Tay Estuary in 2001 were 27 tonnes (Fisheries Research Services, 2004). The total biomass of salmonids using the estuary can only be coarsely estimated, (with no confidence intervals) from these rod and line catches. These estimates are based on Salmon returning in the spring (January to April) being easier to catch compared to those returning later in the year. Abundance is estimated by assuming 30 percent of spring (January to April) fish are caught by anglers (Youngston *et al.*, 2002) and during the summer and autumn this number is reduced to 11 percent (Crozier and Kennedy, 2001). Using these assumptions, the estimated biomass of salmonids using the Tay Estuary in 2001 was 304 tonnes. Using this estimate of harbour seal diet and consumption of salmonids, we can infer that harbour seals may be consuming as much as two thirds of the available biomass. However the wide confidence intervals should be noted.

Figure 4.7 illustrates the seasonal distribution of salmon otoliths found in this study. One salmon ototlith was found in a sample collected at Abertay Sands in September in 2001. All other samples containing salmon otoliths were collected from banks in the Tay Estuary. The majority of otoliths being found in three faeces samples collected in April 2003 and July 2002.

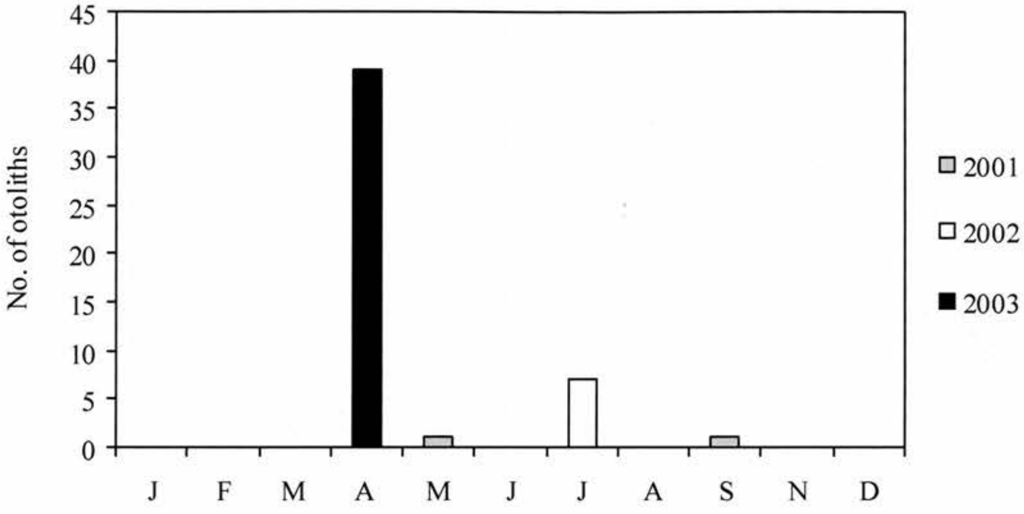

Figure 4.7: Seasonal distribution of salmon otoliths in samples.

The number and geographical distribution of samples in this study are insufficient to be able to say whether the few faecal samples with salmon otoliths present are representative of the population or whether they are from a few individuals specialising on salmonids biasing results.

The otoliths of salmonids are very small and fragile (Boyle *et al.*, 1990) and more maybe completely digested than those corrected for here. The NCFs used were not derived through species-specific experiments and may be underestimated in this case. It has also been suggested that seals may not be eating the heads of large fish such as salmon (Pitcher, 1980; Boyle *et al.*, 1990). The majority of salmon consumed in this study were relatively small, under 60 cm, however there were fish larger than 90 cm consumed so the heads were consumed in this instance (*Figure 4.3).*

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CHAPTER FIVE:

Distribution and habitat use of harbour seals from St Andrews Bay.

5.1 ABSTRACT

The at-sea distribution of harbour seals on the south east of Scotland was investigated using satellite telemetry. 25 animals were tracked between November 2000 and August 2002. This study was the first time that satellite telemetry had been used on harbour seals in Britain and animals were found to be foraging further from haul-outs than previously thought. Foraging activity was densely aggregated into 'hot-spots' of localised foraging activity between 10 and 70 km from the haul-outs.

Telemetry data poses several analytical problems and here data were resampled to represent each individual equally and give locations that could be treated as independent. The distribution of seals was modelled using a binomial generalized linear model including a null model of accessibility, bathymetric and substrate features as explanatory variables. Harbour seals selected sandy substrates with higher percentages of gravel and lower percentages of mud than available. This describes the habitat used by sandeels to burrow, harbour seals main prey species in this area (*Chapter 4*).

5.2 INTRODUCTION

5.2.1 Importance of determining the at-sea distribution of marine mammals

Studying the at sea distribution of seals is of interest not only to helpbecause it helps understand the ecology of the species and how they obtain enough food to survive, but also to inform their conservation and management. In determining the overlap with fisheries and other human activities, maps of at-sea usage could be used in combination with maps of fishing effort to help determine the overlap with fisheries. Under European Union legislation (Council Directive (92/43/EEC) on the Conservation of Natural Habitats and Wild Fauna and Flora), studies of seals at sea are valuable in the context of determining the location and effectiveness of Special Areas of Conservation (SACs). SACs for harbour seals are currently based on terrestrial sites and the extent that they extend into the sea is determined arbitrarily, for example to the 15 m depth contour. Information on the distribution of seals at sea could help delineate an area that would incorporate a given proportion of the populations' at-sea distribution (Matthiopoulos *et al.*, 2004).

In response to European legislation the UK Department of Trade and Industry (DTI) undertakes Strategic Environmental Assessments (SEA) before licensing oil and gas exploration and production. Information on the distribution of marine mammals is needed to inform this process (Hammond *et al.*, 2001, 2002, 2003). Matthiopoulos *et al.*, (2004) used the results of satellite telemetry on grey seals as well as information on the size of the population to determine the population's at-sea usage. This information has been used in SEAs to estimate the percentage of the population's usage within the boundaries of an SEA area. For example, the percentage of the British grey seal population's at-sea usage in SEA 2 area was approximately 1% indicating that activities in the area would have no great impact on the population (Hammond *et al*., 2001). However, SEA 5 was found to contain 39 % of the British grey seal population's at-sea usage and the area to the east of Orkney, Shetland and mainland Scotland was identified as an extremely important area for grey seals (Hammond *et al*., 2003).

5.2.2 Studying at-sea distribution.

Numerous recent studies have used satellite telemetry to provide insights into the offshore behaviour of many species of seal using satellite telemetry (e.g. McConnell, 1986; Stewart *et al*., 1989; McConnell *et al.,* 1992; Folkow, Martensson, and Blix, 1996; Campagna, Fedak & McConnell, 1999; Le Boeuf *et al.,* 2000; Field *et al.,* 2001; Lowry, *et al*., 2001; McConnell *et al.,* 2002; Harcourt *et al.,* 2002; Hindell *et al.,* 2003; Bradshaw *et al*., 2004). These studies have been possible due to the many advances made with telemetry and in the reduction of the size of transmitters (e.g. Fancy *et al.,* 1988; McConnell *et al*., 1986; Stewart *et al.,* 1989; Fedak *et al*., 2002).

The study of seals used to be restricted to their activity at haul-outs and limited to direct observations at sea. Conventional radio telemetry has been used to good effect to study the at-sea distribution of harbour seals in various locations throughout its range (*e.g.* Pitcher and McAllister, 1981; Brown and Mate, 1983; Thompson and Miller, 1990; Thompson *et al*., 1991; Thompson, 1993; Bjørge *et* *al*., 1995; Suryan and Harvey, 1998). These studies found that harbour seals feed locally to haul-outs, rarely travelling further than 25 to 50 km. This technology is however limited in its range to line of sight and therefore some further ranging movements may have gone undetected, seals were not able to be located on all days of some of these studies.

In St Andrews Bay and Orkney, similar studies using VHF radio telemetry to track harbour seals failed to cover the full range of the species distribution. In south east Scotland grey seals have been studied using satellite link telemetry with service Argos (Hammond, McConnell and Fedak, 1993; McConnell *et al*., 1999). Technical advances to reduce the size of satellite relay data loggers (SRDLs) have now permitted the study of harbour seals using satellite telemetry. Lowry *et al.,* (2001) used satellite tracking on harbour seals and found that although the mean haul-out to at-sea distance was 5 to 10 km for adults and 20 to 25 km for juveniles, distances of up to 140 km offshore were recorded and some of the juvenile seals were recorded moving up to 500 km to different haul-out sites.

5.2.3 Habitat selection

Quantifying habitat preference is of key importance when studying a species as it provides fundamental information about the nature of how they meet their requirements to reproduce, survive and persist (Manly *et al*., 1993). Habitat preference is not a straightforward concept to measure. It is not directly observable; it is behavioural, and based on how an animal perceives its environment and how it responds to it. The question being approached in this study was that of habitat selection, defined as resources being used disproportionately to their availability (Manly *et al.*, 1993).

Several studies have used the usage of an area and correlated this directly with environmental variables. The main assumption of this is based on is that all points in space are freely accessible to the animal, which implies unlimited speed of movement or unlimited time for movement (Manly *et al.*, 1993). This assumption might be valid for some free ranging species such as some species of cetacean but not for many species of pinnipeds. This assumption is particularly violated in this instance, as harbour seals are central place foragers, they return to a central place to haul-out in between foraging trips (Matthiopoulos, 2003). Therefore, how availability is determined needs to be considered carefully. Incorrect determination of what habitats are available can lead to an incorrect measure of habitat selection.

5.2.4 Problems associated with the analysis of telemetry data.

Methods of data collection such as VHF and satellite telemetry give rise to several problems in the statistical analysis of the data. Telemetry data provide sequential observations of an animal's position. For each of these locations to be used as independent measurements of an animals' use of an area, the observations must be separated by sufficient time to move between any two points within the study area. Otherwise the animal will be selecting from habitats that are smaller than the defined study area and observations separated by short time intervals will be autocorrelated. If every location were used and treated as independent, the variances of resulting estimates will be artificially small, so null hypotheses are rejected more frequently than at a specified error rate (Neter *et al*., 1985).

The sampling effort is not likely to be balanced between individuals. Different tags provide different numbers of observations due to differences in the duration the tag remains functioning on each animal and to the behaviour of the animal which could facilitate or impede uplinks. It is usually the case that, due to financial and/or logistical constraints, only a very small proportion of the population is tracked. Caution therefore needs to be exercised when inferring population behaviour from a small sample of animals (McConnell *et al.,* 1999).

In this study the problems of serial and temporal autocorrelation in the telemetry data are overcome through resampling of observations. This gives a sample of data that can be treated as independent observations permitting the distribution of foraging activity of individuals to be reliably described, as well as giving each individual equal weighting despite differences in the quantity of data received from different individuals.

5.3 METHODOLOGY

Information on the study site and details of the capture and handling of animals to deploy SRDLs, as well as a description and programing of the SRDLs can be found in *Chapter 2*: Materials and Methods.

5.3.1 Classifying foraging activity

The information collected in this study is insufficient to positively confirm successful foraging events and where they occur as can be done through recording stomach temperature, jaw movements or from camera footage. In this study areas where slower speeds of travel occur were inferred to be areas likely to be important for foraging.

The locations from the SRDLs on seals received by Argos satellites are irregular through time and have error associated with them. For this reason locations were smoothed using a filter developed by Lonergan (unpublished, *Chapter 2*). Locations were then interpolated along the smoothed track, in this case giving locations every two hours.

In this study only those locations thought to be associated with foraging were of interest. To separate at-sea behaviour from near haul-out behaviour the two hourly activity summary data were used (*Chapter 2*). These data consist of the percentage time hauled out, diving or at the surface for each two hourly period, as well as two hourly summaries of dive behaviour. An animal was classified as 'near haul-out' as soon as the percentage time hauled out was greater than zero and classified as 'at sea' as soon as the average dive depth in a two hour period was deeper than 10 metres. The use of alternative haul-out sites was tested for by plotting haul-out events onto the filtered tracks and seeing where they occur.

The locations at sea were classified into 'fast movements at sea' (FAS) or 'slow movements at sea' (SAS) (McConnell *et al.*, 1999). SAS locations were assumed to be indicative of foraging and FAS locations indicative of travelling. Travel rate was explored through visualising tracks using the MAMVIS computer visualisation system (Fedak *et al.*, 1996). Clear trips were evident in the visualisation with directed travel to assumed foraging areas where animals remained for up to ten days. Frequency distributions of speeds of travel, excluding those near the haul-out, were plotted to see if there was a bimodal distribution from those associated with travel and those associated with foraging. Speed of travel was calculated from the filtered track by calculating the length of the hypotenuse between each point. The sensitivity of the threshold was tested for by looking at the separation of the data into SAS and FAS if a slower or faster speed was chosen. The density and distribution of foraging locations could then be presented.

5.3.2 Re-sampling of foraging locations

Data were resampled so that the resulting locations could be treated as independent. Foraging (SAS) locations were resampled taking one location at random per average trip duration (3.2 days); this amounts to 3.4 % of locations from the interpolated tracks. Data were resampled with weightings to compensate for the different frequency of uplinks and in the duration of the tracking period. SAS locations were randomly sampled without replacement with the same number of locations for each individual. The sample size used for the resampling from each individual was the number of 3.2 days in the duration of the animal with the shortest tracking duration. The resultant locations were then treated as independent and were assumed to be representative of the population as a whole.

5.3.3 Environmental data

The environmental information used was sediment type (percentage gravel, sand and mud) and depth (metres) in the format of a 1 x 1 km grid (British Geological Survey, 1989). The area for analysis was a rectangle that encompassed the furthest reaching foraging locations. The resampled foraging locations were converted to a density grid of the same extent. A grid of biological distances from the haul-outs was also constructed, taking into account obstructions to movement, in this case land.

5.3.4 Habitat selection

The environmental characteristics of those areas used for foraging relative to all grid cells were compared. The study area was divided up into 20 km distance bands from haul-outs. Frequency distributions of depths and sediment types were created for each distance band. Co-linearity was tested for between variables and the frequency distributions were compared using Mann-Whitney tests. As multiple tests were used the p-values were penalised using Bonferroni corrections.

A null model was generated to reflect accessibility of locations, this was the same as that determined for grey seal movement by Matthiopoulos (2004). This takes the form of the inverse of biological distance from haul-out squared.

The response variable used in a generalized linear model (GLM) was the presence/absence of seal foraging activity in a grid cell. The null distribution was included as a covariate in a GLM; an approach that helps quantify the power of the null model in explaining the observed usage distribution (Matthiopolous, 2003). The GLMs were fitted to the data with a binomial error distribution using the penalized quasi likelihood method with a logit link function. Other covariates included in the model were sediment type and depth. The most parsimonious model was found using backwards-stepwise selection, the AIC (Akaike information criterion) value was used in model selection. Variance Inflation Factors were used to correct the significance of relationships due to the degree of colinearity between some of the explanatory variables.

5.4 RESULTS

5.4.1 Telemetry

Twenty-five seals were caught between November 2001 and March 2003, mean tracking duration was 131 days, with a range of 86 to 202 days. Details of SRDL deployment are given in *Table 2.1*, *Chapter 2*.

5.4.2 Movements

All but one animal showed repetitive trips to foraging areas returning to within 10 km of the site where they were captured to haul-out. The one exception was a sub-adult male harbour seal, DM, which weighed 51 kg. The movements of this animal are shown in *Figure 5.1*. Seal DM was captured in the Eden Estuary and from here explored the Firth of Forth before remaining in Leith Docks for three weeks. After an extended trip into the North Sea (230 km) it spent four months in the docks in Newcastle upon Tyne. There were reports of fishermen feeding the seal. Our last report of the animal was that it had fishing net around it's neck. The animal was not recovered, but is assumed to have died. This seal was not included in further analysis because the behaviour of scavenging and remaining in docks without going to sea was not thought to be representative of a healthy harbour seal.

The tracks of individuals GF and KF are two typical examples of the type of movements made by animals in St Andrews Bay (*Figure 5.1*). Animals returned repeatedly to the same site off shore to forage and returned to the same haul-out. Seal GF was the only animal that followed the coastline to a foraging site. 16 of the 25 animals tracked follow this pattern of returning repeatedly to the same foraging area, although they vary in the distance travelled to forage. Three animals tracked were found to use two distinct foraging areas.

The track of seal IF shows the same repeated trips to a foraging site, but also exhibits further ranging movements, that might be inferred as exploratory trips or following prey (*Figure 5.1)*. Four other seals tracked also exhibit these further ranging movements as well as repeated trips to one specific area. Seal YF shows very localised foraging, at this scale it is difficult to filter out the error in the locations received by the Argos satellites. The track shows fairly dispersed trips locally along the coast but there may be a more distinct foraging area being used that is not reflected in the filtered track. The smoothed tracks of all animals are shown in *Appendix 1*.

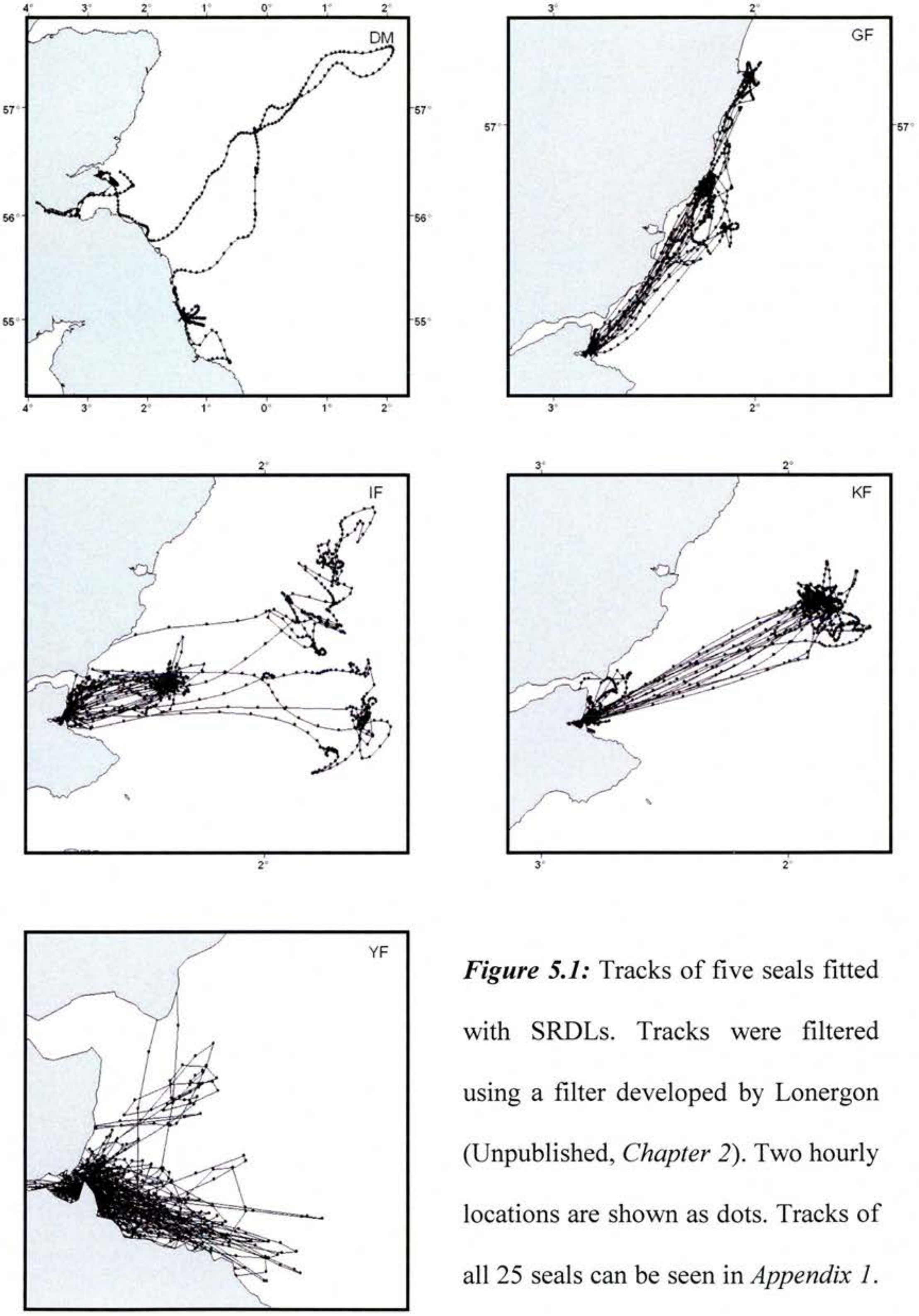

Figure 5.1: Tracks of five seals fitted with SRDLs. Tracks were filtered using a filter developed by Lonergon (Unpublished, *Chapter 2*). Two hourly locations are shown as dots. Tracks of all 25 seals can be seen in *Appendix 1*.

5.4.3 Foraging classification.

Part of the methodology used in classifying locations into foraging activity uses the distance from haul-outs to separate the slow speed activity associated with near haul-out behaviour. The haul-out events presented in *Figure 5.2* illustrate that seals don't appear to be using alternative haul-outs despite foraging close to the coast (*Figure 5.1* – GF) or foraging close to Bell Rock, an offshore area of rock exposed at low tide highlighted in *Figure 5.2*. There are three areas in close proximity being used to haul-out, the Eden Estuary, Abertay Sands and sand banks at Broughty Ferry. The scattering of locations around these is likely to be largely due the amount of error inherent in the locations and the filter being unable to correct for all of this as discussed in *Chapter 2*.

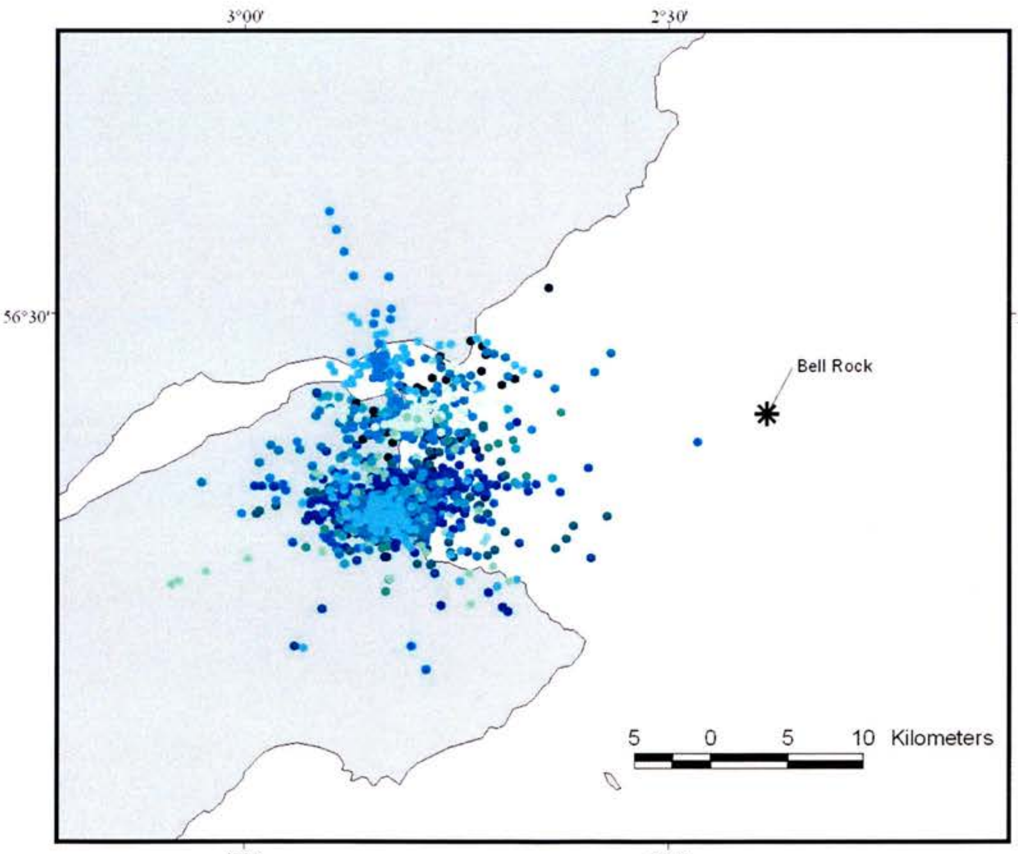

Figure 5.2: Filtered locations of haul-out events. Different shades represent different individuals.

Speed of travel was used to separate locations thought to be associated with foraging and travelling. The rate of travel that appeared to be the most appropriate threshold separating travelling and foraging using the MAMVIS visualisation system (Fedak *et al.*, 1996), fell between 0.4 and 0.6 m s^{-1}.

There was no discontinuity in the frequency distribution of travel rates (*Figure 5.3*).

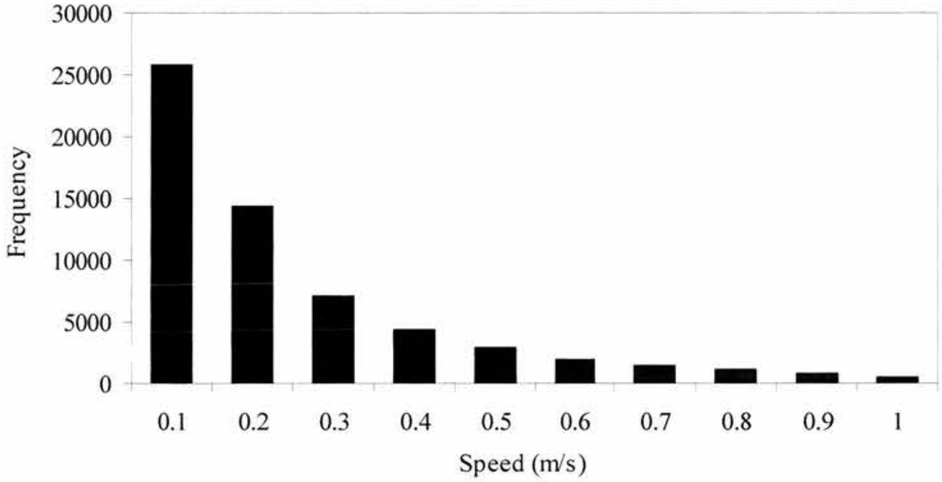

Figure 5.3: Frequency distribution of travel rates at sea.

However when plotting only the speeds of travel from those individuals making longer ranging trips (greater than 40 km) a discontinuity became apparent (*Figure 5.4* and *5.5*).

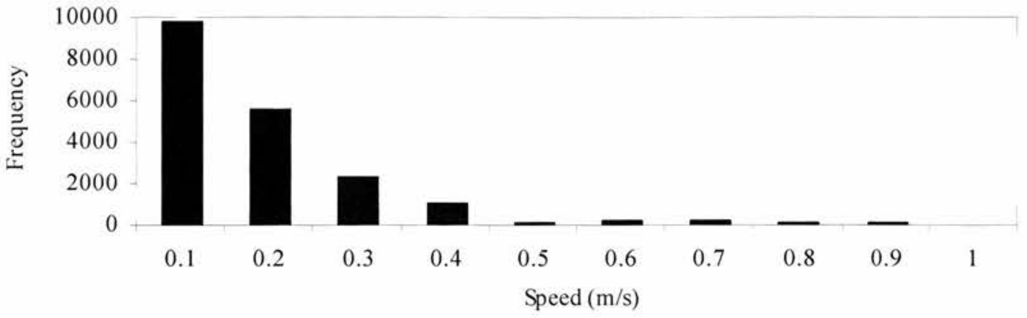

Figure 5.4: Frequency distribution of travel rates associated with animals making further ranging foraging trips (greater than 40 km).

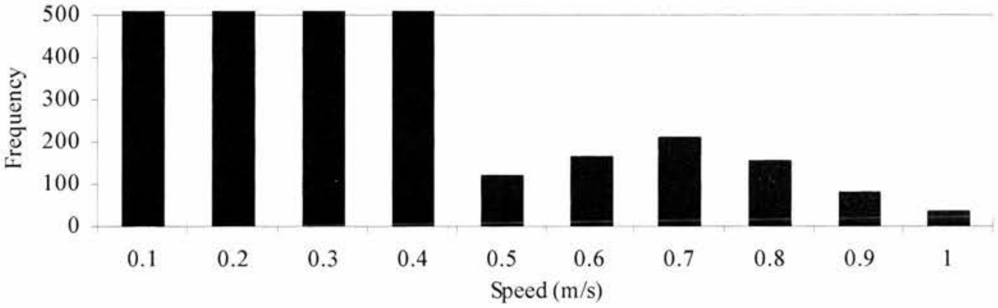

Figure 5.5: Frequency distribution of travel rates associated with animals making longer ranging foraging trips (greater than 40 km), with adjusted scale to illustrate the discontinuity in the distribution.

There was a clear bimodal distribution, the separation between the distributions falling at approximately 0.5 m s^{-1}, confirming the findings observed using MAMVIS. Using this threshold assumes that those animals making shorter foraging trips are travelling at the same speed as those travelling to greater distances. This may not be the case but the degree of error in the locations received from Argos makes it impossible to distinguish a travelling phase when small distances are involved. Speed of movement was estimated from filtered locations. Speed of travel plotted when looking at unfiltered locations has no clear pattern as above, with a much greater proportion of higher speeds of travel associated with low quality locations.

Table 5.1: Sensitivity in selection of threshold speed to distinguish between travelling and foraging

Threshold speed of travel	Near haul-out	Slow at sea movement	Fast at sea movement
0.4 m s^{-1}	38.7 %	48.3 %	6.94 %
0.5 m s^{-1}	38.7 %	51.9 %	9.43 %
0.6 m s^{-1}	38.7 %	54.4 %	13.0 %

5.4.4 Distribution of foraging effort

The SAS locations (those locations with a rate of travel slower than 0.5 m s^{-1}) are presented in *Figure 5.6*. It is clear that there are some areas of dense foraging activity and that foraging is not evenly dispersed across the study area. The majority of foraging for the sampled seals occurred within 75 km of the haul-outs.

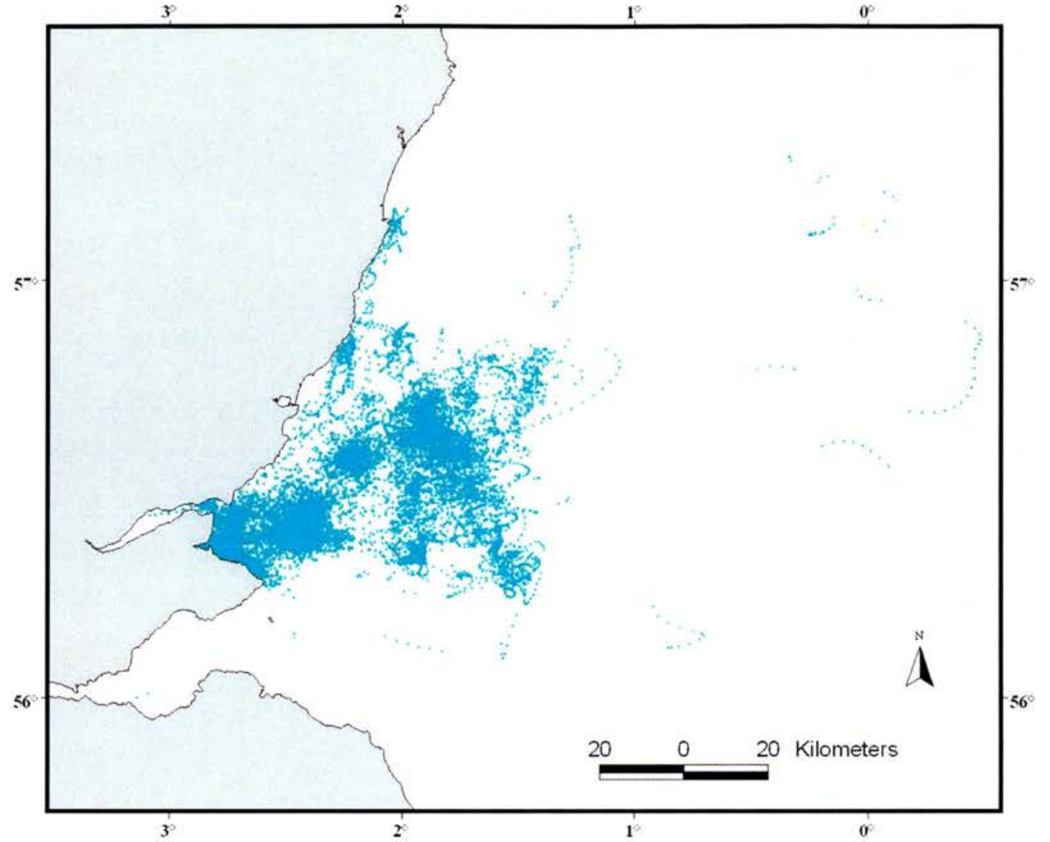

Figure 5.6: *A*ll slow at sea locations (< 0.5 m s^{-1}) inferred to be foraging.

The average SAS location density in each 1 km^2 cell is shown in *Figure 5.7*. Any bias in density that could be caused by seals being tracked for different durations has been removed by using the percentage of points per cell for each individual. This highlights four areas that appear to be 'hot spots' of foraging.

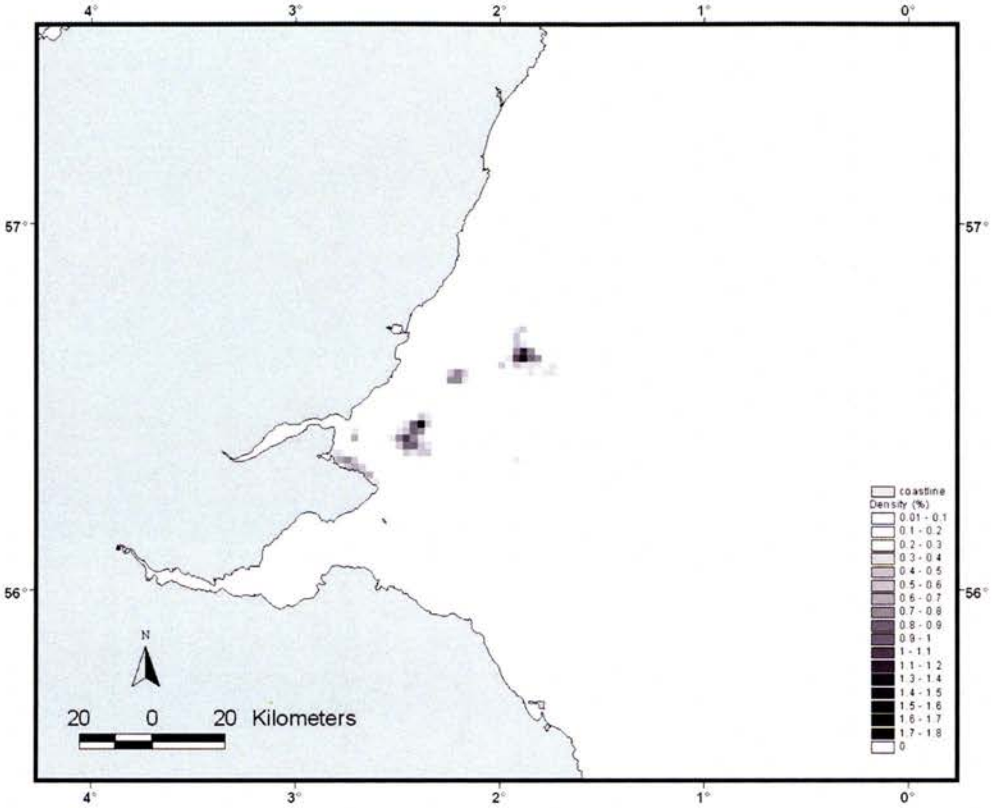

Figure 5.7: Mean percentage density of SAS locations per 1 km^2 for all seals.

A Kernel home range has been fitted to the locations in *Figure 5.8* to further illustrate these 'hot-spots'; 95 % of SAS locations were included within the black areas and 50 % included within the grey areas.

Four foraging 'hot-spots' are apparent, labelled one to four. The two grey areas next to the coast to the north of the haul-outs are from a single seal, GF (*Figure 5.1*). This female did not use the main foraging areas and exhibited very focused foraging activity in these two areas.

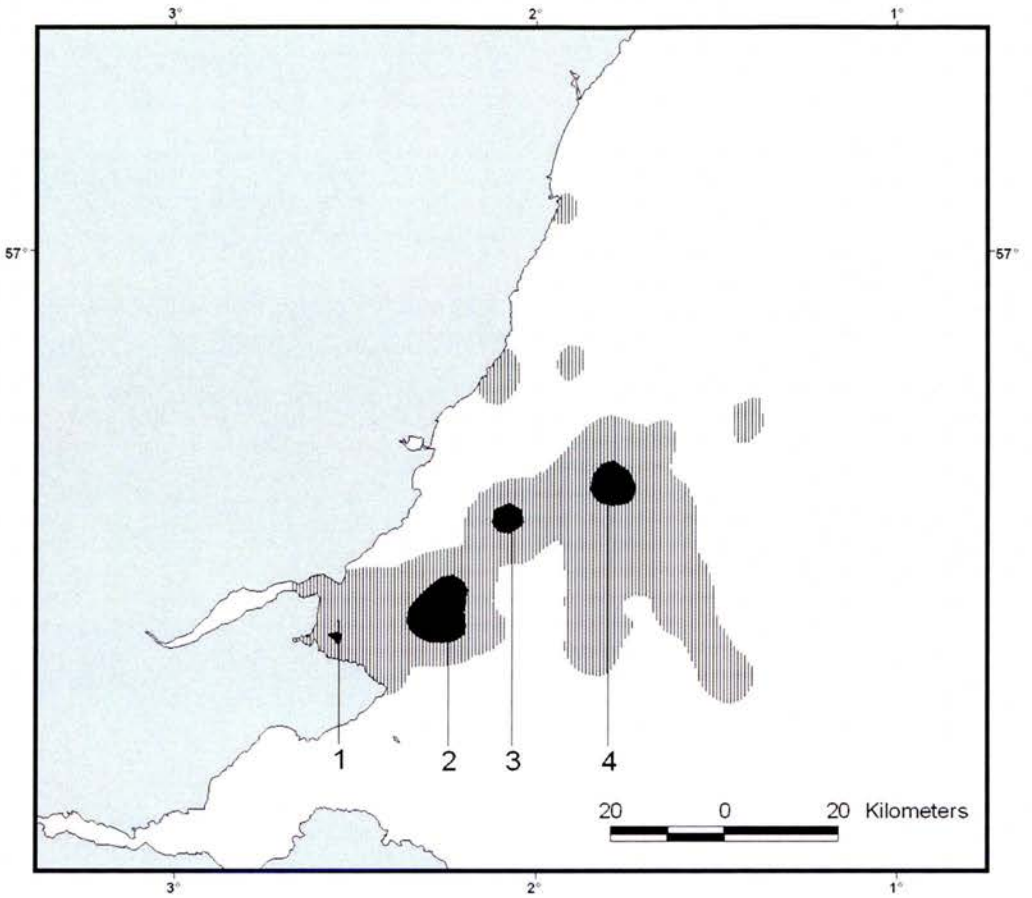

Figure 5.8: Kernel home range illustrating clusters of foraging activity, black = includes 95 % of all SAS locations and grey includes 50 % of all SAS.

Each hot spot was used by between five and ten animals, some of which used more than one of the areas (*Table 5.2*). Four out of the 25 animals tracked did not use any of the densest areas of foraging activity. The depth of the hot spots range from 10 to 50 m depth, depth increases with distance from the haul-outs (*Table 5.2*). All areas are dominated by sand with between five and 25 % gravel being present (*Table 5.2*).

Table 5.2: Number of animals using 'hot-spots' and a description of each area.

Hot-spot (*Figure 5.8*)	Number of seals using area	Description of foraging area
1	8	< 10 km from haul-out, 10 - 20 m depth, Gravelly sand
2	10	20-30 km from haul-out, 30-40 m depth, Gravelly sand
3	5	40-50 km from haul-out, 40-50 m depth, Gravelly sand
4	6	60-70 km from haul-out, 40-50 km depth, Gravelly sand

5.4.5 Habitat selection

Figures 5.9 to *5.12* illustrate the environmental characteristics of the study area, including depth contours and sediment type, together with the resampled locations.

Locations were mostly clustered in shallow (<30 m) and mid range depths (40-60 m) and not in surrounding deeper areas (*Figure 5.9*). They were clustered in areas with a high percentage of sand (80-95 %) (*Figure 5.10*). The locations show a more defined pattern in relation to gravel with foraging activity tending to be concentrated in areas with greater than 5 % gravel (*Figure 5.11*). Seals seem to be avoiding areas with greater than five percent mud (*Figure 5.12*).

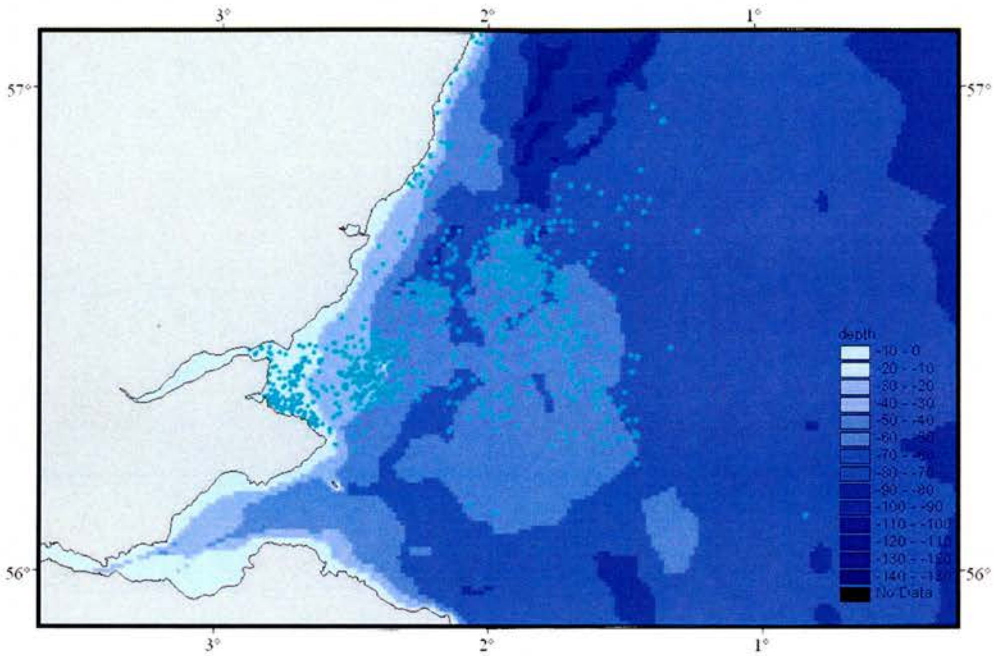

Figure 5.9: Resampled locations presented with depth contours (m).

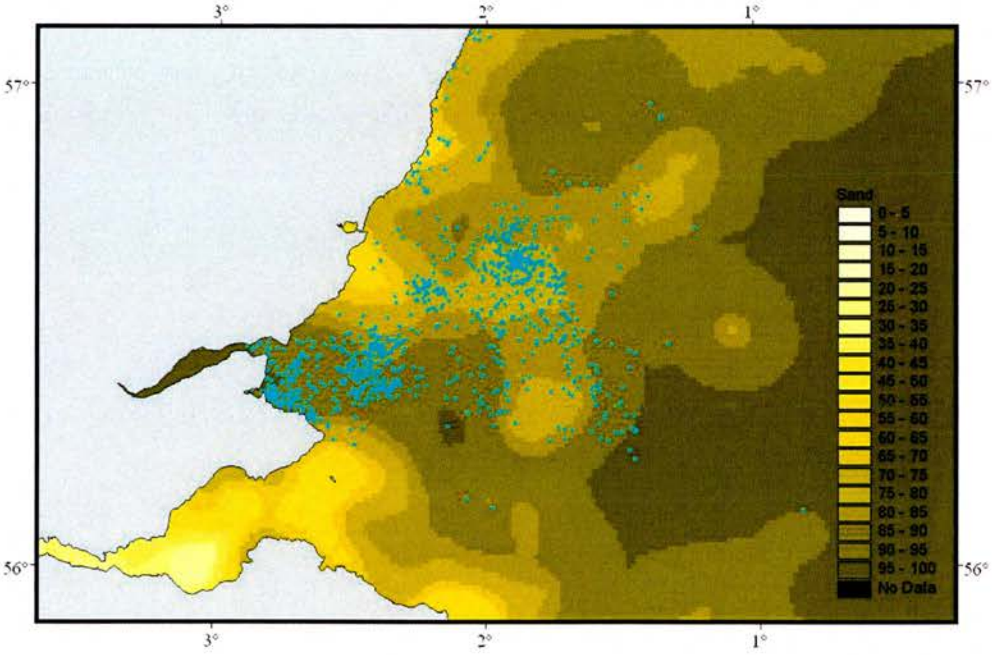

Figure 5.10: Resampled locations presented with percentage sand.

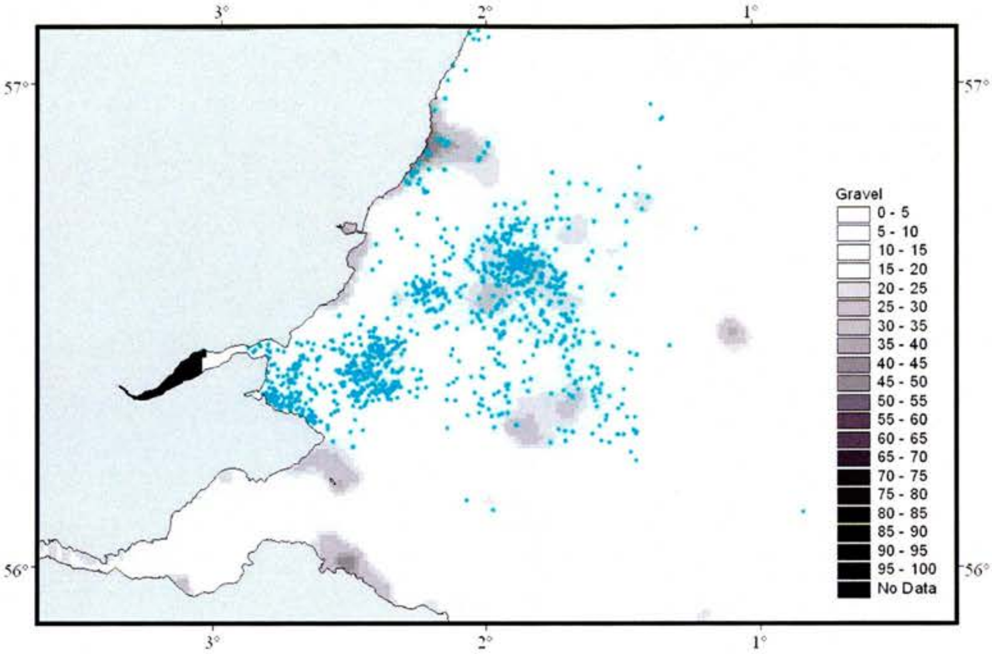

Figure 5.11: Resampled locations presented with percentage gravel.

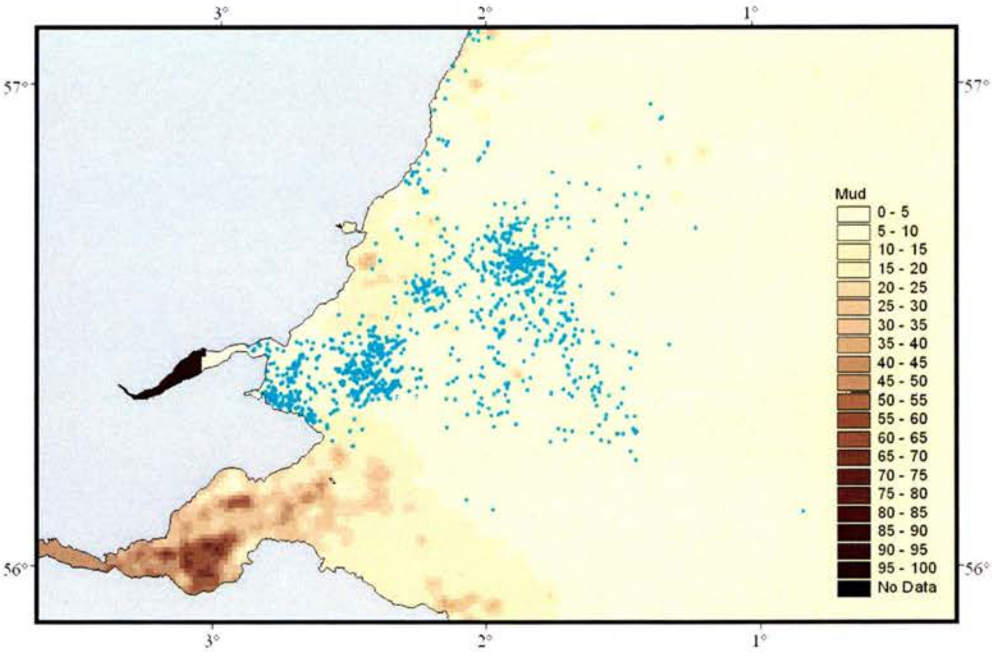

Figure 5.12: Resampled locations presented with percentage mud.

The characteristics of the whole area presented in *Figures 5.9* to *5.12* are represented by the black bars in the histograms below (*Figure 5.13*). The turquoise bars represent the characteristics of those cells containing resampled SAS locations (*Figure 5.13*). The majority of locations were relatively close to the haul-outs. It is not valid to directly compare the whole area with those areas used by seals statistically, as accessibility is not taken into account, however the distributions of the characteristics are illustrative of the differences (*Figure 5.13*).

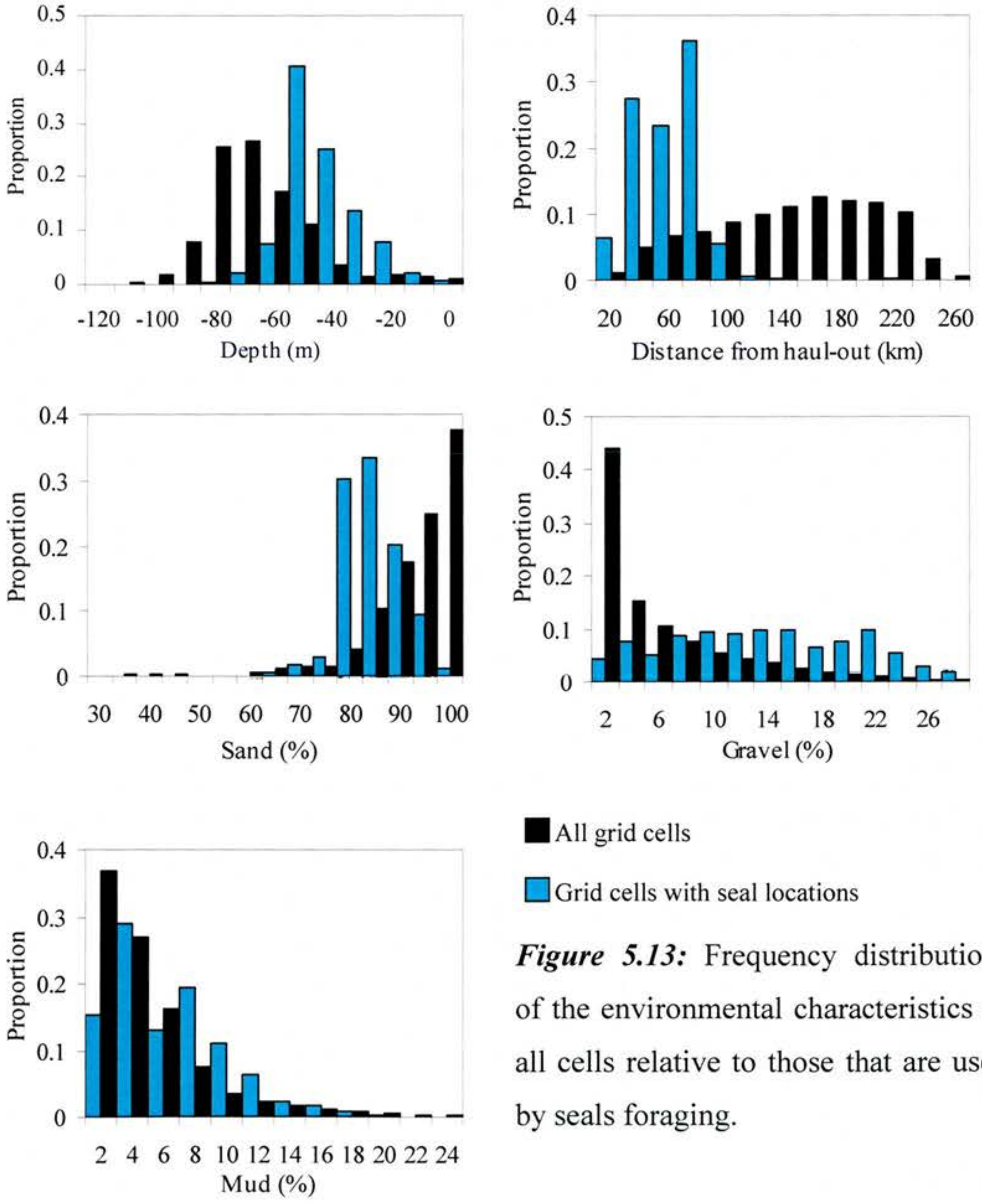

Figure 5.13: Frequency distributions of the environmental characteristics of all cells relative to those that are used by seals foraging.

The most prominent difference between used and all areas in *Figure 5.13* is that lower concentrations of sand were selected more frequently than their distribution and that although the majority of the study site has low concentrations of gravel, areas with slightly higher percentages of gravel were selected.

The mean values of the environmental variables at each distance band from the haul-out are presented in *Figure 5.14* with 95 % confidence intervals. Results of occupied versus all cells for each 20 km distance band from the haul-out, compared using Mann-Whitney test with Bonferroni correction are shown in *Table 5.3*. Little difference was observed between the environmental variables of cells being used by seals relative to all cells when at close distances to the haul-out (within 20 km). However at greater distances from the haul-out there were highly significant differences in the characteristics of the available cells relative to those in which seal locations were observed. Seals were using areas with significantly higher percentages of gravel than were available and significantly lower percentages of mud, with the exception of between 80 and 100 km from the haul-out where the availability of mud was fairly uniform (*Figure 5.12*). The mean depth used by seals between 40 and 100 km from the haul-out was consistently approximately 55 m depth, despite the variation in the available depths.

Table 5.3: Results of Mann-Whitney test for comparing the frequency distributions of the characteristics of those cells with seal locations present and all cells available at a certain distance band from the haul-out. Bonferroni corrections are applied to p-values.

Distance from haul-out (km)	Depth	Gravel	Sand	Mud
0-20 (Deeper than 10 m depth)	W = 6358 p = 0.024	W = 9383 p = 0.023	W = 6962 p = 0.178	W = 8578 p = 0.287
20-40	W = 253871 p = 0.001	W = 263599 p = <0.001	W = 338634 p = <0.001	W = 78084 p = <0.001
40-60	W = 239551 p = <0.001	W = 321756 p = <0.001	W = 211683 p = 0.002	W = 175005 p = <0.001
60-80	W = 544413 p = <0.001	W = 621776 p = <0.001	W = 310055 p = <0.001	W = 344430 p = <0.001
80-100	W = 117544 p = 0.012	W = 86315 p = <0.001	W = 59437 p = 0.006	W = 77522 p = 0.9124

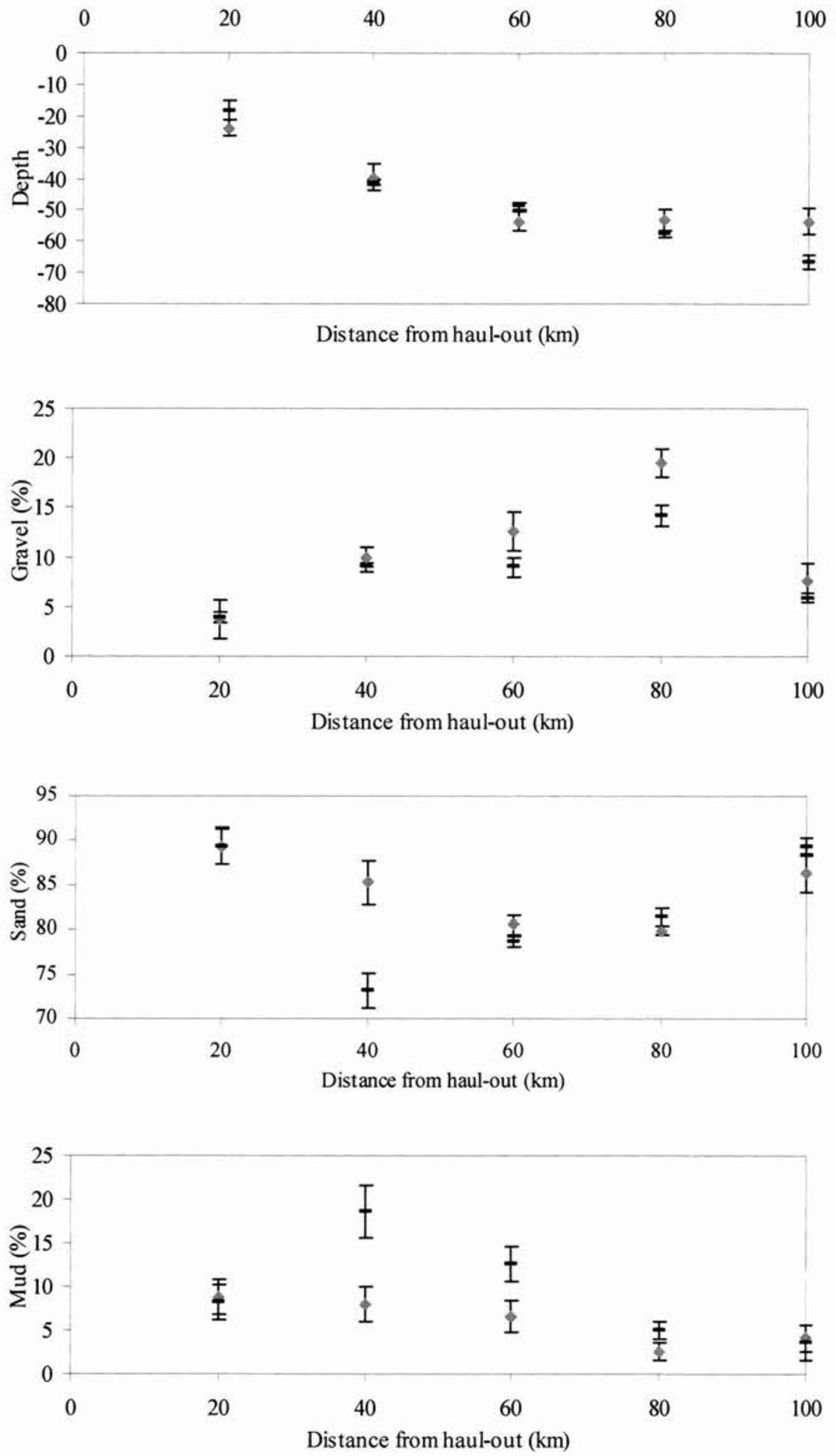

Figure 5.14: Environmental variables as a function of distance from haul-out, with 95 % confidence intervals.

▬ = characteristics of all locations within distance band

◆ = characteristics of where seals are present within distance band

The null model for distribution (Matthiopoulos, 2003) captures the decrease in accessibility as biological distance from the haul-out increases (*Figure 5.15*).

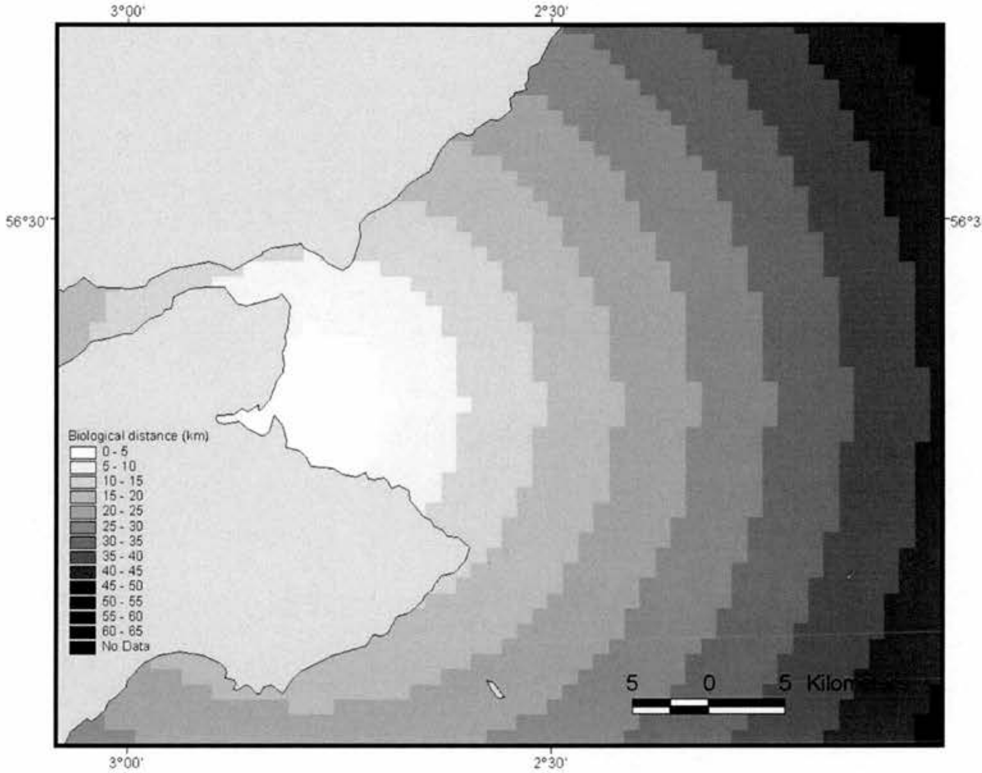

Figure 5.15: Null model of distribution controlling for effects of accessibility.

The best fitting GLM retained all of the variables as well as a quadratic term for depth (*Table 5.4*). In the fitted GLM, the probability of finding SAS (indicative of foraging) locations increased with increasing percentages of gravel and decreased with increasing percentages of mud. The weak positive relationship with sand lost its significance when variance inflation factors were applied. The relationship with depth was best described by including both a linear and a quadratic term, with the greatest proportion of SAS locations being found over shallower depths. This may be an artefact of how near haul-out locations were removed. There is still a large proportion of time spent near the haul-outs still present in the data set, shallow depths occurring closer to the haul-outs. The null model of accessibility was retained in the model and is highly significant, explaining the most variance in the observed distribution of SAS locations (*Table 5.4*).

Table 5.4: Coefficients of the GLM fitted to the re-sampled SAS locations. Corrected p-values gives the p-values having corrected the variance to take account of the degree of co-linearity in the variables using variance inflation factors.

Explanatory Variable	Co-efficient	p-value	Corrected p-value
Depth	5.464×10^{-3}	<0.001	<0.001
Depth^2	2.548×10^{-5}	<0.001	<0.001
Gravel	3.699×10^{-3}	<0.001	<0.001
Sand	7.416×10^{-4}	0.03	0.283
Mud	-2.689×10^{-3}	<0.001	0.006
Null	2.007	<0.001	<0.001

5.5 DISCUSSION

5.5.1 Ecological implications of results

This study is the first in Britain to use satellite telemetry to study the movements of harbour seals at-sea. Prior to this study the population of harbour seals around Britain was thought to forage locally to haul-outs, with the majority of movements being recorded within 50 km of haul-outs (Thompson and Miller, 1990; Thompson *et al.,* 1991). The results of this study show that foraging in St Andrews Bay appears to be densely aggregated into 'hot-spots' of localised foraging activity largely within 50 km of haul-out however the most distant of these is approximately 60 to 70 km from the haul-out (*Table 5.2, Figure 5.8*).

As there are concentrated areas of foraging that the majority of animals appear to use, the consequences of human activity in these localised areas could have significant effects on the population of harbour seals in St Andrews Bay. In this area the most likely impact on these 'hot-spots' would be fisheries activity. If fisheries over exploited these areas the harbour seal population may be unable to find enough energy to make the population viable at its current size (*Chapter 6*). However harbour seals diet varied (*Chapter 4*) and may be able to switch their dominant prey species and forage in other areas of reduced quality (Tollit *et al.,* 1997).

The areas closest to the haul-outs (within 20km) used by seals showed no difference in environmental characteristics to those available within the area. This may be an artefact of how behaviour was split into trips (see *Section 5.5.2*). Some of the SAS locations presented may not be indicative of foraging but of time spent in the water near haul-outs, perhaps during high tide while sand banks are not exposed. Also animals may explore the whole area surrounding the haul-outs to forage during high tides. The density of animals in the area is typically high at this time and little energy is expended in travelling short distances so all habitats could be used, as they do not have to be very profitable energetically to make it worthwhile (*Chapter 6*).

At greater distances from the haul-outs, selection of habitats becomes more apparent. There are significant differences in those environmental variables that were available and those that were used by harbour seals. They avoided sediments that contain mud and selected sediments with higher concentrations of gravel. These habitat characteristics describe the substrate in which sandeels burrow. Sandeels are extremely selective in the types of sediment they occupy, preferring coarse, sandy substrates containing a minimum of silt (Pinto *et al.*, 1984; Macer, 1996; Wright *et al.*, 2000). Indeed, harbour seal diet in this area was dominated by sandeels (*Chapter 4*). Whiting was the second most dominant prey item in the diet and this species is also likely to be found in these areas as one of their main prey items is also sandeels (FRS, 2004).

The species that the population of harbour seals in St Andrews Bay are preying upon (*Chapter 4*) implies that they are feeding largely on or near the seabed. In St Andrews Bay the seabed slopes gently reaching 50 m in depth, in places, approximately 30 km offshore. There are greater depths available within the range at which seals are foraging. However the mean depth where seals were found was approximately 55 m depth between 40 and 100 km from the haul-out.

This suggests that either prey are not so abundant at greater depths or else the energetic gains from capturing prey at greater depths due to a greater proportion of time being used up in reaching greater depths do not make it worth while.

In other areas harbour seals have been found to use a number of different foraging habitats. In the Moray Firth, animals were found to be diving in depths of 10 to 50 m on mainly sandy substrates, an area where sandeels are again a dominant species in the diet (Tollit *et al.,* 1998). Animals in Norway used both shallow kelp areas as well as 150 to 200 m deep basins with a muddy seabed (Bjørge *et al.,* 1995).

5.5.2 Methodological considerations

The way in which the behaviour of seals is classified in this study makes several assumptions. It assumes that slow rates of travel at sea are linked with foraging activity. Information on dive behaviour has been used to consolidate this assumption with square dive profiles representing attempted foraging and triangular dive profiles representing travelling (Le Boef *et al*., 1988; Hindell *et al*., 1991; Thompson and Fedak, 1993). However, with the data received it is not possible to unequivocally identify places where seals are feeding without additional information such as from stomach temperature sensors identifying successful foraging from a drop in temperature (Bjørge *et al*., 1995) or from using underwater cameras (e.g. Baechler *et al.,* 2002; Hooker *et al*., 2002). Using one fixed speed of travel to separate foraging and travelling will misclassify some of the behaviour of animals and does not take account of some foraging activity occurring when near the haul-out and whilst travelling. Despite these limitations, in general the places where animals spend most of their time at sea are likely to represent areas where the majority of foraging is taking place.

Data were resampled in this study in order to avoid problems of non-independence and autocorrelation in the data. In this instance 4.8 percent of observations were used. This means that a lot of information and detail is lost. Due to the large data set, resampling still permitted relationships to be identified in this instance, with smaller data sets this may not be valid. Other approaches may be to use the whole data set in analysis but to account for autocorrelation in the error structure used (*Chapter 3*).

The proportion of the population studied via telemetry was very small. Data collected from 24 seals were used to represent a population of 1746 seals (95 % confidence interval 1238 to 2301, *Chapter 3*). Only approximately 1.5 % of the population has been studied and therefore any conclusions that are made as to the behaviour of the population should be made with caution. Some of the areas of foraging activity are specific to individual seals and it is possible that a larger sample of animals would show a greater spread of foraging activity across more of the study area (*Figure 5.8*). The individual variation in movements could be investigated further to assess the degree of change in the distribution by resampling different subsamples of individuals from the 25 animals tagged.

There was some seasonal variation in the diet observed, for example sandeels were more prominent in the diet in the winter months, relative to summer ones (*Chapter 4*). Season was also retained as an explanatory variable in models explaining factors effecting foraging trip distance and duration (*Chapter 6*). Therefore we would expect the distribution of foraging to alter between seasons. This was something that was not explored here due to the sample size of individuals in each season and the method of resampling the data would leave insufficient sample sizes if reduced further into seasons.

Only substrate type, depth and accessibility were used to try to explain the distribution of foraging observed in the data. These variables were highly significant in explaining some of the observed variation but there are likely to be other explanatory variables that may better explain the variability in the data. For example sea temperature, chlorophyll, currents, prey distributions and slope could be considered as variables that may explain the variation observed in foraging movements as they may capture the productivity of the area.

5.5.3 Conservation and management implications

Sandeel stocks in the North Sea are thought to be able to sustain the current level of fishing, however the North Sea stock of sandeels is composed of several populations that are isolated by the availability of suitable habitat with little migration of adults and limited dispersal of larvae between suitable patches (FRS, 2003). If localised populations of sandeels were over exploited by fisheries, this could have significant effects on the predators of sandeels in these areas. There have already been significant concerns regarding the effect of the sandeel fishery on sea bird populations (Frederiksen *et al.*, 2004; Polozanska *et al.*, 2004) and the current management advice to fisheries is to "aim to prevent local depletions of sandeel aggregations, particularly where predators congregate". (FRS, 2003).

Harbour seal populations were thought to spend the majority of their time close to haul-out sites and this species has not generally been considered at risk from largely offshore activities such as oil and gas exploration and production. This study found concentrated foraging activity occurring as far as 70 km from haul-outs and more dispersed movements beyond this distance. As a result of this, and recent research in Denmark (Tougaard pers. com.) and the Netherlands (Brasseur pers. com.) using satellite telemetry, DTI had funded as part of the Stretegic Environmental Assessments (SEAs) further investigation of the at-sea distribution of harbour seals.

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CHAPTER SIX:

Factors affecting activity budgets and foraging characteristics of harbour seals from St Andrews Bay.

6.1 ABSTRACT

Harbour seals live in a variety of habitats and the proportion of time they spend hauled-out and the characteristics of their foraging trips vary both within and between regions. Here we investigate the variation in the activity of harbour seals within St Andrews Bay and the degree to which this variation can be explained by endogenous characteristics such as sex and body size.

Foraging trip duration (mean = 6 days, SE = 0.39 days, n = 24) was strongly correlated with the distance travelled to forage (mean = 41 km, SE = 1.27 km, n = 24). The distance travelled was significantly shorter for females (males: mean distance = 50.25 km, SE = 1.13km, n = 12; females: mean distance = 31.56 km, SE = 1.26 km, n = 12; t = 1.28, $p<0.01$). Both the proportion of time at sea and foraging trip duration were positively related to body length for both sexes. Endogenous factors do appear to affect foraging behaviour, and will therefore have important implications in assessing the populations' energy requirements and diet composition.

6.2 INTRODUCTION

6.2.1 Pinniped activity budgets

To understand the ecology of a species it is necessary to know how individuals allocate time to different activities. In particular the characteristics of foraging provide details of how the species gains enough energy to survive. It is well known that the characteristics of foraging trips vary considerably among pinniped species. Elephant seals (*Mirounga* sp.) can spend several months thousands of kilometres away from haul-outs (e.g. Le Boeuf *et al*., 1993; McConnell and Fedak, 1996), whereas individual harbour seals have been recorded making trips of a few hours within five kilometres from their haul-out (Bjørge *et al.,* 1995; Thompson *et al*., 1998). These extreme differences may reflect responses to different distributions of prey and/or differences in endogenous characteristics of the species.

Considerable differences in foraging behaviour have also been found within species. Thompson *et al* (1998), found that foraging trip duration ranged from 17 hours to over ten days and that the recorded distances travelled to forage ranged from 4.3 km to over 50 km in harbour seals captured in the Moray Firth. Some of this variation was explained by the body size and sex of the animals. Grey seals in the North Sea were found to be making both long and distant movements (up to 2100 km away), and repeated return trips from haul-outs to discrete offshore areas. Of the return trips there was considerable variation between individuals, from 20.4 km to 180 km (McConnell *et al.,* 1999).

Telemetry studies provide a means to observe seal behaviour where previously observations could only be made of animals when they were hauled out on land or opportunistically from boats at sea. The majority of a seal's time is spent at sea, largely underwater. As a result, only a very limited understanding of the species can be obtained without information about their at-sea behaviour. The ability to collect continuous data on the activity and geographical location of an animal using telemetry can provide a detailed insight into the energetic balance involved in its foraging behaviour.

In harbour seals the proportion of time spent at-sea during the moult or breeding season is widely studied with the aim of correcting counts for the proportion of time animals are in the water to derive estimates of absolute abundance (*Chapter 3*; Eberhardt *et al.*, 1979; Pitcher and McAllister, 1981; Harvey 1987; Thompson *et al.*, 1987; Yochem *et al*, 1987; Thompson and Harwood, 1990; Mathews and Kelly, 1996; Thompson *et al.*, 1997; Ries *et al.*, 1998; Huber *et al.*, 2001; Simpkins *et al.*, 2003) as well as determining the variables that effect haul-out behaviour (e.g. Schneider and Payne, 1983; Slater and Markowitz, 1983; Kreiber and Barette, 1984; Stewart, 1984; Yochem *et al.*, 1987; Thompson *et al.*, 1989; Thompson and Miller, 1990; Grellier *et al.*, 1996). There have been few studies of activity budgets outwith the breeding season and moult (Thompson *et al.*, 1997).

6.2.2 Effects of endogenous characteristics on activity budgets

Body size is positively related to dive duration and depth in pinnipeds (Boyd and Croxall, 1996). Larger animals have greater oxygen storage capacity and lower mass-specific energy demands through allometric effects and can therefore remain submerged for longer than smaller conspecifics. It is possible that pinnipeds use the available habitat in accordance with their diving capabilities in such a way that there is niche separation within a population related to body size (Mori, 2002). For example larger animals may be able to forage further from shore and/or at greater depths.

Harbour seals are sexually dimorphic. Adult females and adult males weigh on average about 85 kg and 110 kg, respectively (Coltman *et al.*, 1998). Differences in foraging behaviour may be expected due to this body size dimorphism. Beck *et al.* (2003) found that in grey seals there were seasonal differences in diving behaviour between males and females, but these were not attributed to body-size dimorphism, or niche separation. Instead the differences were attributed to the need for females to recover condition earlier in the year than males, to support the energetic costs of reproduction (Beck *et al.* 2003). Foraging behaviour during the breeding period has been omitted in one previous study to eliminate the potential differences attributed to varying timings and costs of reproduction (Thompson *et al.*, 1998). Harbour seals have shown an increase in the time spent ashore and a restriction in range throughout the lactation and the mating period (Thompson *et al.*, 1994; Van Parijs *et al.*, 1997; Thompson *et al.*, 1998). However, the study still found that the foraging range and trip duration were significantly shorter for females (Thompson *et al.*, 1998).

6.2.3 Wider application of data on activity budgets

The current information used to inform management decisions on levels of fish consumption by harbour seals is not sex or age specific. Estimates of fish consumption are based on the metabolic rate inferred from the average size of an individual in a species. An estimate of three to five kilograms of fish per harbour seal, depending on whether feeding on fatty fish or whitefish, has most recently been reported (SCOS, 2003).

If variation in foraging behaviour can, in part, be explained by the endogenous characteristics of individuals, knowledge of the population structure can improve predictions of how the population utilises an area to forage. This would be extremely valuable in informing conservation and management decisions.

Detailed field based knowledge can be utilised in combination with laboratory based studies of metabolic rates of harbour seals to create energetic models to estimate the energy requirements of the population given their activity patterns. This would permit more reliable estimates of the level of food consumption by a population of harbour seals.

6.2.4 Activity budgets of harbour seals in St Andrews Bay

In this study satellite telemetry was used to describe the activity budgets and foraging trip characteristics of 24 harbour seals captured in St Andrews Bay. Characteristics such as sex, body mass and body length are used to try to explain variation in foraging behaviour. Results are compared with data collected in the Moray Firth, which lies north of the St Andrews Bay study site to further explore how much of the variation in activity may be due to endogenous or environmental factors.

6.3 METHODOLOGY

Information on activity budgets and foraging characteristics were obtained from satellite relay data loggers (SRDLs). Data were collected from 25 seals between October 2001 and July 2003 in St Andrews Bay. Further details of the study site, methods for capturing and handling seals and a description of SRDLs are given in *Chapter 2*: Materials and Methods. One of the seals (DM) was excluded from the analyses because it made no distinguishable foraging trips, instead spending the majority of time within the confines of harbours, where it was observed scavenging.

There were few data collected in summer months because the majority of tags had been shed by this time. Data that were collected in the months of June and July were excluded from further analysis, to keep the focus on foraging behaviour, and excluding behavioural changes associated with the breeding season.

The data used to estimate the proportion of time an animal spent ashore were the proportions of time hauled out during each two hour period. Further details of how these data were collected are given in *Chapter 2* – Materials and Methods.

To study characteristics of foraging behaviour, the smoothed tracks (see *Chapter 2*) for each animal were separated into individual foraging trips. The start of a trip was defined as the first time an animal was recorded diving to ten metres or more. The trip ended when the animal hauled out.

To determine the mean distance travelled to forage on each trip, the at sea behaviour was first classified as either foraging or travelling. Speed of travel was used to distinguish between travelling and foraging as travelling is assumed to be associated with greater speeds (McConnell *et al.,* 1984). The transit and foraging phase of trips was separated using a speed threshold of 0.5 m s^{-1}; the reasoning behind this choice is described in *Chapter 5*. The sensitivity of the threshold speed chosen is also investigated in *Chapter 5*. To obtain the mean distance travelled to forage within each trip, the geographical area used for foraging was first determined by removing locations associated with faster speeds of travel. The average of the remaining, locations, assumed to be associated with foraging, was then calculated. The distance to this average location was then used to calculate the distance travelled to the foraging area for each trip. Splitting travelling and foraging using travel speed alone is inaccurate, and some locations from the travelling phase of the trip may not be removed. However the vast majority of points are likely to be from the foraging phase and this simple method is unlikely to significantly shorten the foraging distance. There may be multiple foraging areas visited within a trip. If this is the case the mean distance travelled to forage should still reveal the relationships between the distances travelled to forage and the endogenous characteristics explored here.

Activity at sea was not split into foraging and travelling, due to the inaccuracy in dividing the two behaviours. Separating behaviours using one fixed speed for all seals does not accurately distinguish between the two behaviours, but can be beneficial in determining broad areas used for foraging. The behaviours can easily be classified for those animals travelling further afield, but for those animals making short distance and duration trips the inaccuracy of locations prevents the travelling and foraging phases of a trip from being determined.

Analysis

The mean proportion of time spent at sea by males and females was normally distributed (KS = 0.163, p <0.01) and was compared using an unpaired t-test. The effect of seal length and weight on the proportion of time hauled out was explored using linear regression analysis. Departure from linearity was tested using a runs test.

Relationships between mean duration of foraging trip for each animal and body mass or body length were examined using a Spearman rank correlation coefficient, because the data were not normally distributed (Kolomgorov and Smirnov test for normality, KS = 0.189, p = 0.018, *Figure 6.1*). A Mann-Whitney U test was used to test for any differences in the duration of foraging trips between the sexes.

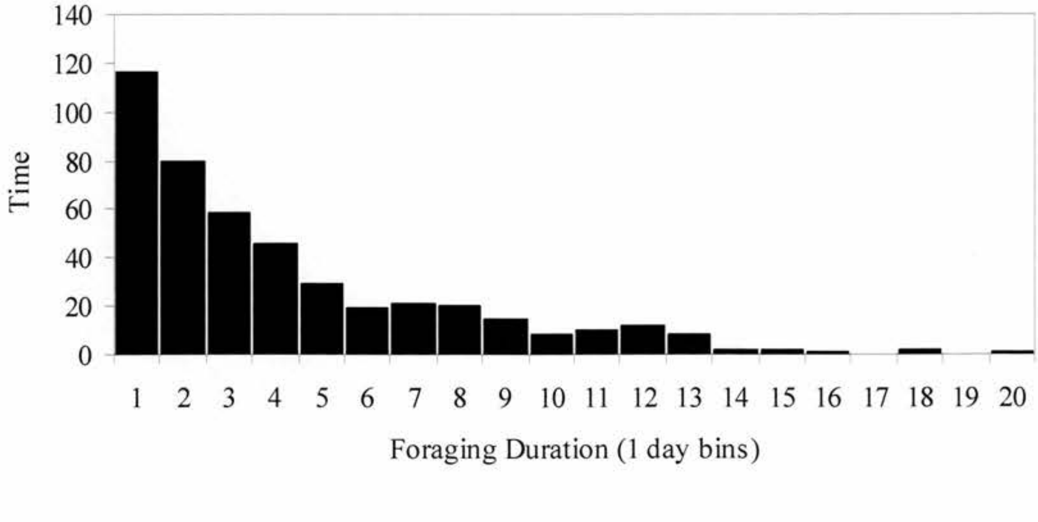

Figure 6.1: Frequency distribution of foraging trip durations.

The effect of body size on the mean distance travelled for each individual to foraging areas was investigated using Spearman rank correlation coefficients, as above, the data were not normally distributed (Kolomgorov and Smirnov test for normality, KS = 0.213, p = 0.017, *Figure 6.2*).

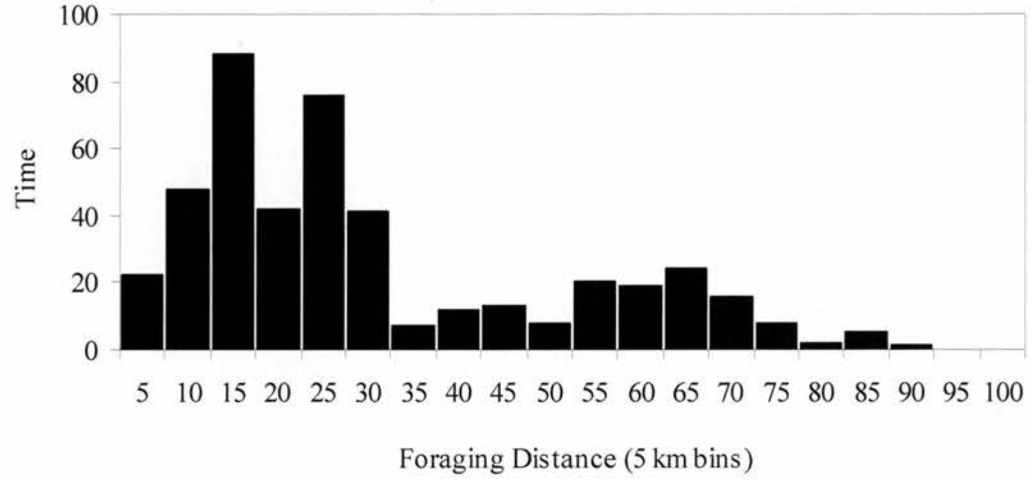

Figure 6.2: Frequency distribution of the mean distance travelled per foraging trip.

As the frequency distributions of both trip durations (*Figure 6.1*) and trip distance (*Figure 6.2*) appear to have a bimodal distribution, the characteristics of animals making longer distance and duration trips were compared with those making shorter distance and duration trips. Animals making trips of more than 40 km were classed as 'long' and those animals making trips to distances less than 40 km were classed as 'short'. Three individuals made a mixture of both long and short trips and were excluded from this analysis. A t-test was used to compare the lengths and masses of animals making long and shot trips.

The endogenous characteristics explored as explanatory variables for both trip duration and distance travelled to forage were weight, length and sex. A mean of each response variable (distance and duration) was taken for each individual. An index of body condition was also used to further explore these relationships. To assess body condition, mass was regressed against length for each sex (females: $y = 58.5 - 0.83x$, $r^2=0.65$, p=0.05, n=52; males: $y = 51.35 - 0.64x$, r^2=0.62, p=0.05; n=68). The observed mass was then divided by predicted weight to produce an index of body condition (BCI) (Schulute-Hostedde *et al.*, 2005).

Generalized linear mixed models (GLMMs) fitted with the penalized quasi-likelihood method, Schall, (1991), were used to further investigate these relationships. In this instance the characteristics of each trip made by an individual were used rather than the mean, giving repeated measures for each individual. A random term was included in the model to allow the intercept to vary for each individual animal. The explanatory variables included were year of study, season, sex, body length and body mass. Model fitting was conducted in R (version 1.9.0.) using both forward and backward stepwise selection to assess which fixed effects should be retained in the model. Akaike's Information Criterion (AIC) was used as a criterion to assess which model best explained the data. Overall model fit was assessed from plots of residuals against fitted values, residuals against the fixed effects included in the model, and fitted versus observed values.

6.4 RESULTS

6.4.1 Overview of foraging characteristics

The breakdown of activity budgets into trips at sea and periods near haul-outs and the distance travelled to forage varied considerably between individuals *(Figure 6.3* and *6.4)*. Between four and 40 trips were recorded for each animal (mean = 18.9 trips); 452 trips were recorded in total (*Table 6.1*). Trip durations ranged from under a day to 23 days (mean = 6 days, *Table 6.1*). Mean foraging trip distances for individual seals ranged from 7 to over 70 km (mean = 40 km, *Table 6.1*).

Table 6.1: Details of foraging trips

Animal	No. of trips	Trips per month	Mean trip duration	Mean trip distance
		males		
AM	10	2.14	13.99	70.41
BM	4	2.16	13.9	67.20
CM	8	3.60	8.33	53.81
FM	28	10.03	2.99	20.19
LM	15	5.43	5.52	49.68
MM	8	3.74	8.03	48.98
NM	18	5.42	5.54	61.05
OM	16	4.55	6.59	41.06
PM	33	11.19	2.68	24.91
QM	10	4.19	7.16	55.63
TM	9	5.22	5.75	51.69
VM	9	5.03	5.97	58.39
		females		
EF	40	10.53	2.85	20.37
GF	9	3.61	8.3	53.19
HF	5	2.54	11.82	60.43
IF	17	6.44	4.66	30.66
JF	17	4.86	6.17	39.73
KF	9	3.03	9.89	55.02
RF	54	25.21	1.19	14.76
SF	48	20.27	1.48	12.64
UF	7	5.60	5.36	47.84
WF	36	18.18	1.65	10.50
XF	11	7.48	4.01	26.14
YF	32	34.88	0.86	7.47

There was a large amount of individual variation in foraging behaviour exhibited by the seals tracked, as demonstrated in *Figures 6.3* and *6.4*. Some seals showed highly consistent foraging behaviour throughout the duration of the tracking period, for example seal PM (*Figure 6.3*) and seal KF (*Figure 6.4*). Although these seals travelled different distances for differing durations when compared to each other, each seal had a consistent pattern of foraging, travelling to approximately the same distance from the haul-out and for the same duration. Other seals switched between different trip types, from short ranging, short duration trips to further distance, longer duration trips (e.g. seals IF and RF, *Figure 6.4*). Distances travelled in trips ranged considerably from 7 km to over 150 km.

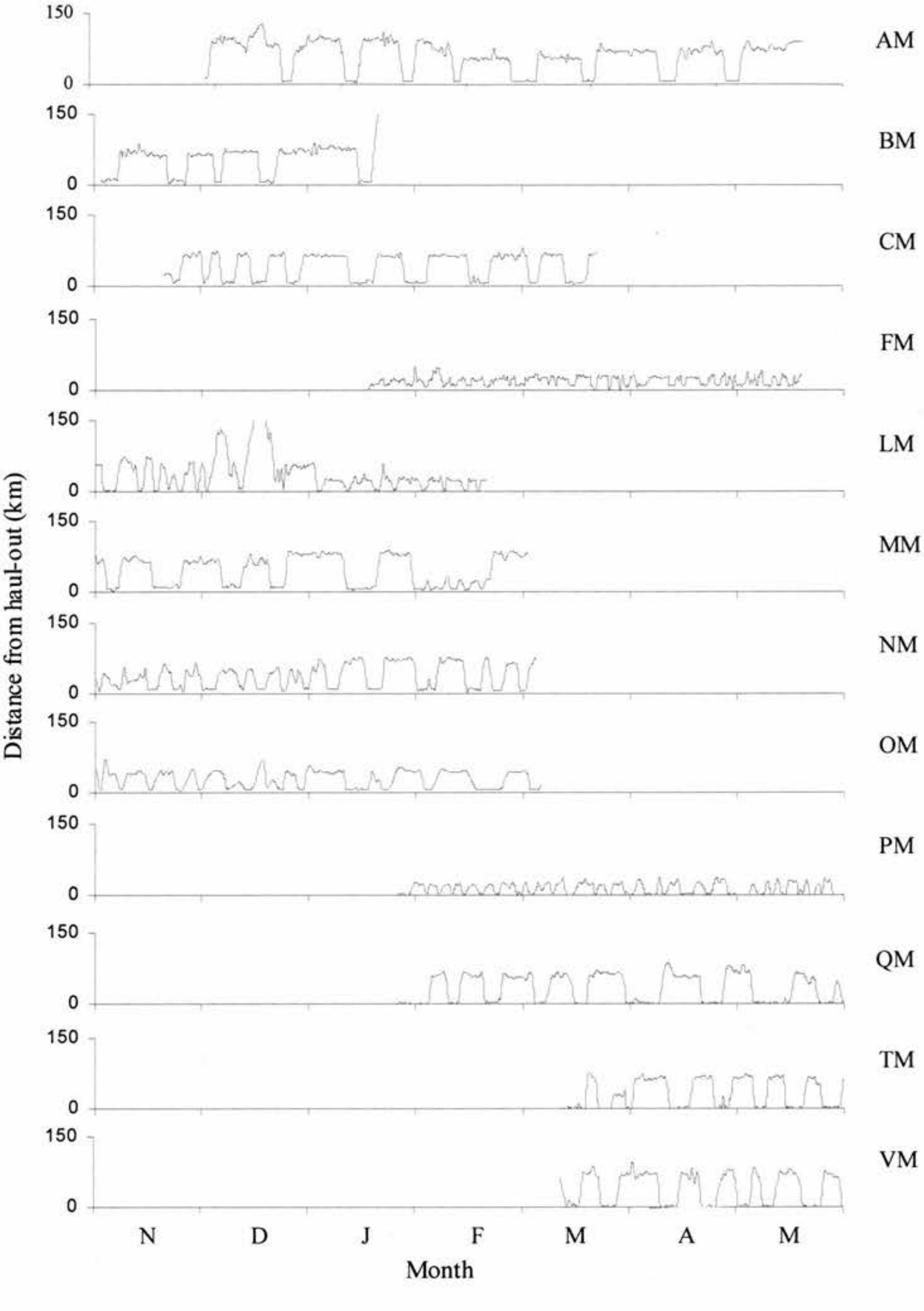

Figure 6.3: Movement/foraging trip patterns of 12 male harbour seals.

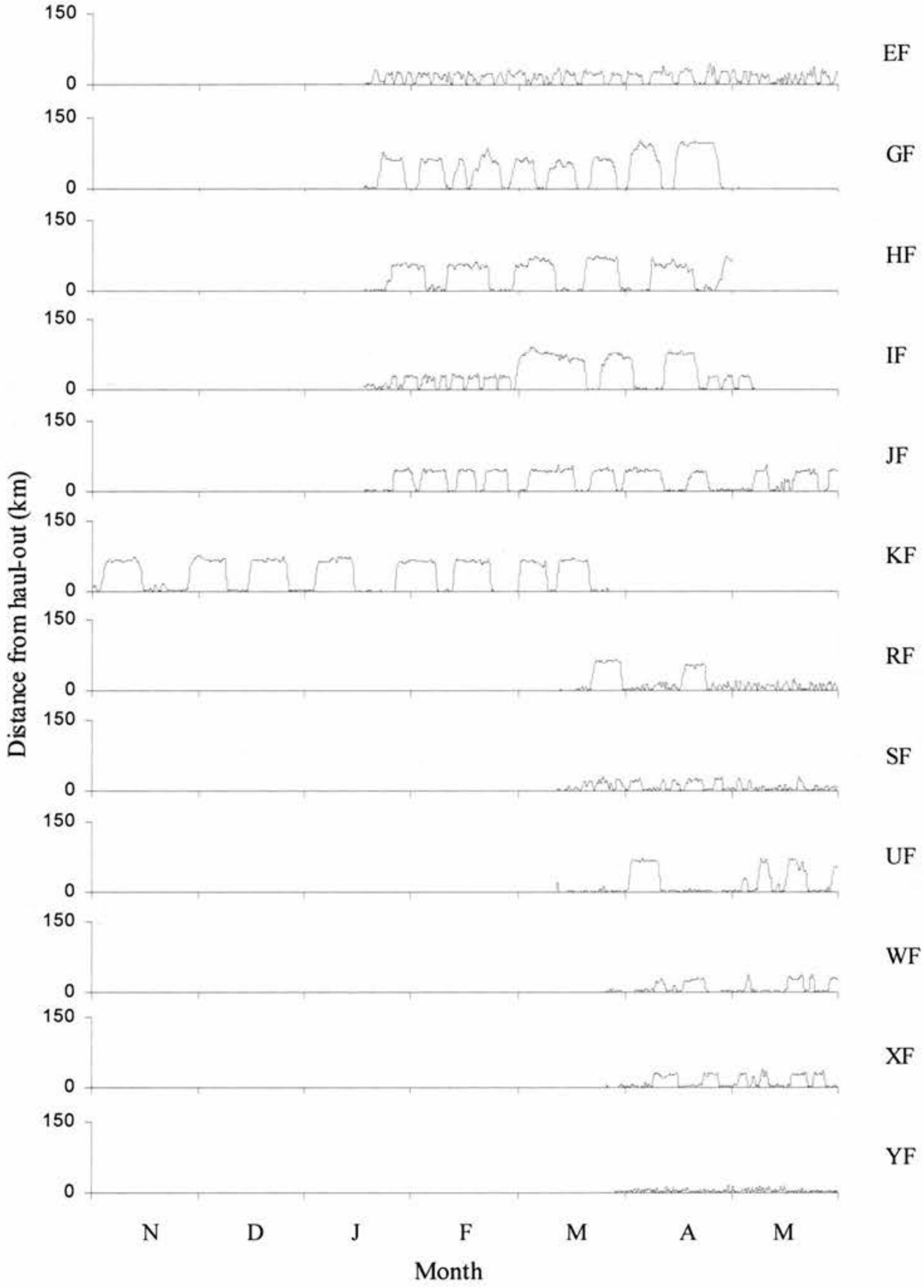

Figure 6.4: Movement/foraging trip patterns of 12 female harbour seals.

The distribution of lengths and masses of the male and female tagged animals are shown in *Figure 6.5*. There was no significant difference in the mass (males: mean = 71 kg, SE = 1.8, n = 12; females: mean = 70 kg, SE = 2.0, n = 12; $t = 0.15, p = 0.88$), length (males: mean = 135 cm, SE = 2.3, n = 12; females: mean = 135 cm, SE = 2.3, n = 12; $t = 0.08, p = 0.94$) or body condition (males: mean = 0.99, SE = 0.04, n = 12; females: mean = 0.99, SE = 0.04, n = 12; $t = 1.89^{-18}$, $p > 0.99$) of males and females tagged in this study.

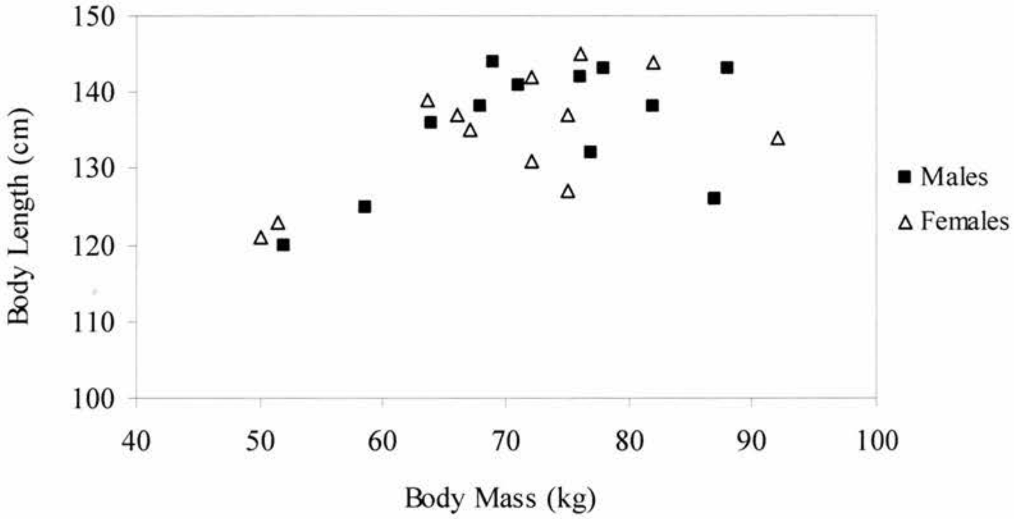

Figure 6.5: Mass and length of both male and female study animals captured in St Andrews Bay.

6.4.2 Proportion of time spent at sea.

All study animals spent the majority of time at sea, spending on average between 11 and 29 % of time hauled out on land. There was no significant difference in the proportion of time males and females spent at sea (males: mean = 0.83, SE = 0.05, n = 12; females: mean = 0.80, SE = 0.05, n = 12; $t = 1.08, p = 0.29$). There was no significant relationship between the proportion of time at sea and body mass (*Figure 6.6*), however there was a significant positive relationship with body length (*Figure 6.7*). Relating the proportion of time spent at sea to body condition index showed no significant relationship for females (*figure 6.8*), however there was a clear significant, negative relationship with males (*figure 6.9*), those males with a higher body condition index spending a reduced proportion of time at sea.

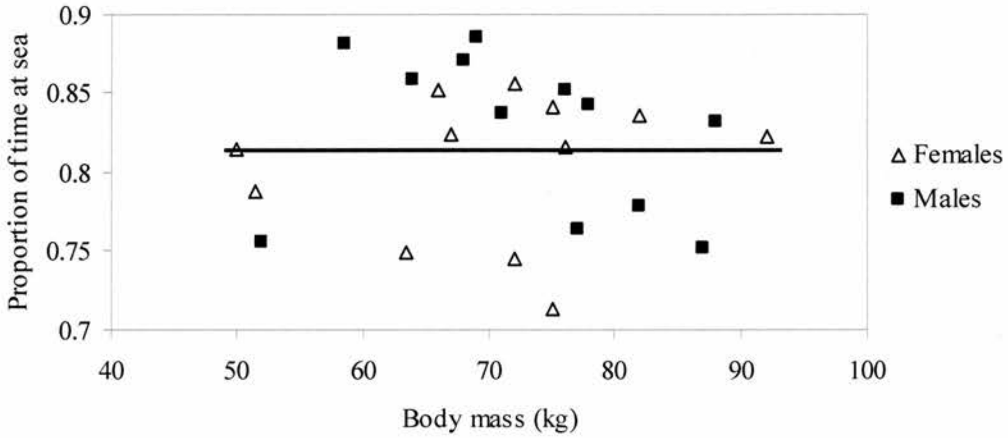

Figure 6.6: Proportion of time spent at sea as a function of mass (regression equation for males and females combined: $y = 0.8274 + 0.0002x$, $r^2 = 0.0022$, $p = 0.83$).

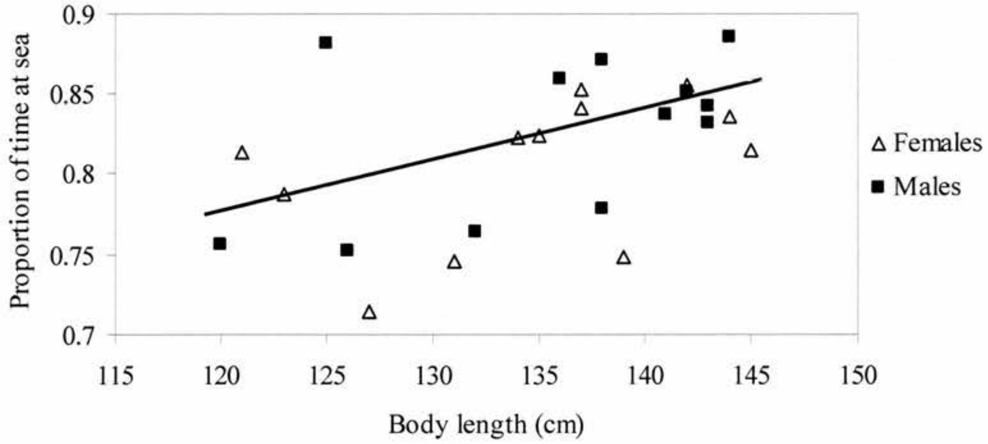

Figure 6.7: Proportion of time spent at sea as a function of body length (regression equation for males and females combined: $y = 0.7616 + 0.0026x$, $r^2 = 0.244$, $p = 0.014$).

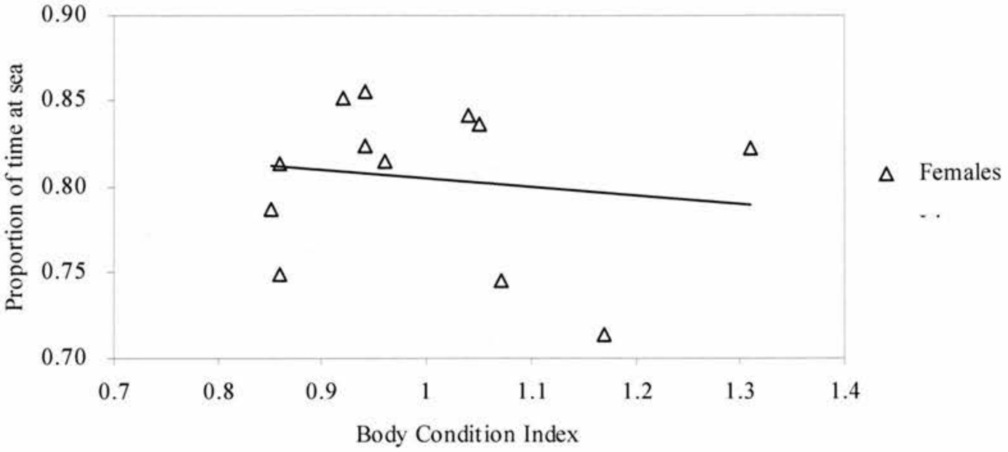

Figure 6.8: Proportion of time females spent at sea as a function of body condition index ($y = 0.86 - 0.054x$, $r^2 = 0.026$, $p = 0.62$).

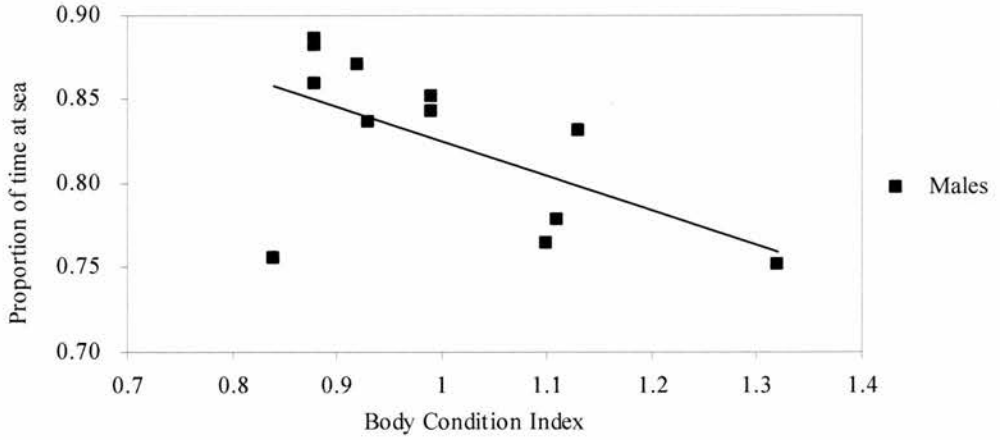

Figure 6.9: Proportion of time males spent at sea as a function of body condition index ($y = 1.04 - 0.22x$, $r^2 = 0.38$, $p = 0.03$).

The individual monthly activity budgets of the 12 male and 12 female harbour seals illustrate the seasonal variation and trends in the proportion of time spent hauled out and at sea (*Figure 6.10* and *6.11*). Only months where the animals were tracked for the entire month are displayed. Two adult males, CM and LM, spent no time hauled out in November and December respectively. The minimum percentage time hauled out was 0 % (CM and LM), the maximum was 35 % in May. The seasonal increase in time hauled out was not apparent when individual haul-out patterns were examined. However, when all individuals were combined seals spent a greater proportion of time at sea in winter months, and less time at sea in spring and summer.

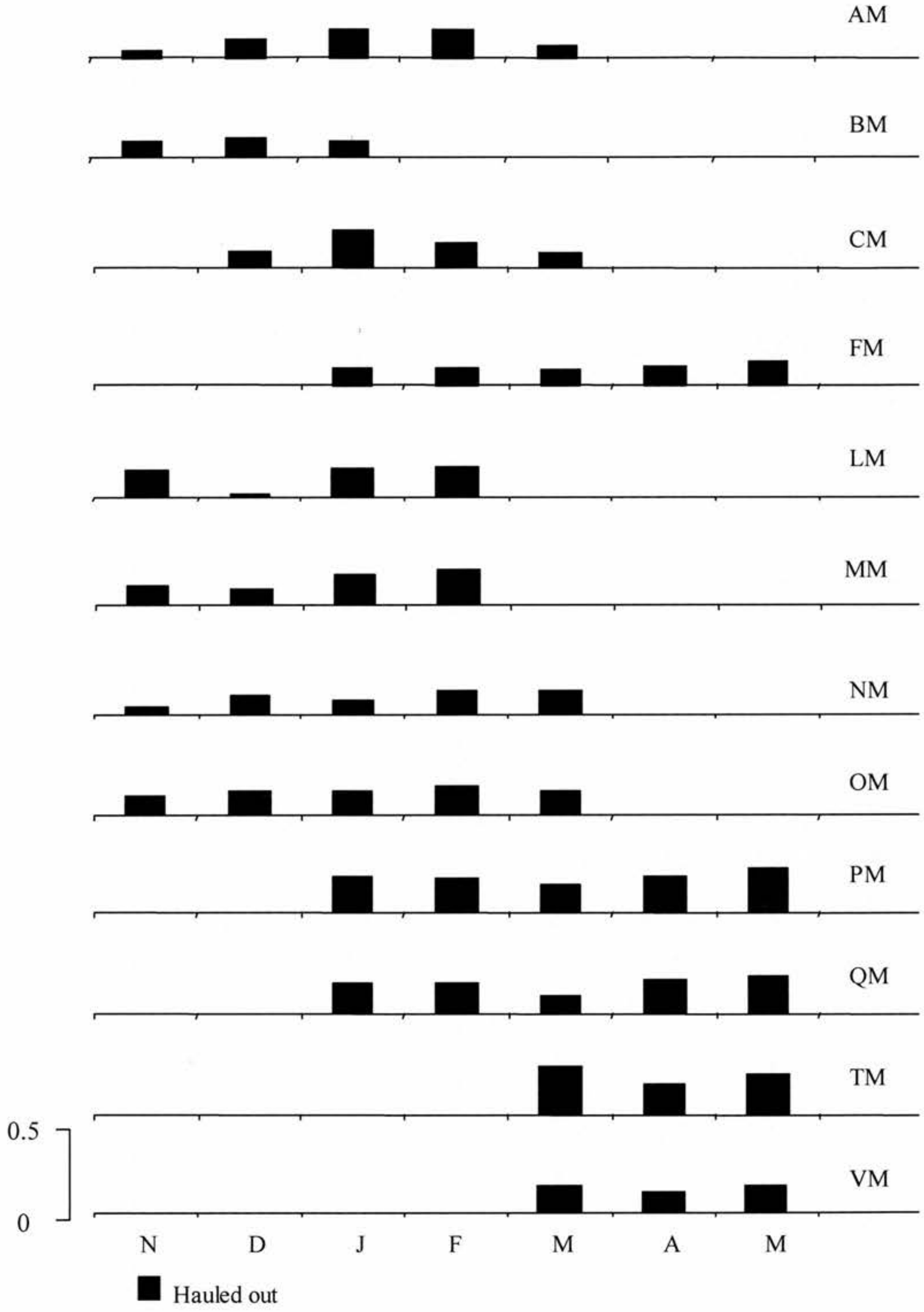

Figure 6.10: Monthly proportion of time hauled out and at sea of 12 male harbour seals. Those months where a black bar is absent indicate months where no data were collected, with the exception of CM in November where the animal didn't haul-out.

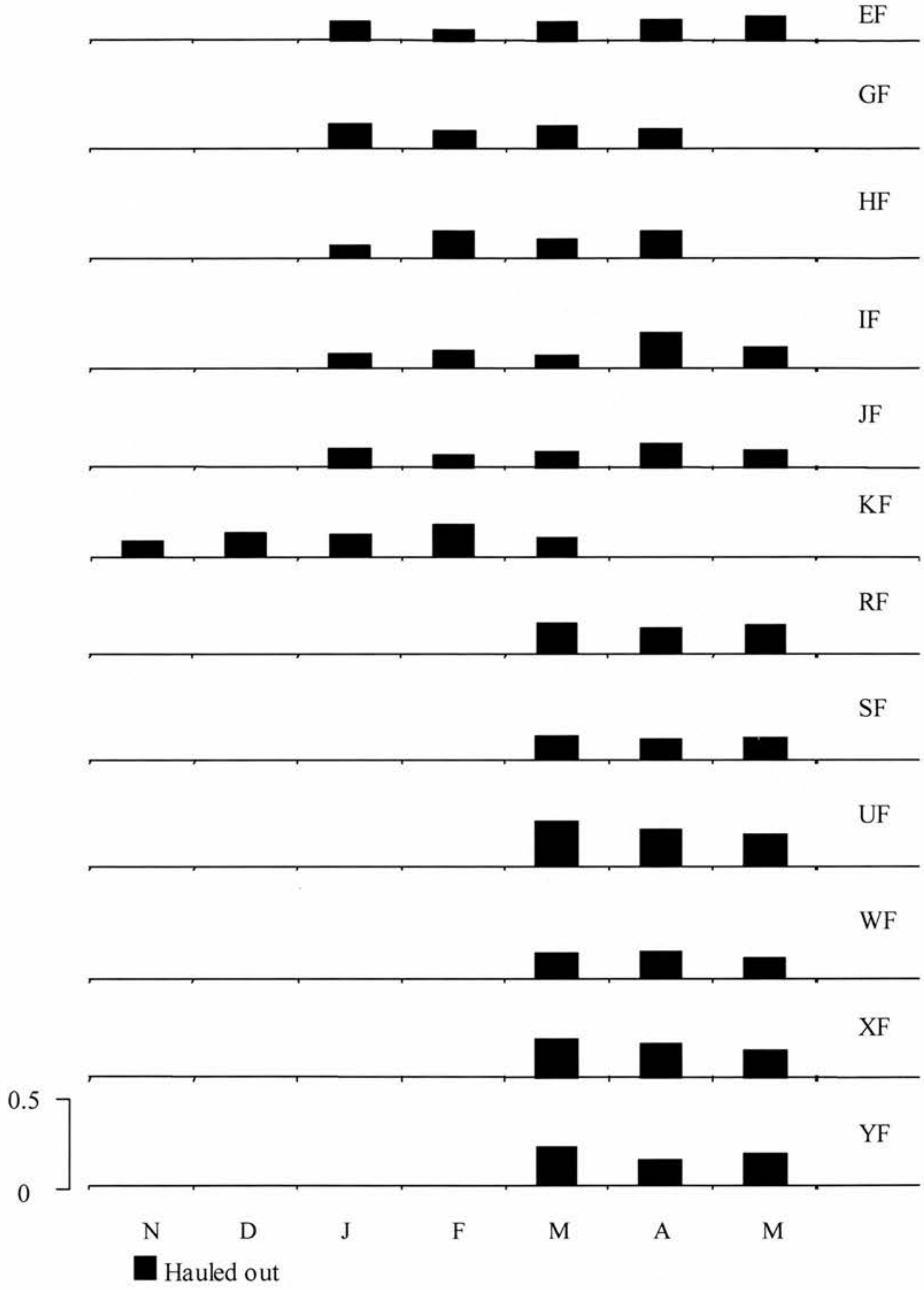

Figure 6.11: Monthly proportion of time hauled out and at sea of 12 female harbour seals. Those months where a black bar is absent indicate months where no data were collected.

The mean time that males hauled out increased from 9 % to 21 % from November to May (*Figure 6.12*). This relationship is further explored in *Chapter 3* when estimating population size. There was an insufficient sample size of females tagged throughout November and December to look at how the proportion of time hauled out varied in these months. There was however a slight increase in the percentage of time hauled-out from 15 % in January to 21 % in April (*Figure 6.13*). Males and females showed a similar seasonal trend in the proportion of time hauled out.

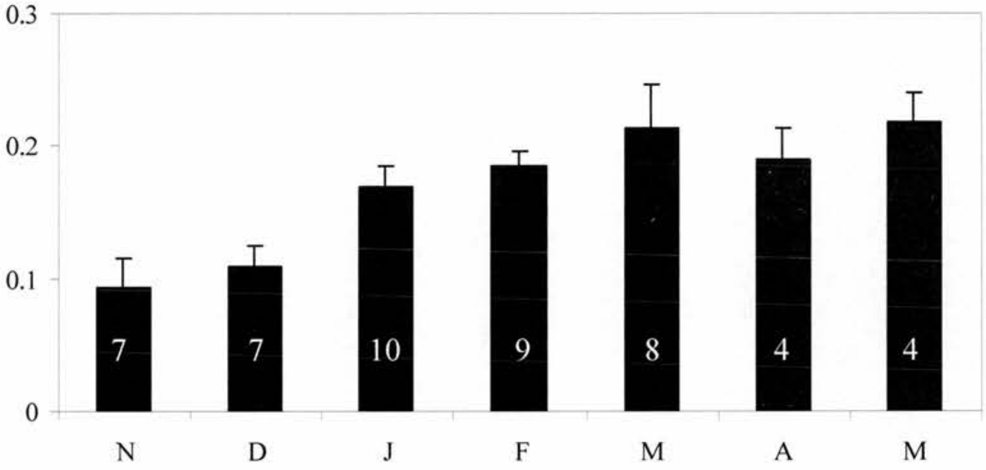

Figure 6.12: The seasonal time budget of males. Proportion of time spent hauled-out per month with standard error (n = value in white).

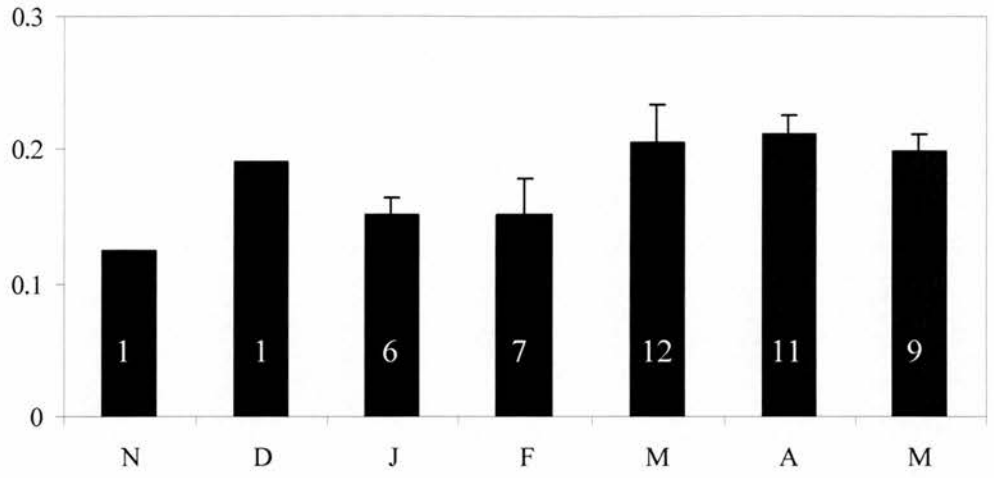

Figure 6.13: The seasonal time budget of females. Proportion of time spent hauled-out per month with standard error (*n* = values in white).

6.4.3 Distance and duration of foraging trips

Males travelled significantly further to forage than females (males: mean distance = 50.25 km, SE = 1.13km, *n* = 12; females: mean distance = 31.56 km, SE = 1.26 km, *n* = 12; *t* = 1.28, $p<0.01$). However, the difference in the duration that males and females spent on foraging trips was less significant (males: mean = 7.20 days, SE = 1.03 days, *n* = 12; females: mean = 4.85, SE = 1.04 days, n = 12; *t* = 1.60, *p* = 0.12).

Mean trip duration was positively related to body length (Spearman's rank correlation = 0.47, *p* = 0.019, *Figure 6.14*) but not to body mass (Spearman's rank correlation = 0.233, *p* = 0.274, *Figure 6.15*) or body condition index (Spearman's rank correlation = -0.157, *p* = 0.464, *Figure 6.16*).

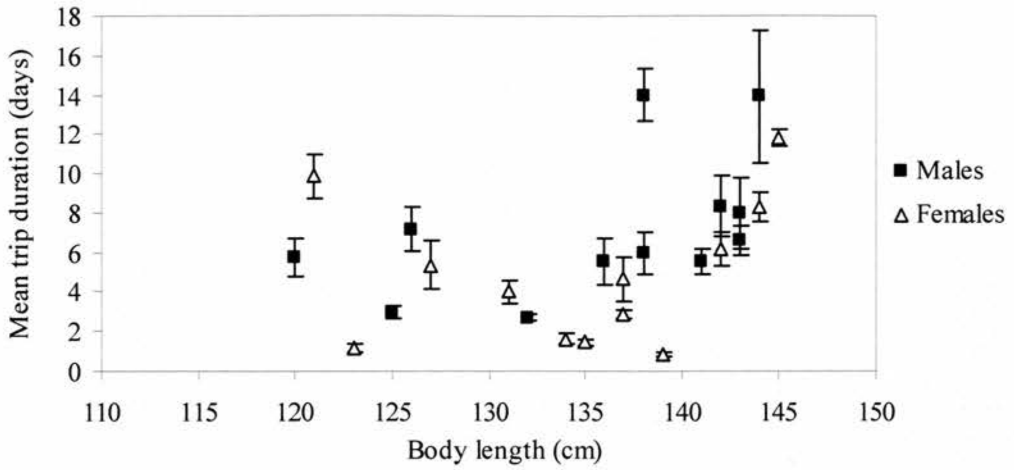

Figure 6.14: Mean foraging trip duration versus body length for 24 harbour seals with standard error (12 males, 12 females).

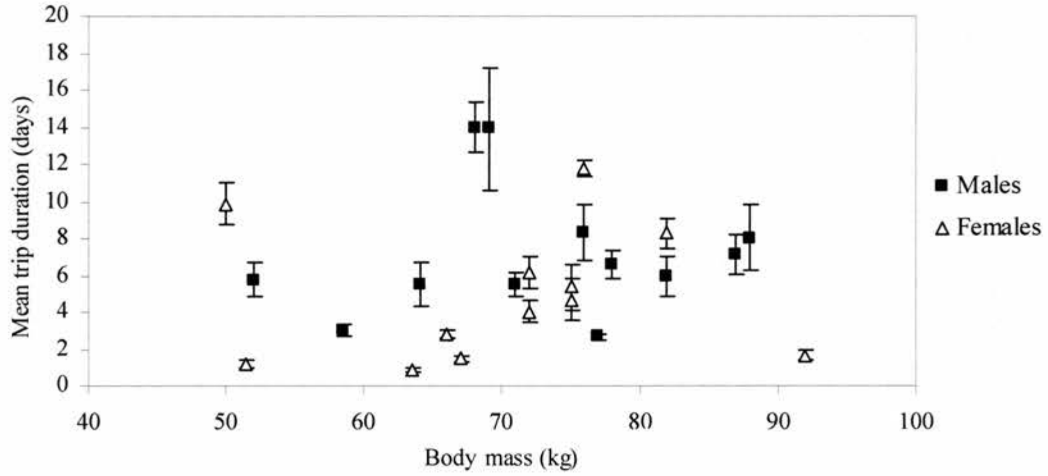

Figure 6.15: Mean foraging trip duration versus body mass for 24 harbour seals with standard error (12 males, 12 females).

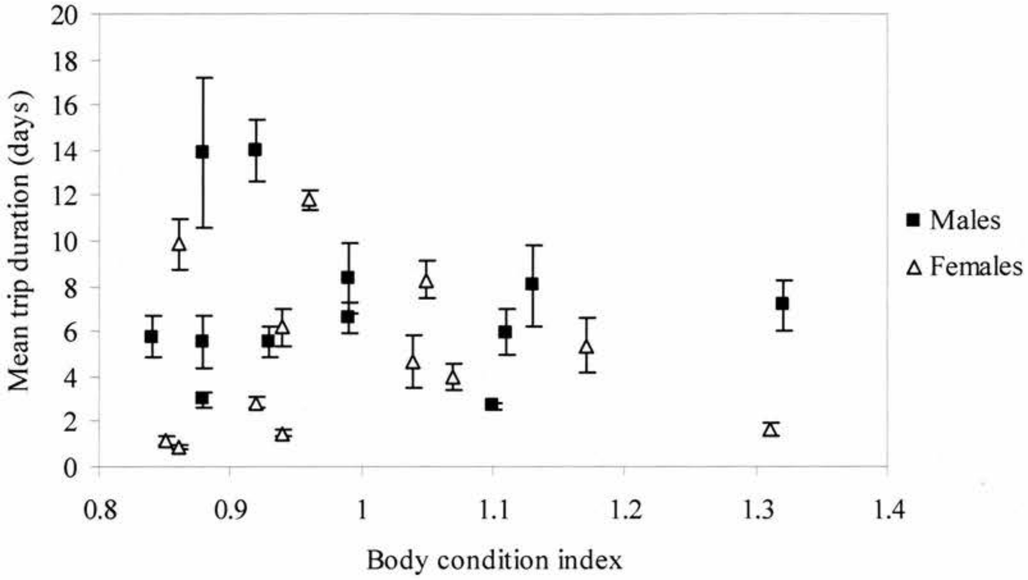

Figure 6.16: Mean foraging trip duration versus body condition index for 24 harbour seals with standard error (12 males, 12 females)

Mean foraging distance showed no significant relationship with body mass (Spearman's rank correlation = 0.469, p = 0.469, *Figure 6.17*) and a weak correlation with body length (Spearman's rank correlation = 0.351, p = 0.093, *Figure 6.18*) and no correlation with body condition index (Spearman's rank correlation = -0.197, p = 0.355, *Figure 6.19*).

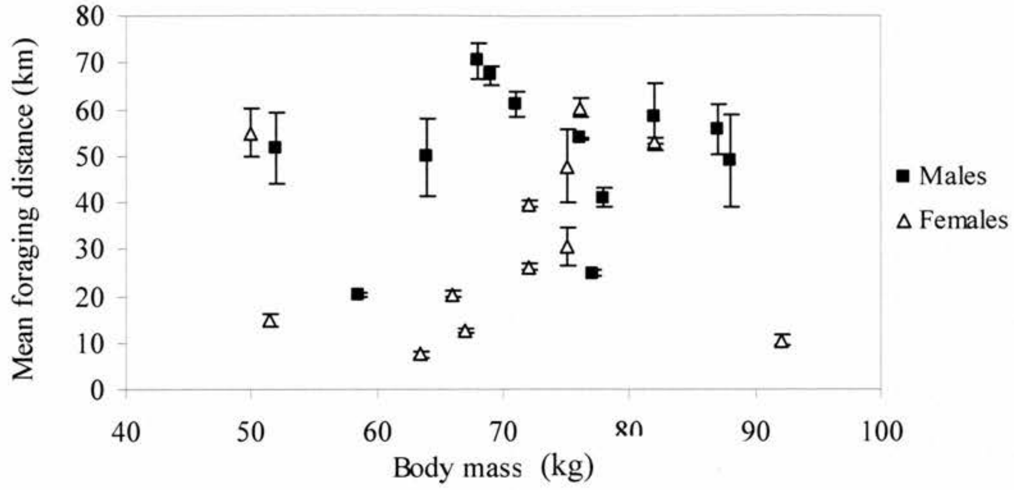

Figure 6.17: Mean distance travelled to forage versus body mass for 24 harbour seals with standard error (12 males, 12 females).

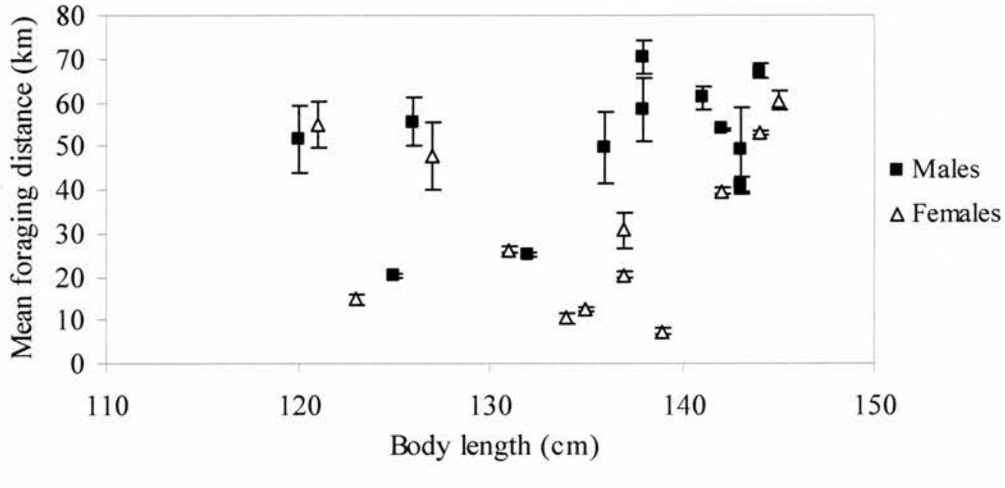

Figure 6.18: Mean distance travelled to forage versus body length for 24 harbour seals with standard error (12 males, 12 females).

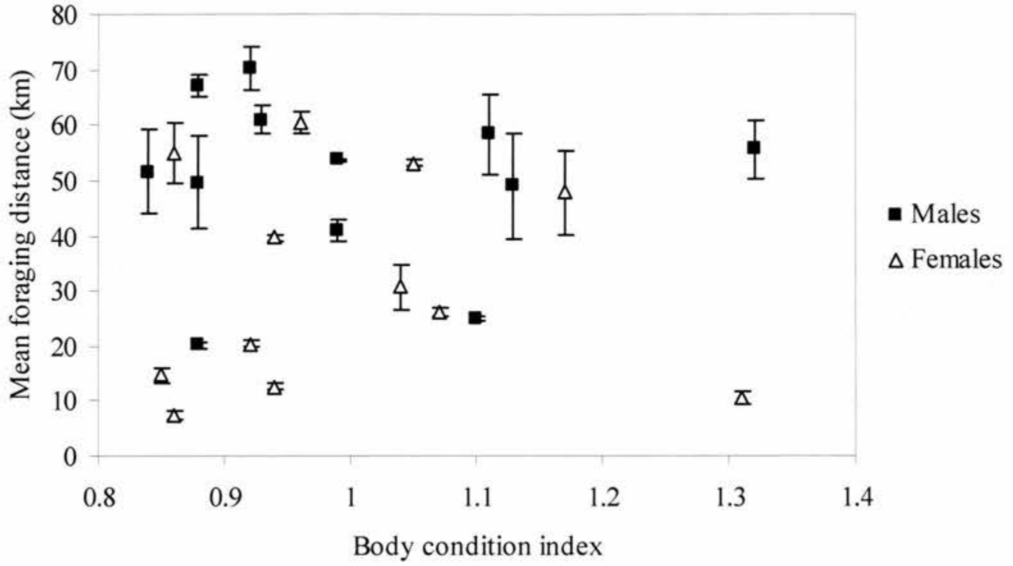

Figure 6.19: Mean distance travelled to forage versus body condition index for 24 harbour seals with standard error (12 males, 12 females).

There was a highly significant positive relationship between the distance travelled and the duration of a trip (*Figure 6.20*). There appears to be an upper cut off in the maximum distance travelled to forage, approximately 75 km excluding a few anomalies. There also appears to be two different distributions apparent in this graph. Those trips shorter than approximately five days and less than 40 km appear to have a quite a direct linear relationship where as those trips longer than this have a more scattered distribution. The characteristics of those animals making 'long' trips were compared with those making 'short' trips, there was no significant difference found between their length ('short': mean = 133 cm, SE = 1.99, n = 6; 'long': mean = 135 cm, SE = 2.03, n = 15; t = 0.52, p = 0.61) or mass ('short': mean = 67.56 kg, SE = 5.29, n = 6; 'long': mean = 71.58 kg, SE = 4.23, n = 15; t = 0.17, p = 0.87).

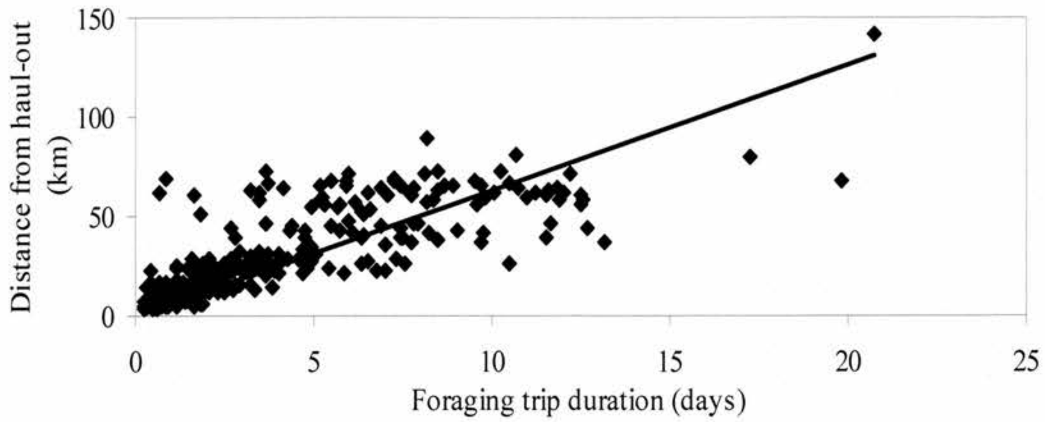

Figure 6.20: Relationship between distance from haul-out and foraging trip duration (Regression equation: $y = 4.943x$, $r^2 = 0.78$, $p < 0.0001$).

The GLMM with trip duration as the response variable only retained season and body length in the model using backwards selection, with season being highly significant ($p < 0.01$) and explaining most of the variance (*Table 6.2*). Body length did not show a significant relationship with trip duration, however its inclusion slightly improved the model fit.

Table 6.2: Coefficients, standard errors and significance of those variables included in the GLMM to model the duration of foraging trips.

Explanatory Variable	Coefficient	Stnadard Error	Significance
Season	0.133	0.062	$p < 0.01$
Body Length	0.002	0.005	0.923

The GLMM that best explained the variation in the distance travelled to forage retained season and length in the model, again using backwards selection. Again season explained the majority of the variation and was the only variable to show a significant relationship with the distance travelled to forage ($p < 0.01$) (*Table 6.3*).

Table 6.3: Coefficients, standard errors and significance of those variables included in the GLMM to model the distance travelled to forage.

Explanatory Variable	Coefficient	Standard Error	Significance
Season	0.003	0.001	$p < 0.01$
Body Length	0.0003	0.0006	0.257

6.5 DISCUSSION

Studies of activity budgets tend to be focused on the breeding or moult period when the maximum number of animals is hauled out and this information is then applied to estimate population size (e.g. Eberhardt *et al.,* 1979; Harvey, 1987; Thompson and Harwood, 1990 Härkönen *et al*., 1999; Huber *et al*., 2001; Simpkins *et al*., 2003). However, because males and females behave differently throughout these periods (Thompson *et al*., 1994; Van Parijs *et al*., 1997; Thompson *et al*., 1998), data collected from seals over the breeding period were excluded to focus solely on foraging behaviour.

Endogenous characteristics do explain some of the variation in foraging behaviour. Sex of the animal influenced the distance travelled by individuals with males travelling significantly further. It has been suggested that this difference may partly be explained by females being smaller in length, on average than males. The sex difference has also been attributed to differential cost of travel due to females being heavily pregnant for some of the study period (Thompson, *et al*., 1998). In this study, however, the males and females in this sample of animals were not significantly different in mass, length or body condition at the time of capture (*Figure 6.5*).

The proportion of time spent at sea and the duration of trips at sea were found to be positively correlated with body size and specifically with length rather than mass. This may be because the stage of the maturity of the animal is the best descriptor and that length captures this better than mass. Also the body condition index in male seals was negatively related to the proportion of time spent at sea, whereas no such pattern was apparent with females. There may be an optimum condition, above which buoyancy and diving capabilities are effected, below which may adversely effect growth and reproductive success. The relationship may not be apparent in females due to the maternal investment being made, energy attained foraging is being utilised in pregnancy rather than purely improving over all body condition.

GLMMs explaining the variance in both foraging trip distance and duration found that the time of year explained most of the variation in the trip characteristics observed. Endogenous characteristics of the animals added little to the models, although those explanatory variables that were retained in the models did reflect the results of the nonparametric statistical analysis. It is likely that the number of individuals sampled was insufficient, given the high degree of individual variation, to elucidate further the relationships between time at sea, foraging distance and trip duration in this instance.

Foraging distance was directly related to foraging duration. This is consistent with both theoretical studies (Stephens and Krebs, 1986; Boyd, 1996) and previous field studies of harbour seals (Thompson *et al.*, 1994). This is to be expected due to the increased travel time incurred to reach patches at greater distances, however the relationship persists beyond the additional travel time incurred. Optimal foraging theory predicts that as travel time to a patch increases, the optimal time that should be spent in a patch also increases (Stephens and Krebs, 1986). There was an upper limit in the distance travelled to forage by animals of approximately 75 km (*figure 6.20*). There are a number of possible reasons for this. The bathymetry of the study site means that with increasing distance from the haul-outs there is generally an increase in depth, so the time incurred in travelling to depth in the dive may prohibit these foraging dives from being very profitable at greater depth. There are a number of sandbanks throughout the study site known to house large populations of sandeels, one of the harbour seals main prey items. The distance travelled to forage may be reflecting the distribution of these sandbanks. Alternatively the upper limit of distance travelled to forage may reflect a necessity to be within a certain range of haul-outs. Animals in this area are spending extended periods at sea not hauling out. Animals are likely to be able to compensate for not being able to haul-out to a degree by resting at sea, inactive dives at sea are frequently observed, particularly at night. However there are likely to be many other benefits associated with hauling out, it provides an opportunity for social interaction, protection from marine predators, it may help prevent marine parasites and may provide thermal benefits in some seasons.

6.5.1 Foraging characteristics of harbour seals in different locations.

Information on foraging behaviour (Pitcher and McAllister, 1981; Harvey 1987; Thompson and Miller, 1990; Thompson *et al.,* 1994) and activity budgets (*Chapter 3*; Eberhardt *et al*., 1979; Thompson *et al*., 1987; Yochem *et al*, 1987; Thompson and Harwood, 1990; Mathews and Kelly, 1996; Thompson *et al*., 1997; Ries *et al*., 1998; Huber *et al*., 2001; Simpkins *et al*., 2003) of harbour seals has been collected throughout their range. However the two are rarely inclusive. Information on activity budgets tends to be focused on the haul-out behaviour throughout the breeding and moult season with an interest in estimating population size (e.g. Eberhardt *et al.,* 1979; Harvey, 1987; Thompson and Harwood, 1990 Härkönen *et al*., 1999; Huber *et al*., 2001; Simpkins *et al*., 2003). Foraging behavioural studies have focused on diving, diet or the horizontal movement of animals in relation to fisheries and environmental characteristics. There is little published data investigating foraging characteristics in relation to endogenous characteristics. However, comparable data on foraging behaviour has been published from north of a study site in the Moray Firth, on the north east coast of Scotland (57°41'N, 4°0'W) using VHF telemetry.

The influence of body size and sex on the characteristics of harbour seal foraging was investigated in the Moray Firth. However this study focused on a much smaller time period. Animals were tagged in April and May and as the study was focussing on foraging behaviour, data were excluded from adult females (>60kg) during the lactation period (June) and from adult males (>60kg) during the mating period (July-August) (Thompson *et al*., 1998). Comparing the foraging behaviour of animals in St Andrews Bay with those in the Moray Firth for the same months gives small sample sizes of animals in the St Andrews Bay, particularly males, as this study was looking at year round foraging behaviour.

St Andrews Bay is an open bay with the Eden and Tay estuary feeding into it. The sea-bed slopes gently, reaching 50 m in depth approximately 30 km offshore, and the sediment is largely sand with gravel. The Moray Firth is a more enclosed area, a triangular embayment consisting of three sheltered estuaries. The sea-bed slopes to 50 m in depth approximately 15 km offshore with the exception of deep basins (30-50m) created at tidal constrictions in the mouths of the estuaries. The sea-bed sediments are predominantly sand and muddy sand with patches of sediment containing mainly gravel, mud or rock (Tollit *et al*., 1998).

Both the foraging trip durations and distances of the seals tagged in St Andrews Bay were high compared to harbour seals studied in the Moray Firth and Norway (Bjørge *et al.*1995; Thompson and Miller, 1990; Thompson *et al.*, 1998). Data collection techniques differed in that VHF radio telemetry was used in these other studies and the period of data collection was much earlier (between 1988 and 1995) (Thompson *et al.*, 1998). When mean foraging distances travelled by animals in the Moray Firth and St Andrews Bay were compared using an unpaired t-test with Welch correction, the St Andrews Bay animals were found to travel significantly greater distances, when comparing females (Moray Firth females: mean = 14.87 km, SE = 1.63 km, $n = 14$; St Andrews Bay females: mean = 24.86 km, SE = 5.15 km, $n = 9$; $t = 1.86$, p=0.046) and males (Moray Firth males: mean = 25.52 km, SE = 2.97 km, n = 22; St Andrews Bay males: mean = 41.78, SE = 7.75, $n = 5$; $t = 2.26$, $p = 0.048$).

These differences could be confounded by the different technologies used. Satellite telemetry has associated error with Argos locations (*Chapter 2*). However VHF radio telemetry relies on triangulation from coastal vantage points. The 95 percent confidence intervals for each bearing taken were estimated to be ± 12 of the estimated bearing. This resulted in 90 percent of the error polygons associated with locations being an area smaller than 25 km^2, and all less than 100 km^2 (Thompson and Miller, 1990). This method does result in an increasing amount of error associated with locations obtained at greater distances from vantage points. Radio telemetry is also restricted in range to line of sight. Therefore, further ranging movements may have been missed. However, there is also a significant difference in the duration of trips in the two areas between females (Moray Firth females: mean = 30.38 hrs, SE = 2.78 hrs, $n = 14$; St Andrews Bay females mean = 72.14 hrs, SE = 14.41 hrs, $n = 9$; $t = 2.85$, $p = 0.022$) and males (Moray Firth males: mean = 61.07 hrs, SE = 12.68 hrs, $n = 23$; St Andrews Bay males: mean = 102.58, SE = 19.70, $n = 5$; $t = 2.59$, $p = 0.039$) from each area, providing evidence that the observed difference in distances travelled is real, as there was a direct relationship with foraging trip duration and distance in both studies.

Significantly longer trip durations and distances travelled to forage in St Andrews Bay suggest that foraging in the Moray Firth is more profitable closer to haul-outs than in St Andrews Bay. This could be due to more abundant prey in the Moray Firth or due to differing distributions of prey relative to the haul-outs in the two areas. Also the study in the Moray Firth study was conducted between 1988 and 1995 as apposed to 2000 to 2003 in this study, differences observed could be due to the differences in fish stocks between the times of study rather than geographical differences. Further studies of animals from the Moray Firth have been conducted in 2004-2005 with the same technology used in St Andrews Bay. Initial analysis of the data suggest that animals in the Moray Firth are being observed to be travelling further than in the previous study in this area, adding weight to the hypothesis that the differences observed are due to the different years of study rather than geographical differences.

6.5.3 Inter and intra specific competition

It is also possible that there are varying degrees of both intra and inter specific competition in the Moray Firth and St Andrews Bay. Harbour seals disperse from a central place to forage. If the population size is larger, animals may disperse further on average to avoid intra specific competition. In this situation, larger animals may be able to afford to travel further and dive deeper. However larger animals may be able to dominate those prime foraging areas closest to haul-outs excluding smaller animals, forcing them to travel further. This does not appear to explain the differences in foraging observed in the two areas because the minimum population estimates for the Moray Firth and St Andrews Bay in August 2002 were comparable, 789 and 668 respectively, (Duck and Thompson, 2003). Population estimates made using two different techniques of correcting counts using telemetry data are also comparable, 1653 in the Moray Firth (95 % CI, 1471 – 1836, Thompson *et al.*, 1997) and 1746 in St Andrews Bay (95 % CI 1238 - 2301 – Chapter 3).

Harbour seals are sexually dimorphic and the difference in foraging distances travelled between males and females may be a result of differing energetic constraints (Thompson *et al.*, 1998). Although body size was not significantly different between the sexes, in this sample of tagged animals males travelled further on average, implying that there may be a degree of niche partitioning between the sexes.

In both areas grey seals (*Halichoerus grypus*), harbour porpoises (*Phocoena phocoena*) and bottlenose dolphins (*Tursiops truncatus*) are also commonly seen. It is not clear what degree of interspecific competition there is between these marine predators and to what extent this affects the foraging behaviour of harbour seals in either of these areas.

6.5.4 Potential affect of increased drag on foraging behaviour

The deleterious effects of externally attached tags on the foraging efficiency of marine mammals and the parameters of interest that are being studied are rarely discussed. A study of female Antarctic fur seals carrying either a radio transmitter or a radio transmitter and a time-depth recorder found that those seals carrying both tags made significantly longer duration foraging trips to compensate for the effect of the additional drag (Walker and Boveng, 1995). There are no dedicated studies to investigate the effect the tagging devices have on marine mammals, partly because the tags are relatively small compared to the body size of the mammals, but also the logistics of laboratory based experiments with marine mammals in flumes is problematic. There have been several studies looking at the effect of tagging devices on penguins. The shape of tags was found to be very important, tags with a greater volume but with a reduced cross sectional area were found to improve swimming efficiency by 87 % relative to previous models of tags (Bannasch, Wilson and Culik, 1994). A recent study on Magellanic penguins (*Spheniscus magellanicus*) examining the impact of different antennae on transmitters found that those birds equipped with rigid antenna (3mm by 200mm) had a foraging efficiency five times less than that of unequipped birds (Wilson *et al.*, 2004).

The different technologies used in St Andrews and the Moray Firth may provide an alternative hypothesis explaining some of the differences in the time spent at sea and trip durations observed between regions. SRDLs (305 g) are larger than the radio transmitters (either 80 or 200 g) used previously in the Moray Firth and are positioned on the neck of the animal at the base of the skull (see *Chapter 2*), whereas the radio transmitters were glued to the top of the head.

The tags also differ in that the radio transmitters have a much longer and thicker but more flexible antenna. It is unknown how these differences in transmitters affected the behaviour of seals. SRDL technology is currently being used to update information on the offshore distribution of animals in the Moray Firth, this data will provide a more comparable data set as the effect of drag will be consistent in both data sets.

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CHAPTER SEVEN:

General Discussion

7.1 Overview of study

The main objective of this study was to improve our knowledge of the ecology of the population of harbour seals in southeast Scotland as well as the species as a whole. Prior to this study there was little information on the population of harbour seals hauling out within St Andrews Bay. A technique was developed (*Chapter 3)*, using satellite telemetry and counts of animals made at haul-outs to estimate absolute abundance of harbour seals throughout the year. This technique provides both the first estimates of absolute abundance of harbour seals in this area throughout the year as well as a methodology that can be applied to telemetry data from other areas or from other species. Year-round estimates of absolute abundance are useful for the conservation and management of the species, partly because they allow levels of prey consumption by the population in the area to be estimated, but also because levels of immigration or emigration to or from the area can be assessed. This study suggests that haul-out behaviour is not consistent between areas as the population estimate for St Andrews Bay is considerably higher than would be obtained if data on haul-out proportion from the Moray Firth (Thompson and Harwood, 1990) and the Wadden Sea (Ries *et al.,* 1998) had been used.

The diet of harbour seals was previously unknown for this area and using existing methodologies to study the contents of scat samples collected throughout the area the diet and annual consumption of the population has been estimated (*Chapter 4*). Six prey species made up more than 85 percent of the total prey consumed by weight. Overall the diet was dominated by sandeels (45%) and whiting (22%). There were significant seasonal trends in the consumption of sandeels, peaking in winter months when sandeels are dormant in the sand or spawning. Few sandeels were consumed in the summer months when the diet was dominated by flatfish, primarily flounder, as well as salmonids. There was considerable uncertainty surrounding the estimates of consumption largely due to small sample sizes; results should only be presented alongside an explanation of the various assumptions and sources of bias and error that are associated with them.

This study is the first in Britain to use satellite telemetry to study the movements of harbour seals at-sea (*Chapter 5*). Prior to this the population of harbour seals in Britain was thought to forage locally to haul-outs, based on studies in the Moray Firth where the majority of foraging occurring within 50 km of these sites (Thompson and Miller, 1990; Thompson *et al.,* 1991). The results of this study show that the foraging of animals from haul-outs in St Andrews Bay appears to be densely aggregated into 'hot-spots' of localised foraging activity, the most distant of these is approximately 60 to 70 km from the haul-out (*Table 5.2, Figure 5.7*). Harbour seals were found to be foraging in certain habitats significantly more often than would be expected from their availability compared to other habitat types, inferring preference. Dense foraging activity was found to be associated with gravelly sand in depths shallower than 55 m, which corresponds to the burrowing habitat of sandeels (Pinto *et al.*, 1984; Macer, 1996; Wright *et al.*, 2000) the seals main prey item (*Chapter 4*).

Activity budgets of individuals were correlated to their endogenous characteristics (*Chapter 6*). The distance travelled was significantly shorter for females (males: mean distance = 50.25 km, SE = 1.13km, n = 12; females: mean distance = 31.56 km, SE = 1.26 km, n = 12; t = 1.28, $p<0.01$). Both the proportion of time at sea and foraging trip duration were positively related to body length for both sexes. Endogenous factors are affecting foraging behaviour, and will therefore have important implications in assessing a population's energy requirements and diet composition.

7.2 Implications of findings

Harbour seals in southeast Scotland were found to be spending a greater proportion of their time at-sea than expected and the size of the population was therefore greater than expected from studies in other areas (*Chapter 3*). One implication of this is that the population has greater energetic requirements than might previously have been assumed. This is not only because estimates of abundance are higher, but also because of the high proportion of time animals are spending at sea, presumably reflecting increased foraging effort. A greater proportion of time at sea doesn't necessarily reflect increased foraging effort, it may be due to increased time spent resting at sea due to the proximity of profitable foraging grounds to the haul-out sites. Further analysis of the data received on diving behaviour would help elaborate on the level of activity while at sea.

Higher population estimates equate to greater estimates of fish consumption, therefore the potential impact on fish stocks, and interactions between this marine predator and fisheries are also greater. The species composition of the diet of harbour seals from St Andrews Bay was estimated in

Chapter 4, highlighting the degree of overlap with commercially exploited species of fish. The main concern expressed is over the impact of pinniped predation on stocks of salmonids (Harwood and Croxall, 1988). In St Andrews Bay the importance of salmon in the overall diet of harbour seals appears to be relatively minor, contributing about 5% by weight. However this amounts to two thirds of the estimated available biomass of salmonids in the River Tay catchment. The confidence intervals around the estimate of salmonids consumed using this method are very wide. Greater sample sizes and a more even geographical coverage are needed to be able to say whether these figures are representative of the population or whether samples from a few individuals specialising on salmonids were collected, biasing the results. Salmonid otoliths were only found in a few scats collected from haul-outs in the Tay Estuary in spring and summer and they were not found consistently across years (*Figure 4.7*). The observed distribution of foraging activity (*Chapter 5)* does not show areas of foraging within the Tay Estuary, however no animals were tagged from haul-outs within the Tay so the foraging locations are unlikely to represent those animals potentially foraging within the Tay on salmonids. If salmonids were a substantial part of the diet of the populations of harbour seals in St Andrews Bay we would have expected to see animals entering the Tay estuary from the surrounding haul-outs to forage, this was not observed.

As there are concentrated foraging areas that the majority of animals appear to be using, the consequences of human activity in these localised areas could have significant effects on the population of harbour seals in St Andrews Bay. In this area the most likely impact on these 'hot-spots' would be fisheries activity. If fisheries over exploited these areas the harbour seal population may be unable to find enough energy to make the population viable at its current size (*Chapter 6*). The sandeel fishery off the east coast of Scotland was closed in 2002 due to concerns about the effects that local concentrated fishing effort has on the predators in areas where they congregate (FRS, 2003). This was in relation to sea birds in particular, but if reopened this may also effect the harbour seal population.

The discovery in this study that animals are spending time further offshore than expected, alongside recent research carried out in Denmark (Tougaard pers. com.) and the Netherlands (Brasseur pers. com.) using satellite telemetry, has highlighted the at-sea distribution of harbour seals as an area that requires further study. Recently, DTI sponsored Strategic Environmental Assessments (SEAs) have supported research in Orkney, Shetland the Moray Firth and the Wash to determine any potential impact of offshore oil and gas exploration and production and wind farms on harbour seals. These SEAs have partly been fuelled by the recognition that seals are using more offshore areas and these ongoing satellite telemetry studies should provide a better understanding of the main areas of the North Sea being used by harbour seals, giving much greater geographical coverage rather than extrapolating results across areas. The information on harbour seals' at-sea distribution can be used in delineating conservation areas. Areas have previously been delineated by, for example, the 15 metre depth contour, which these results show this would not be very helpful in protecting harbour seals at sea covering only a very small proportion of their at-sea distribution.

There are many techniques that can be applied to gain further information on the ecology of harbour seals to help inform conservation and management decisions, the combination of scat analysis and telemetry used here do provide a wealth of information on the diet, population size and distribution of this population. To collect any detailed information on the areas animals are using to forage requires some form of telemetry and in this instance VHF radio tracking is insufficient in range to monitor all movements making satellite telemetry the one practical means to monitor the full extent of harbour seal distribution. Telemetry does however require the capturing and handling of seals (*Chapter 2*), which is quite invasive and not without risks. Throughout the course of this study there was one seal fatality. A healthy, pregnant, adult female harbour seal drowned in the net prior to it being hauled in, probably because the net was set across the current and the strength of current in the area was too strong, which put too much tension on the net, thus preventing the seal surfacing as is usually possible. This area was avoided in future trips and every effort was made to haul in the net as quickly as possible. There are other non-invasive techniques that could be used to carry out some aspects of this work, for example, use of natural markings on the pelage to identify individuals can be used to study aspects of activity budgets and in estimating population size, however this is very time consuming and not effective in all locations (Mackey, 2004; Hiby and Lovell, 1990). Other aspects of pinniped ecology cannot be studied effectively without attaching telemetry devices to them, in particular the at sea distribution and diving behaviour.

In this study, the ecology of harbour seals has been investigated, highlighting some of the interactions with their prey as well as identifying relationships with some physical attributes of their environment. Some of the results indicate that the quality of the marine ecosystem in St Andrews Bay does not match that in other areas, and in order to maintain the population at it's current size animals are having to spend longer foraging and travelling further to forage.

This study has highlighted some potential interactions with fisheries. There are concerns that localised exploitation of sandeels may impact on this marine predator and concerns that harbour seals may be impacting on the decreasing population of Atlantic salmon in the Tay River. It has also highlighted the need to study the at-sea distribution of this species prior to coastal developments, as foraging behaviour could be effected by developments occurring as much as 70 km from haul-outs and further in other areas. The data presented here provide much of the information needed to inform the conservation and management of the species.

7.3 Future Work

In the St Andrews Bay area there is further analysis that can be done with the telemetry data already collected. For example there are a lot of data on dive behaviour that has barely been used in the breadth of this thesis. Diving information can be used to help confirm the areas that are likely to be related to foraging as well as highlighting the part of the water column that is being utilised for foraging if related to the known bathymetry of the area. Dive behaviour can also be related to the endogenous characteristics of individuals to gain a better understanding of whether physiological constraints are effecting the observed diving and hence foraging behaviour.

There is also further information that would further the understanding of the ecology of harbour seals in southeast Scotland. Combining information on the distribution and abundance of prey with the movements of seals would help provide further insights into how harbour seals behave in response to the availability of prey. Greater sample sizes of scats in the area are required to gain a better understanding of the diet in this area, in particular in relation to the consumption of salmonids. This information is required to help inform the decisions of designating the Tay Estuary as an SAC for harbour seals considering the potential level of salmonid consumption highlighted in *Chapter 4*.

It would be valuable to quantify the effect satellite tags have on the behaviour of individuals due to increased drag. Particularly if satellite telemetry is being used to help estimate the size of the population (*Chapter 3*), increased drag could cause animals to increase their foraging effort and therefore the proportion of time at sea which leads to an overestimate of population size.

There are now many areas in Britain where satellite telemetry has been used, to study the at-sea distribution of harbour seals. Satellite telemetry has been used to track harbour seals from the west coast of Scotland, Orkney, Shetland, the Moray Firth and the Wash. These data sets provide a valuable opportunity to compare many attributes of behaviour in these different areas and different habitats. There are future plans to combine all the telemetry data in Britain with that collected in Norway and the Netherlands to look at North Sea wide usage by harbour seals.

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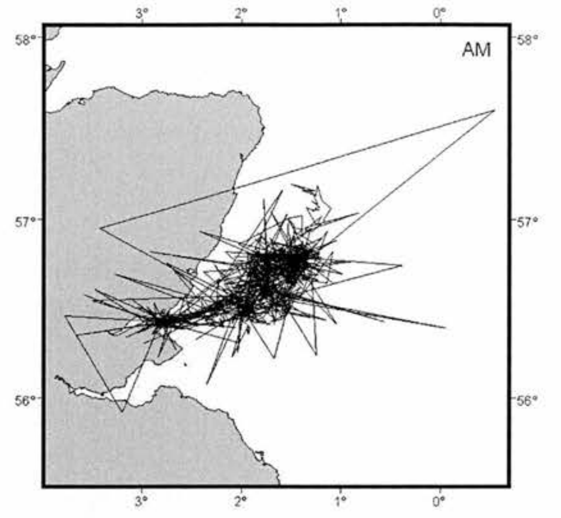
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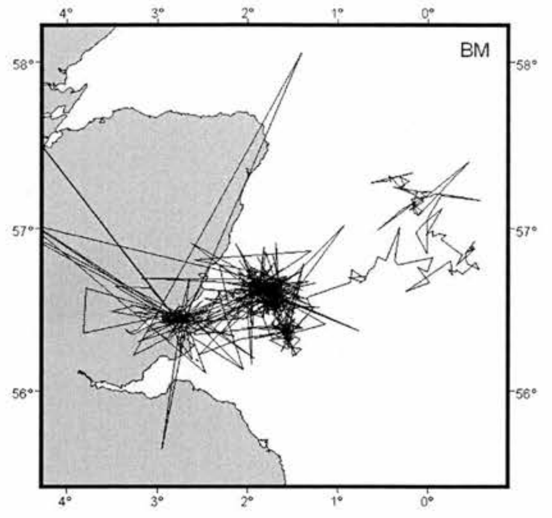
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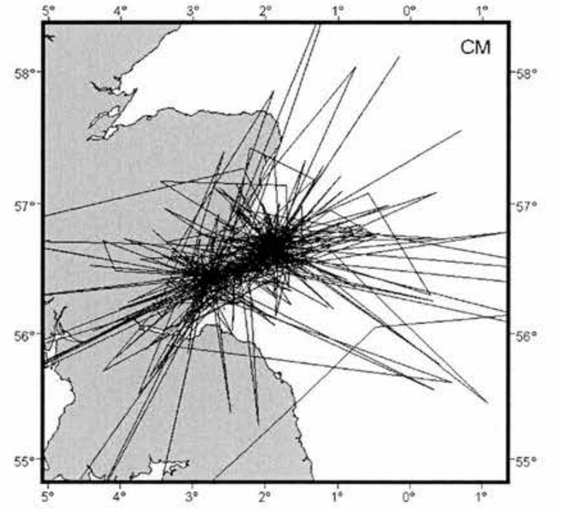
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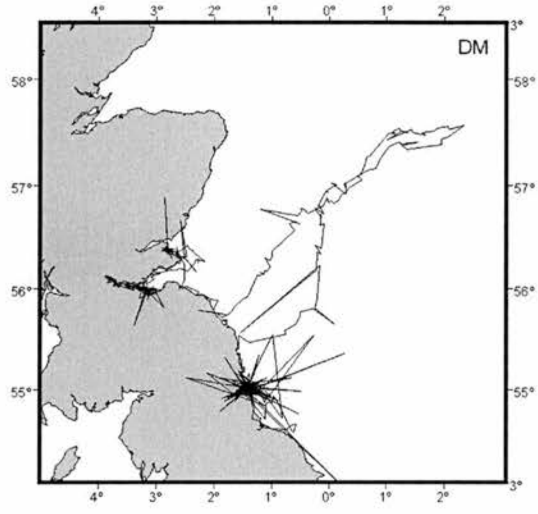
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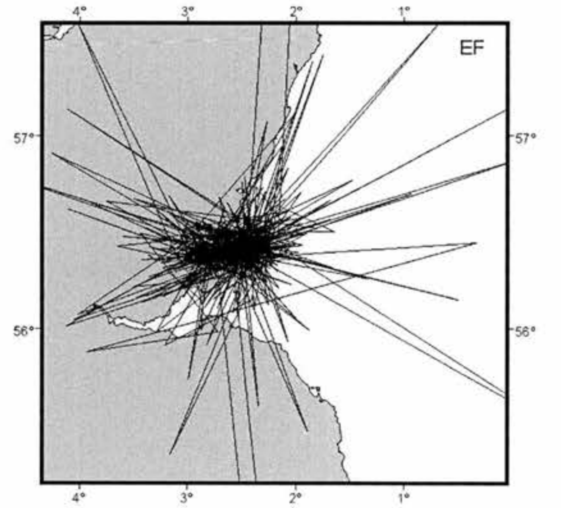
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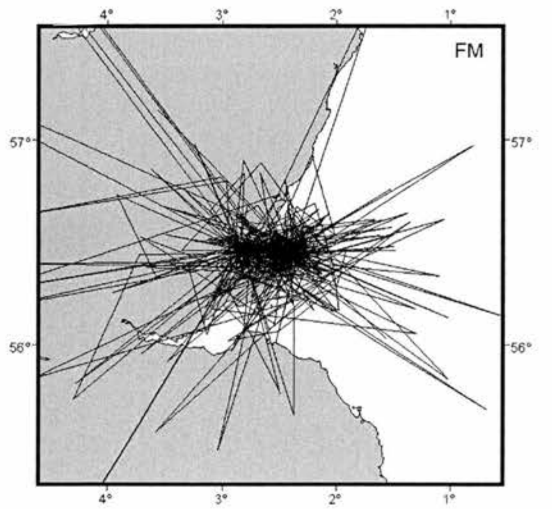
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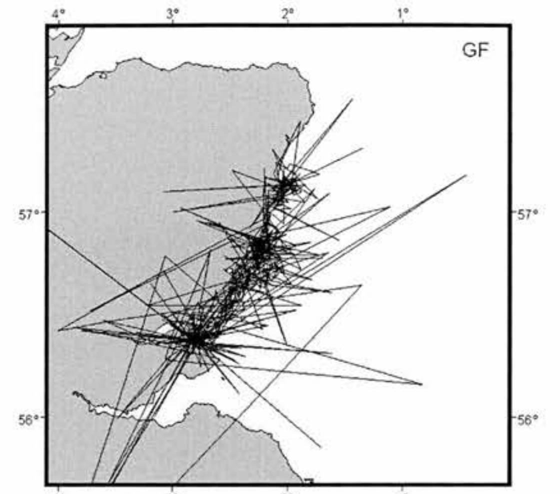
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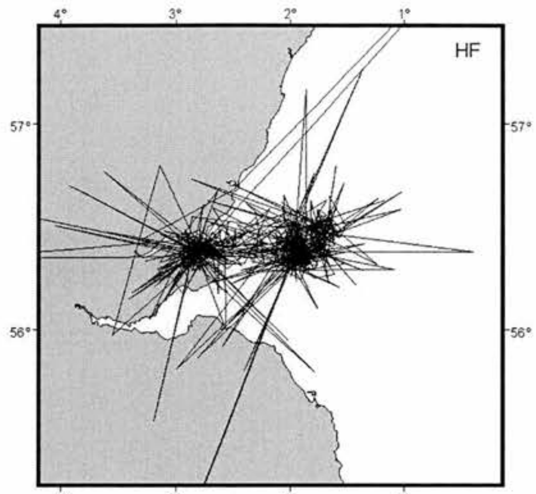
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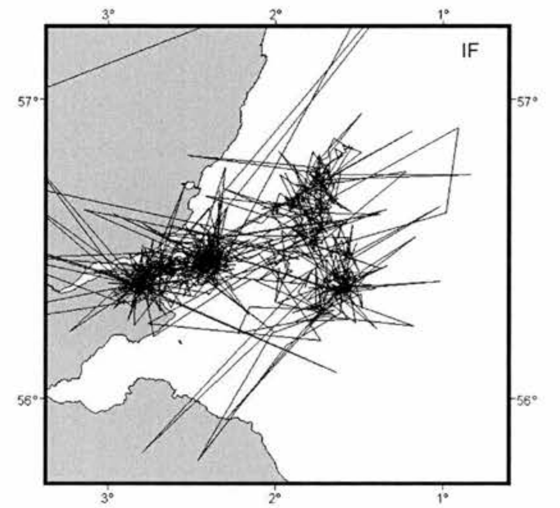
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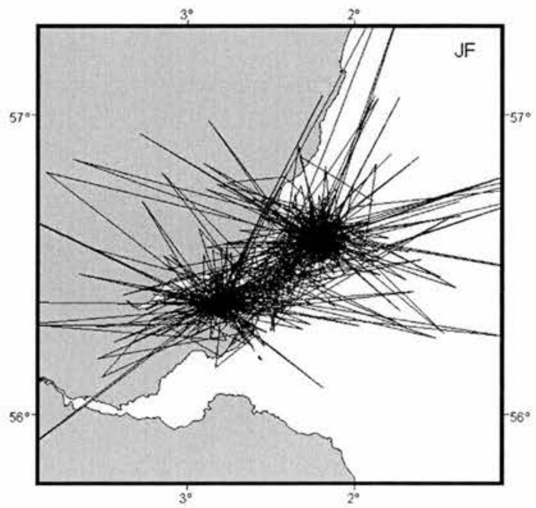
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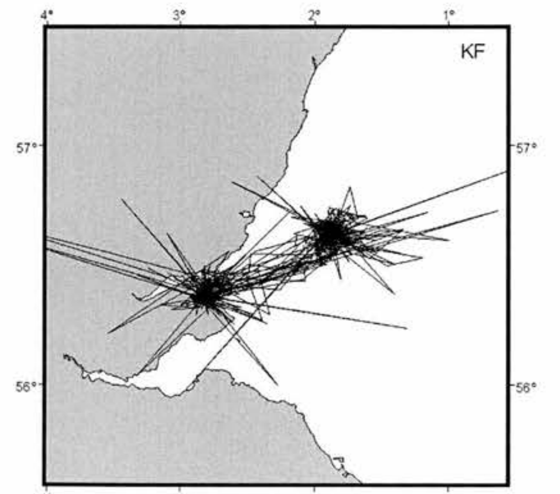
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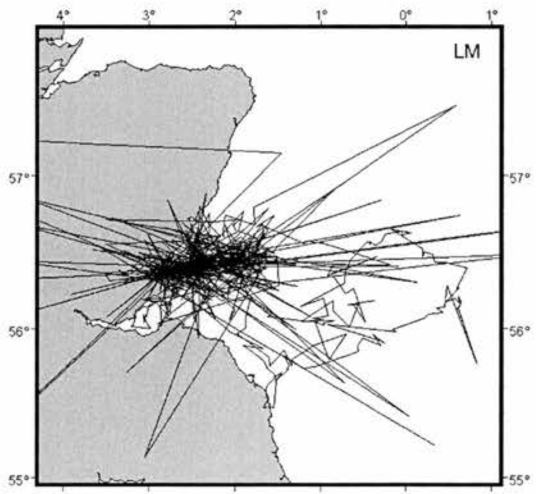
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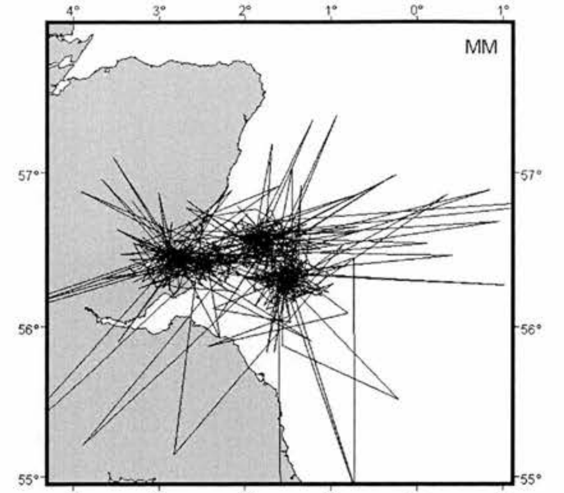
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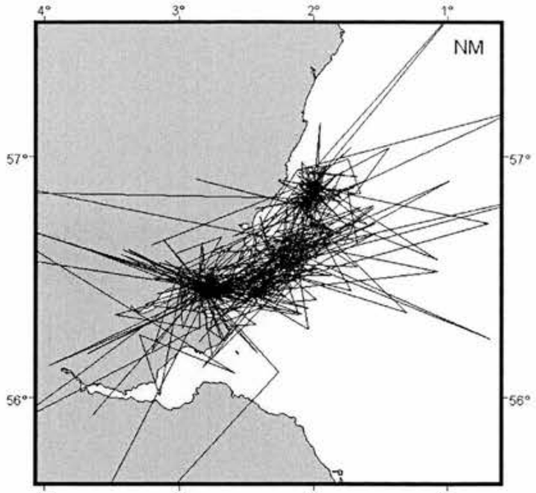
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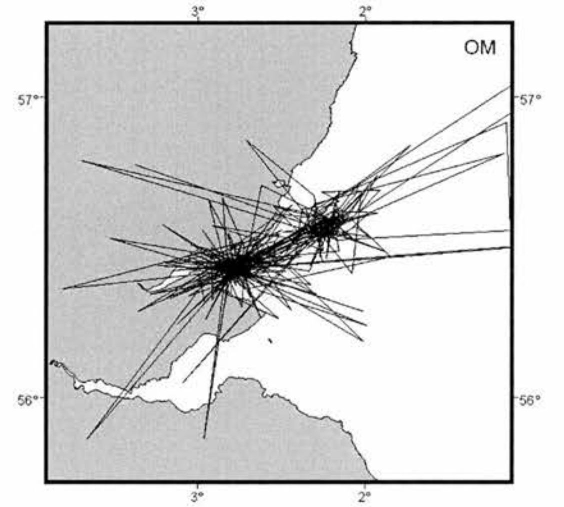
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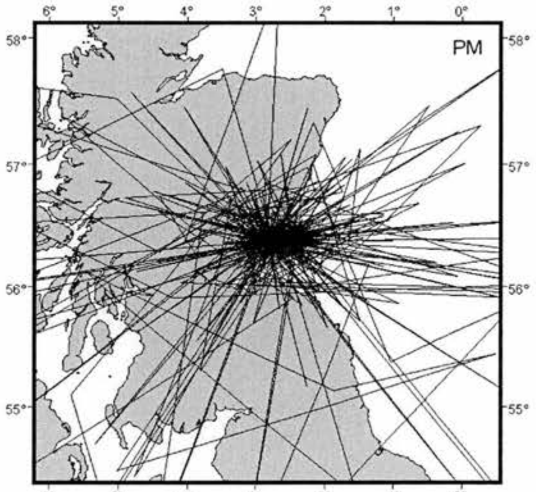
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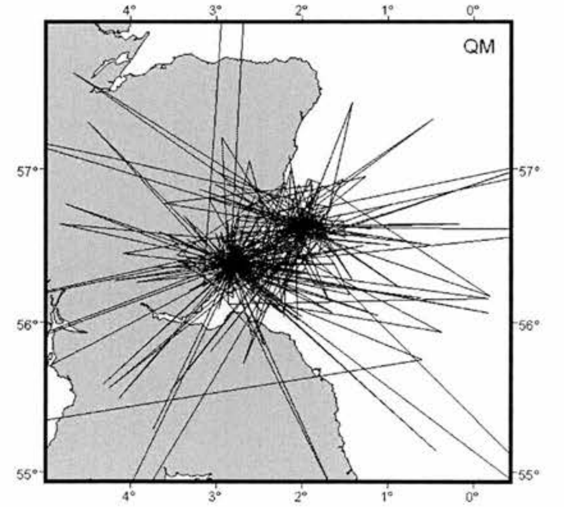
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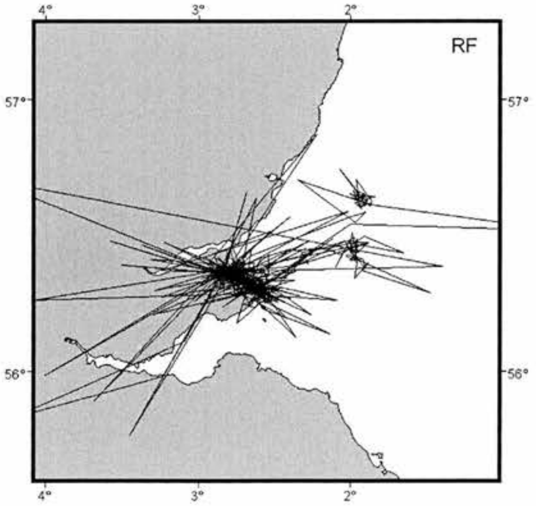
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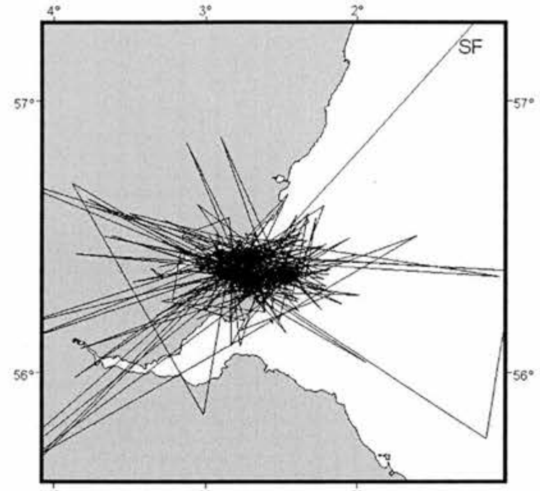
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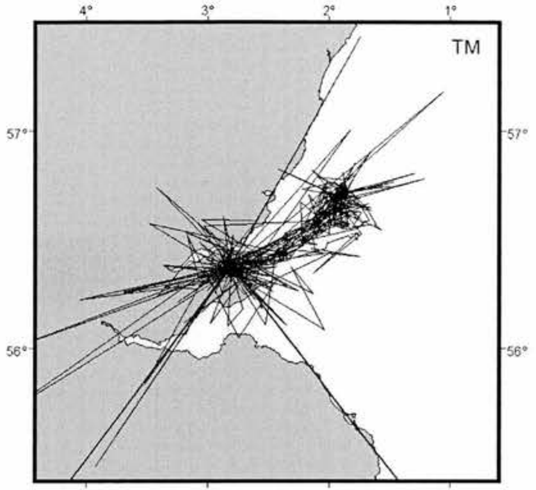
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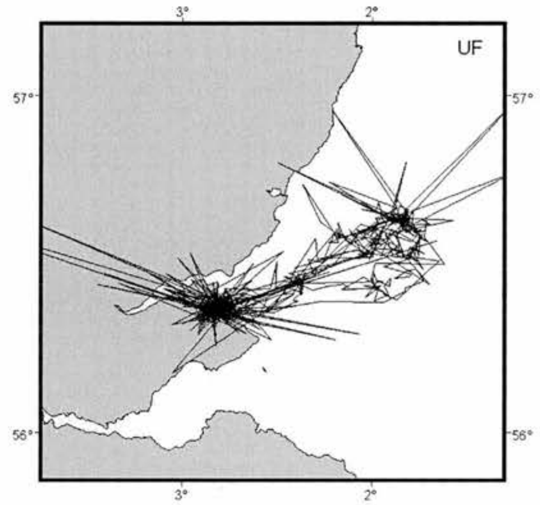
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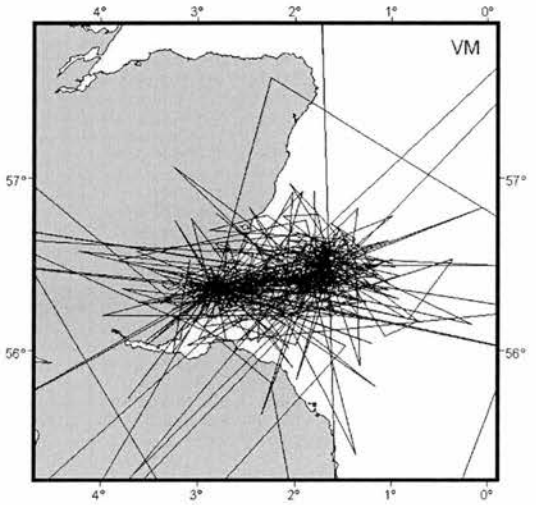
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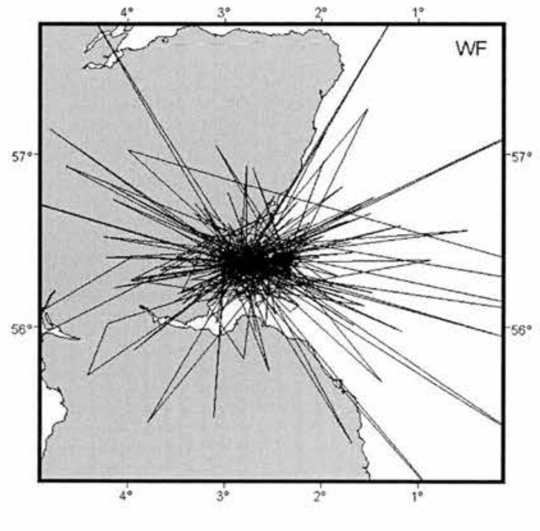
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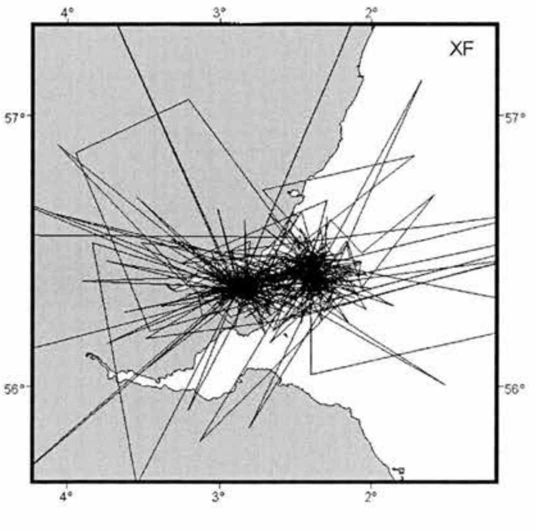
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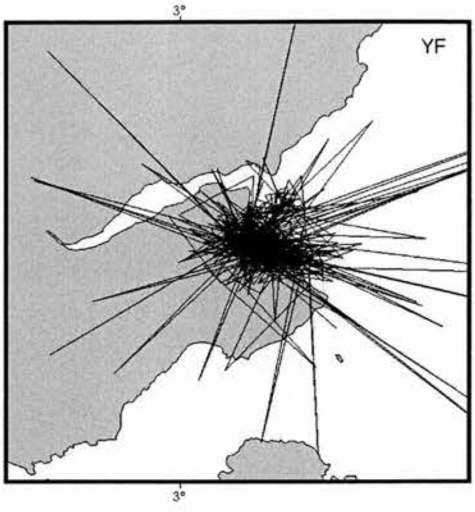
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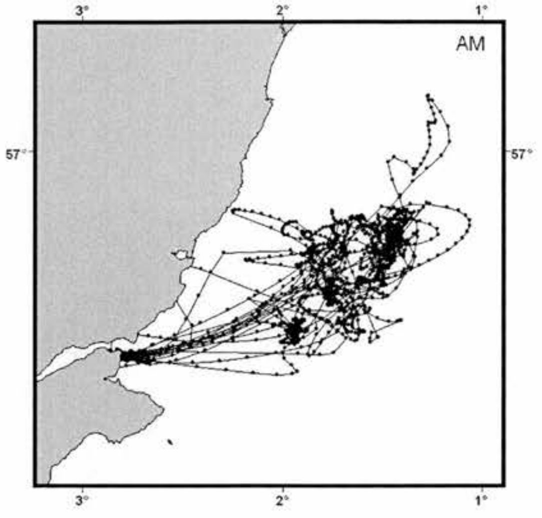
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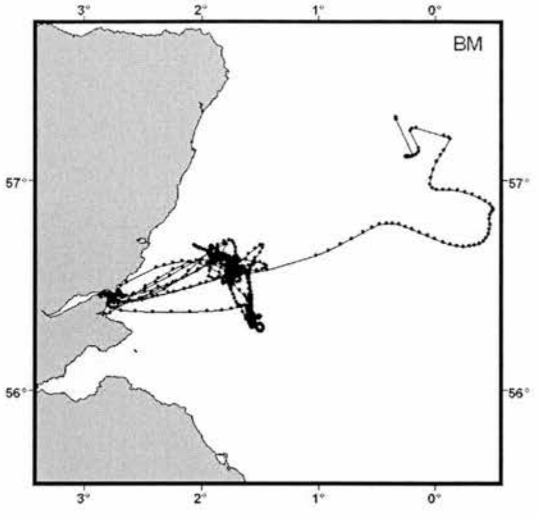
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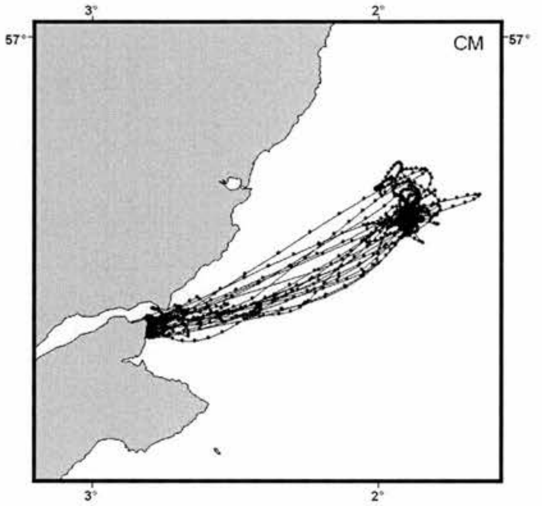
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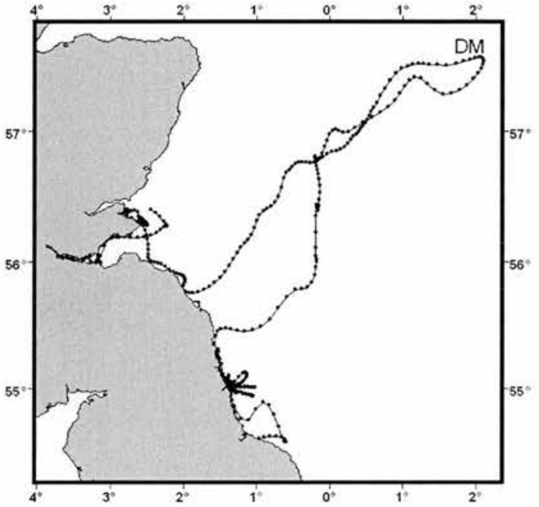
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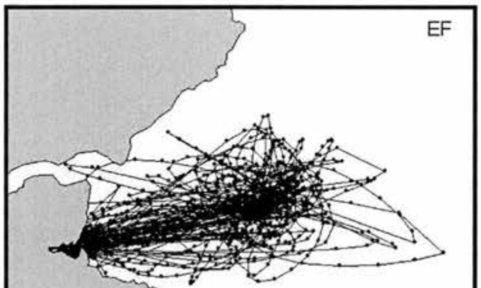
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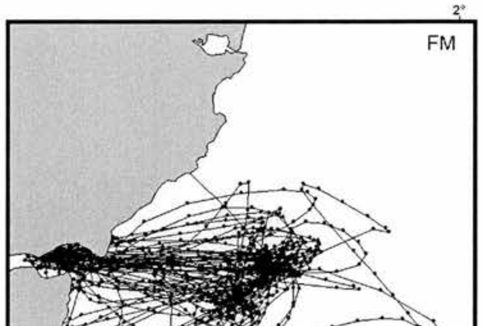
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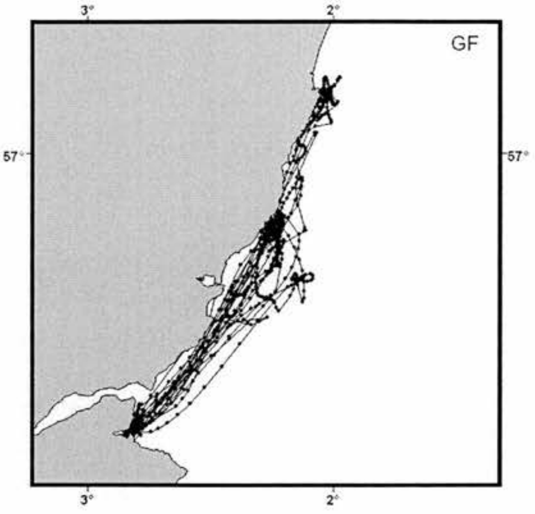
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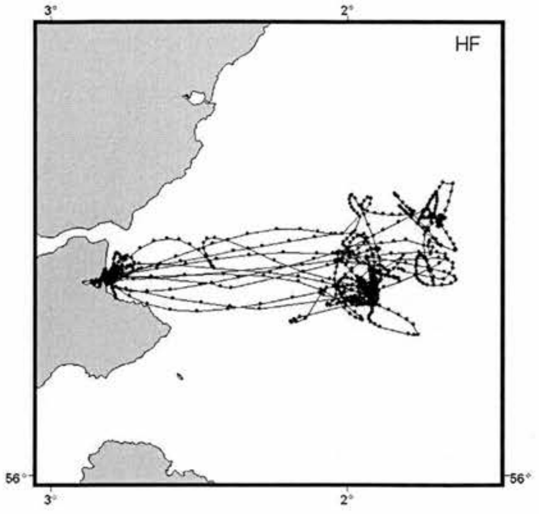
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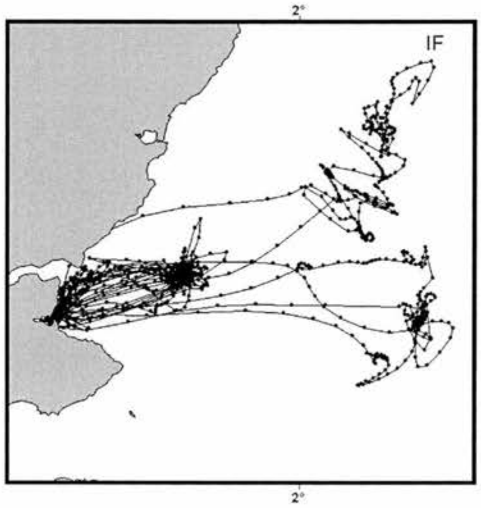
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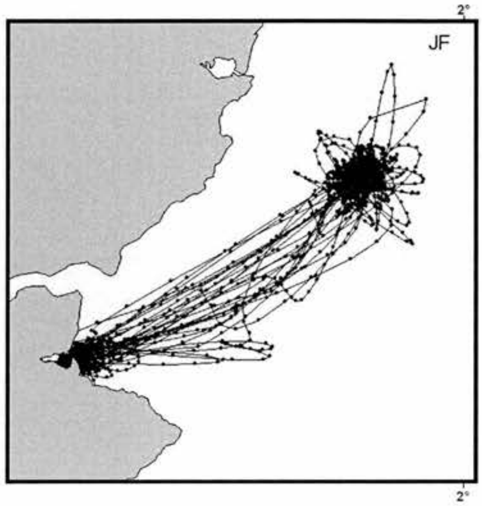
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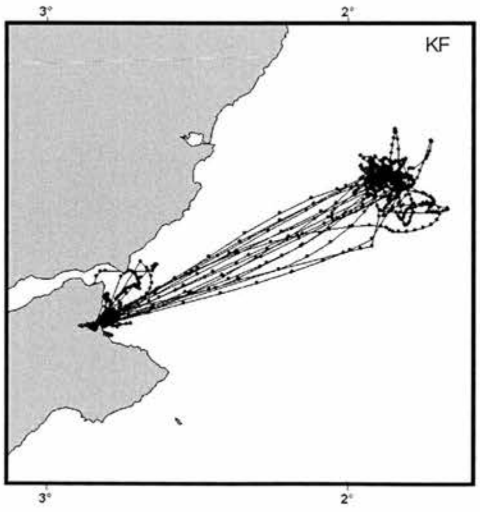
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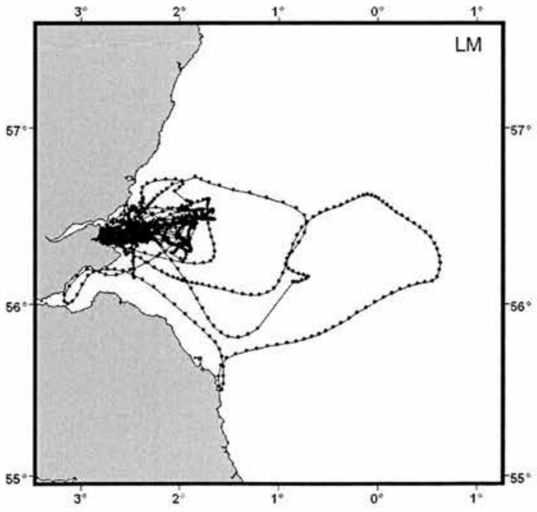
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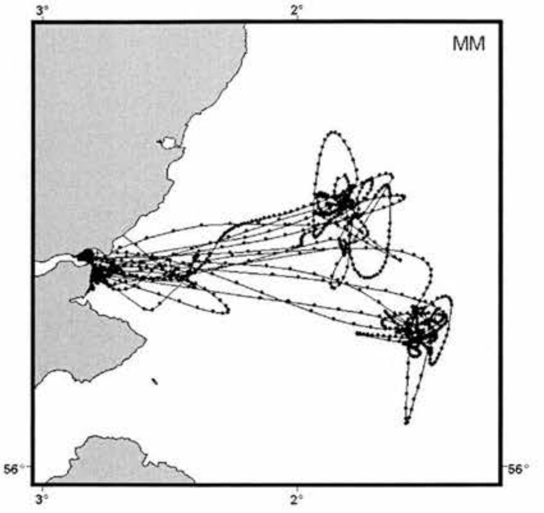
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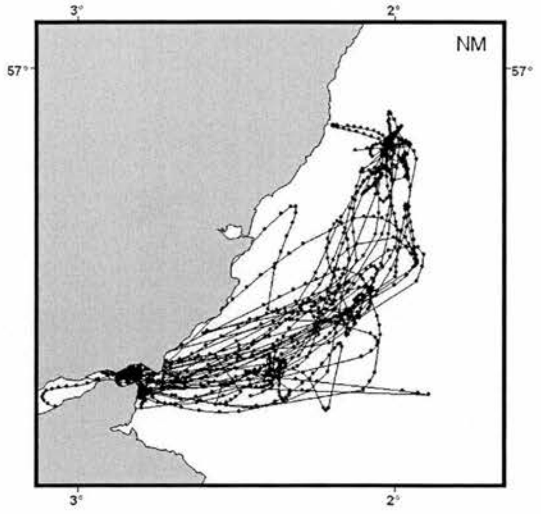
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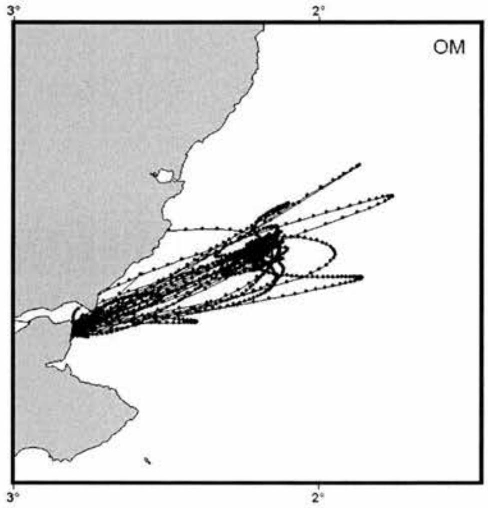
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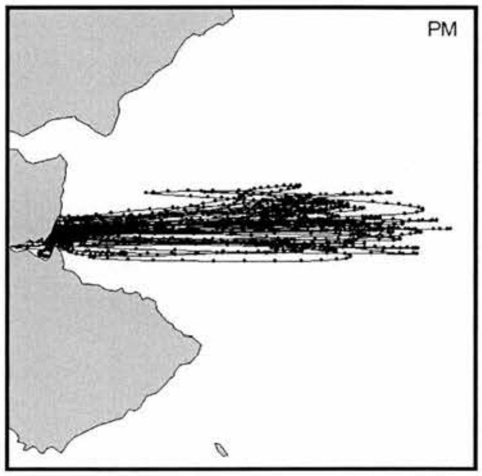
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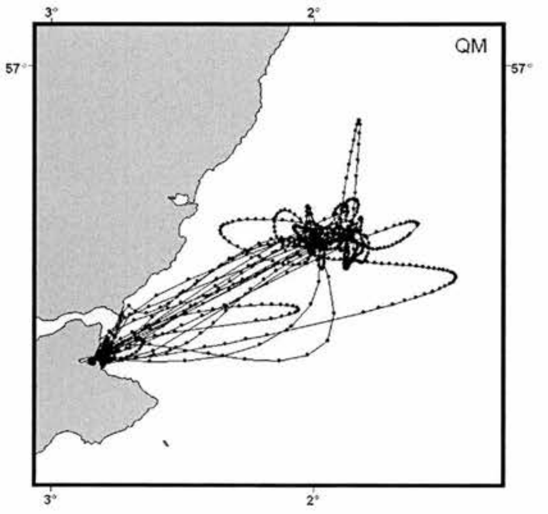
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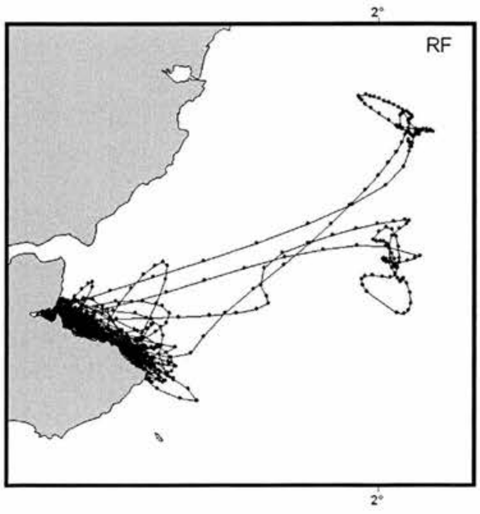
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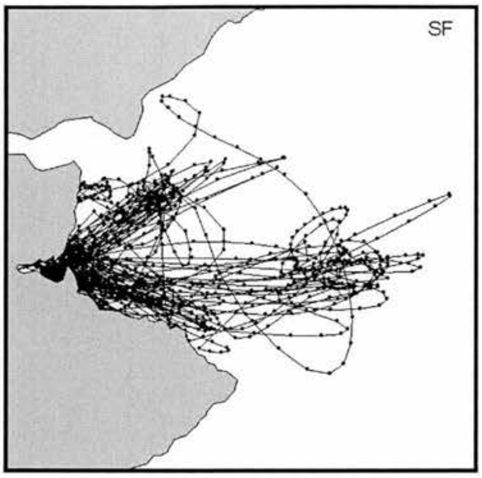
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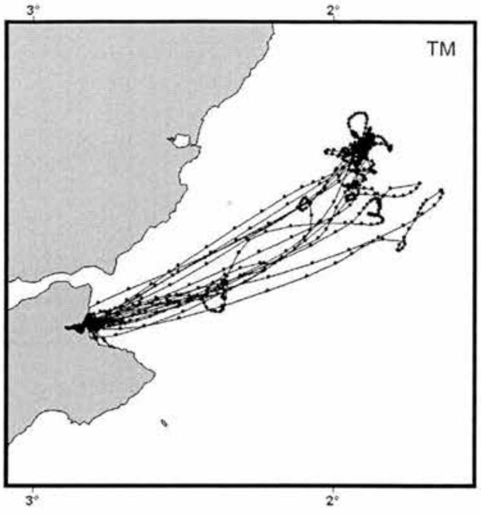
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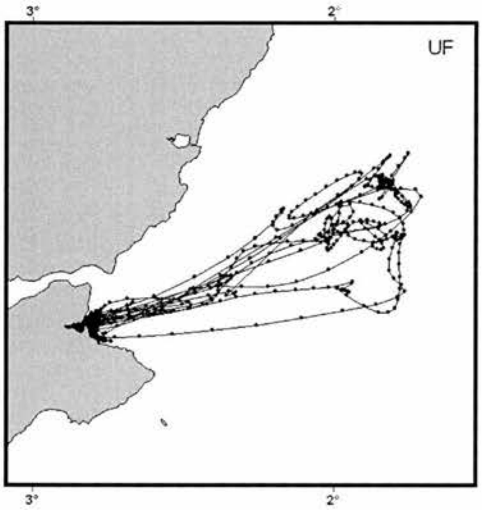
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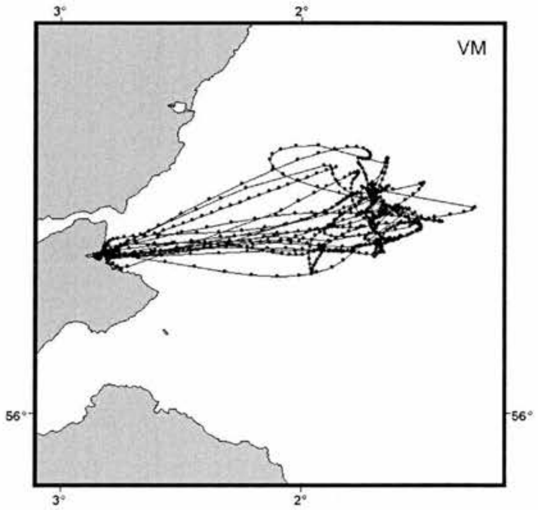
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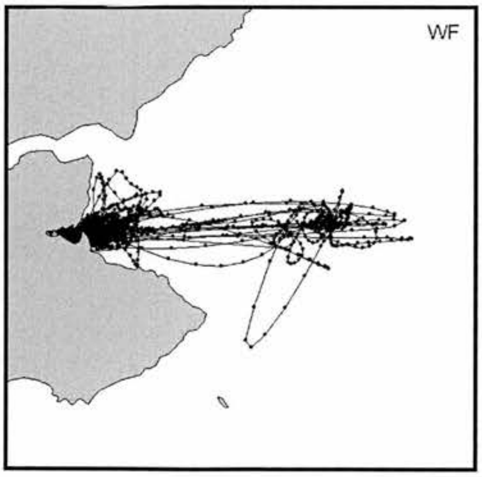
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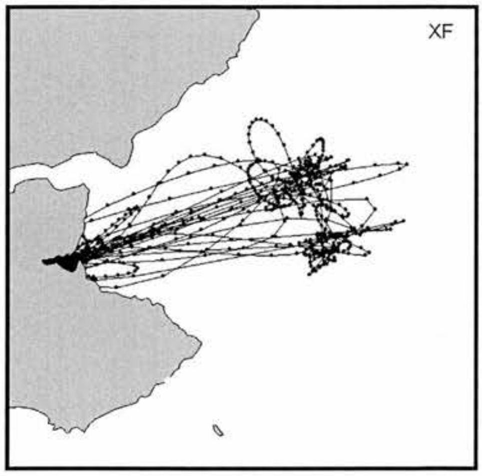
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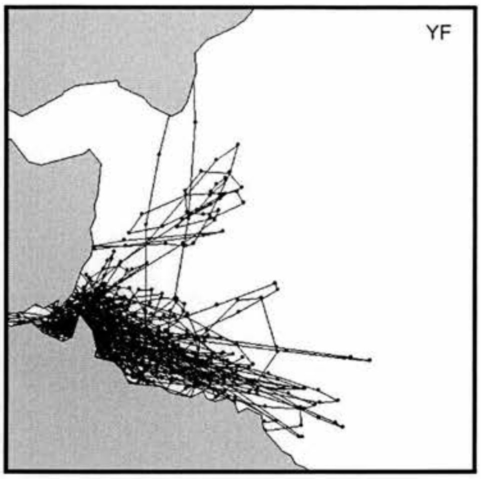
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