ASSESSING GREY SEAL (*HALICHOERUS GRYPUS*) DIET IN WESTERN SCOTLAND

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

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Contents

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Abstract

Grey seal diet was last comprehensively studied in western Scotland in 1985. Since then, the grey seal population has increased by approximately 30% and relative abundance of fish stocks in the area has changed markedly. The aim of this study was to provide a current assessment of diet to inform policy issues related to the impact of the still increasing grey seal population on commercial fish populations. During 2002, nine sampling trips totalling 56 days were completed around western Scotland, resulting in the collection of 1,589 grey seal scats. Forty-nine prey species were recorded in these samples revealing that grey seals on the west coast of Scotland remain highly catholic in their diet. Seasonal and regional variation in diet composition was assessed and the annual consumption of commercial fish species estimated. Proportions, by weight, of prey species indicated that gadoids were the main prey. Sandeels were also an important component of the diet. Comparisons between 1985 and 2002 revealed many similarities in diet composition but declines in the importance of sandeels, ling and megrim were balanced by increases in haddock, lemon sole, pelagic species and several benthic species. Changes in the size of fish stocks partially explain some of these changes. One exception is cod, which, despite very low abundance in 2002, formed a significant part of grey seal diet in western Scotland. Results from this study highlight the need for better methods for assessing absolute stock abundances for 'critical' fish species west of Scotland. Reducing the uncertainty over estimates of grey seal population size would also improve consumption estimates. The results from this study will be important to conservation and fisheries managers in Scotland.

1. Introduction

The study of marine ecology attempts to understand the interrelationships between organisms and their biological and physical environments and how these interactions affect their distribution and abundance within their ecosystems (Levinton 2001). Ecological studies have provided important information on nature and many underlying mechanisms, which have lead to increased concerns over the effects man's activities are having on the environment, prompting awareness for the importance of conservation.

Studying the dynamics of single species alone is not enough when it comes to managing a fishery, as the fishery not only affects the target species but many other species through interspecies interactions (Laevastu et al. 1981). Marine ecology is overwhelmingly complex, there is rarely a definitive answer to any scientific investigation; by improving our knowledge of how these links within ecosystems work we can constantly update and improve our working knowledge of these systems (Mann et al. 1996). This in turn better allows us to inform policy and action, conservation and management.

There is a long history of conflict between commercial fishing interests and marine top predators, which have been likened to a competing fishery (Harwood 1992). It is important that we have a good understanding of the role predators play within marine ecosystems, as this will provide the bases for evaluating any potential impact, as will the function of all other aspects of marine ecosystems, biological and physical. The removal or decline of one species may not necessarily mean an increase in another (Punt & Butterworth 1995).

If we are to maintain biodiversity and extract certain species at a maximum level then it is essential that we have a complete understanding of these processes to better manage the resources. It is clear that the distribution and abundance of top predators does have important consequences on the structure and function of some systems. Developing a better understanding of the role these populations play within ecosystems will only be developed slowly with long-term research and will remain one of the greatest challenges facing ecologists (Bowen & Siniff 1999).

West Coast of Scotland

The marine environment west of Scotland is a highly heterogeneous zone, with physical and biological features constantly changing. This results in a patchy rather than even distribution of marine organisms. As the distribution of predators, during foraging periods, generally relates to that of their prey species (Pollock et al. 2000), whether that be due to movements or abundance of fish stocks, or the presence of high productivity in the case of areas of upwelling or fronts (Barnes & Hughes 1988), it is important to first provide a brief description of the physical and oceanographic features of the area of interest: International Council for the Exploration of the Seas (ICES) sea area VIa (Figure 1).

The underlying seabed of ICES sea area VIa comprises a wide variety of substrate types and topography. The continental slope runs south-west to north-east, with water over 1,000m deep in many areas. The shelf edge lies approximately 65km north-west from the Western Isles, where deep water rises steeply to shelf waters of around 200m. In many areas, as the coastal zone is approached, the bathymetry often fluctuates widely giving rise to underwater channels, holes, ridges, banks and reefs (Macmillan Reeds Nautical Almanac 2002). Amongst this plethora of marine features and associated islands, a wealth of habitat types can be found.

The currents of the North Atlantic Ocean are the main influence on the west coast of Scotland, where nutrient rich waters of the Atlantic are forced to the surface at the continental slope and carried into shelf or neritic water (Barnes & Hughes 1988). Within these waters the myriads of small-scale currents, back eddies, gyres, upwellings and overfalls, created by tidal action on marine topography are important at a local scale (http://www.jncc.gov.uk/page-2531).

Water temperature and salinity in the study area can vary with large-scale changes in hydrographical conditions occurring within and between years (Dooley et al. 1984). Such seasonal changes play an important role in many biological processes. Within neritic waters variation in water depth and tidal influences result in mixing of the water column. Where this meets thermally stratified water or wherever water depth suddenly alters, resulting in changes in current speeds, frontal systems may occur (Mann & Lazier 1996).

The outcome of this environment is a complex ecosystem made up of a wide range of habitat types that support a high biodiversity of marine organisms. Although much is known about some aspects of this system, especially those of commercial relevance, our knowledge of most is poor.

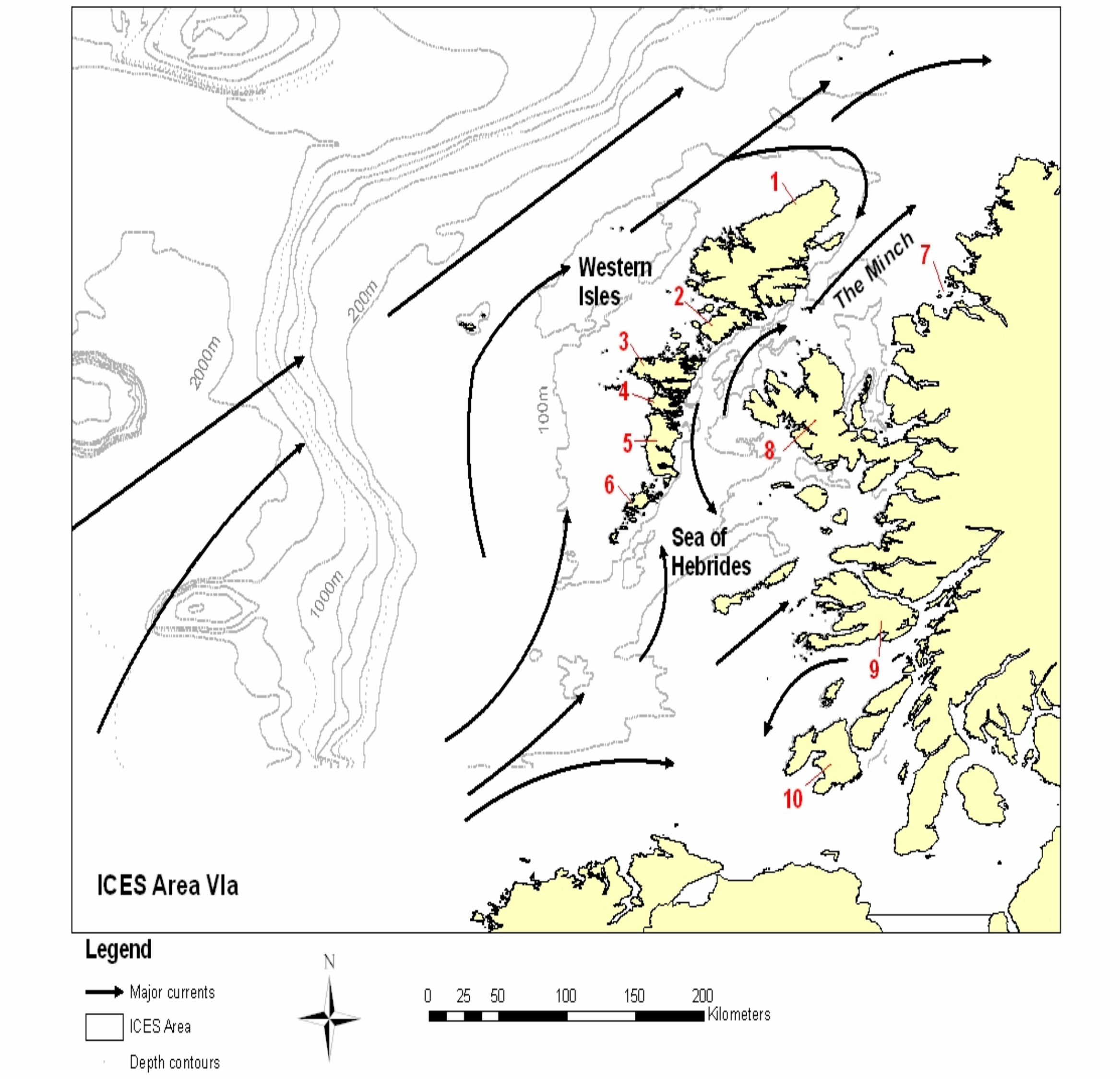

Figure 1. ICES area VIa west of Scotland showing major currents, sea areas and island groups; Lewis 1, Harris 2, North Uist 3, Benbecula 4, South Uist 5, Barra 6, Summer Isles 7, Skye 8, Mull 9, Islay 10.

ICES VIa's fishing fleets

Many of the species that thrive in these seas have commercial value, generating a large fishery. The main fleets operating in this area include the mixed roundfish otter trawl fleet, fishing for cod, haddock, monkfish and whiting with bycatches of saithe, megrim and lemon sole, the *Nephrops* otter trawl fleet, the otter trawl fleet targeting monkfish, megrim and hake and the fleet targeting saithe and/or deep sea species. The latter three fleets also land small quantities of haddock, cod, whiting and small saithe, but often discard large amounts of the whiting and haddock. In addition a pelagic fishery for herring operates at a low level, probably due to a weak market. There are also fisheries for mackerel and blue whiting. The sandeel fishery on the west coast, unlike in the North Sea, is irregular because abundance and distribution of sandeels fluctuates widely, and the fishery is dependent on the availability of processing plants (ICES 2004).

Stock assessments

Around the UK the Centre for Environment, Fisheries and Aquatic Sciences (CEFAS) and the Fisheries Research Service (FRS) of the Scottish Executive are responsible for carrying out the annual International Bottom Trawl Survey (IBTS), which is coordinated by ICES, to provide data for the assessment of stocks. IBTS are carried out in a standardised way with consistent methods and are regularly distributed in time and space covering all ICES rectangles in quarter 1 and/or quarter 3 each year. Some additional surveys are conducted during quarters 2 and 4. Data produced from these include calculated Catch per Unit Effort (CPUE) for a given prey class. However, because trawls only sample a fraction of the water column and there is large variability in the catchability of many species and their year classes, converting catches to estimates of abundance is far from straightforward (Harley et al. 2001).

Cod stocks west of Scotland are thought to be close to or at historically low levels during the 2000-2003 period and are below precautionary levels (http://www.jncc.gov.uk/page-2531). Haddock however have shown a temporary recovery after a single strong year class. The whiting stock size is uncertain but is thought to be at historical low levels after being in decline since 1981. Megrim stocks are uncertain as pressure has increased as fleets have moved further offshore. Fishing pressure on herring stocks in this area is thought to be low and the stocks have shown signs of increase and are thought to be above the precautionary level (ICES 2004). Status of the west of Scotland sandeel fishery is uncertain and is protected by closing the fishery after 31 July each year in an attempt to protect a food source for breeding seabirds (DEFRA 2005).

The coverage of IBTS is very limited, with respect to the distance between survey trawls and the areas that they can trawl. For example, vessels are unable to trawl over rocky bottom types, which are especially prevalent close to shore and the west coast of Scotland as a whole. These are likely to be the areas that are particularly important to piscivorous predators such as seals.

Fish species often display changes in their behaviour during their life cycles. For example, some species change their habitat use, such as sandeels which spend part of the year buried in sediments and as a result are a notoriously difficult species to survey with IBTS (Wright et al. 2000; Greenstreet et al. 2006). Other species make migrations between different areas that may take them away or closer to a central placed forager or a trawl survey. Fish/prey abundance is particularly difficult to estimate accurately and as a species becomes scarcer this is likely to be exaggerated. However, predators are likely to be better at finding their prey than human surveyors. Predators may utilise less abundant but more accessible species. Conversely, even if a particular species is abundant it may not always be very accessible to predators, such as seals, cetaceans and seabirds. Predators, compared to a fishery or survey that covers wide areas, may therefore perceive availability of prey very differently (Greenstreet et al. 2006).

Grey seals and their populations

The grey seal (*Halichoerus grypus*) is one of the major piscivorous predators in the marine environment on the west coast of Scotland. Grey seals are from the family Phocidae and the order Pinnipedia and they are found across the North Atlantic and in the Baltic Sea (King 1983). The species is distributed mainly in two areas; Nova Scotia and the Gulf of St Lawrence in Canada (approximately 52% of the population); and Britain (approximately 39%), mainly around the Scottish coastline. These populations are increasing although the Baltic population remains low, being the last to recover from over-hunting (SCOS 2005).

Grey seals come ashore to breed, moult and rest between foraging trips, breeding takes place in the autumn and moulting in the winter or spring. Pregnant females come ashore for approximately two to three weeks to give birth to a single white-coated pup at traditional breeding colonies (Figure 2). This behaviour enables accurate counts to be made of the number of pups born each year at selected sites, which provides the raw data, along with other biological parameters, for input into population models to estimate the overall population size. The population of grey seals around Britain is thought to have increased from very low levels, perhaps as low as 500 animals in the early 1900's as a result of over-hunting (Harwood 1984), to approximately 105000 seals in 2004 (SCOS 2005).

In order to accurately assess or manage a population it is essential that an accurate estimate of its size be obtained. However converting counts of pups born each year to give an overall population size is not straightforward. Thomas & Harwood (2005) fitted a range of models to the pup count data that resulted in widely differing results, with population estimates ranging from 105000 to 234000. The models allowed for a number of different forms of density dependence in either pup survival or fecundity, as well as fitness-dependent movement of recruiting females between regions (Thomas & Harwood 2005). All models fitted the data equally well, but the NERC Special Committee on Seals agreed at their 2005 meeting that the model incorporating simple linear density dependent pup survival provided the best estimate. These estimates are used here. It should be noted that this model provided the smallest population estimates out of all the models fitted and that there still remains uncertainty over the right choice of model.

Thomas and Harwood (2005) produced estimates for the Inner and Outer Hebrides based on the colonies that are surveyed regularly. For colonies that are not surveyed regularly the most recent pup count was taken and multiplied by the ratio of estimated population size to pup count for the appropriate region from the Thomas & Harwood (2005) results. This increased the estimates by approximately 5% (Hammond & Harris 2006).

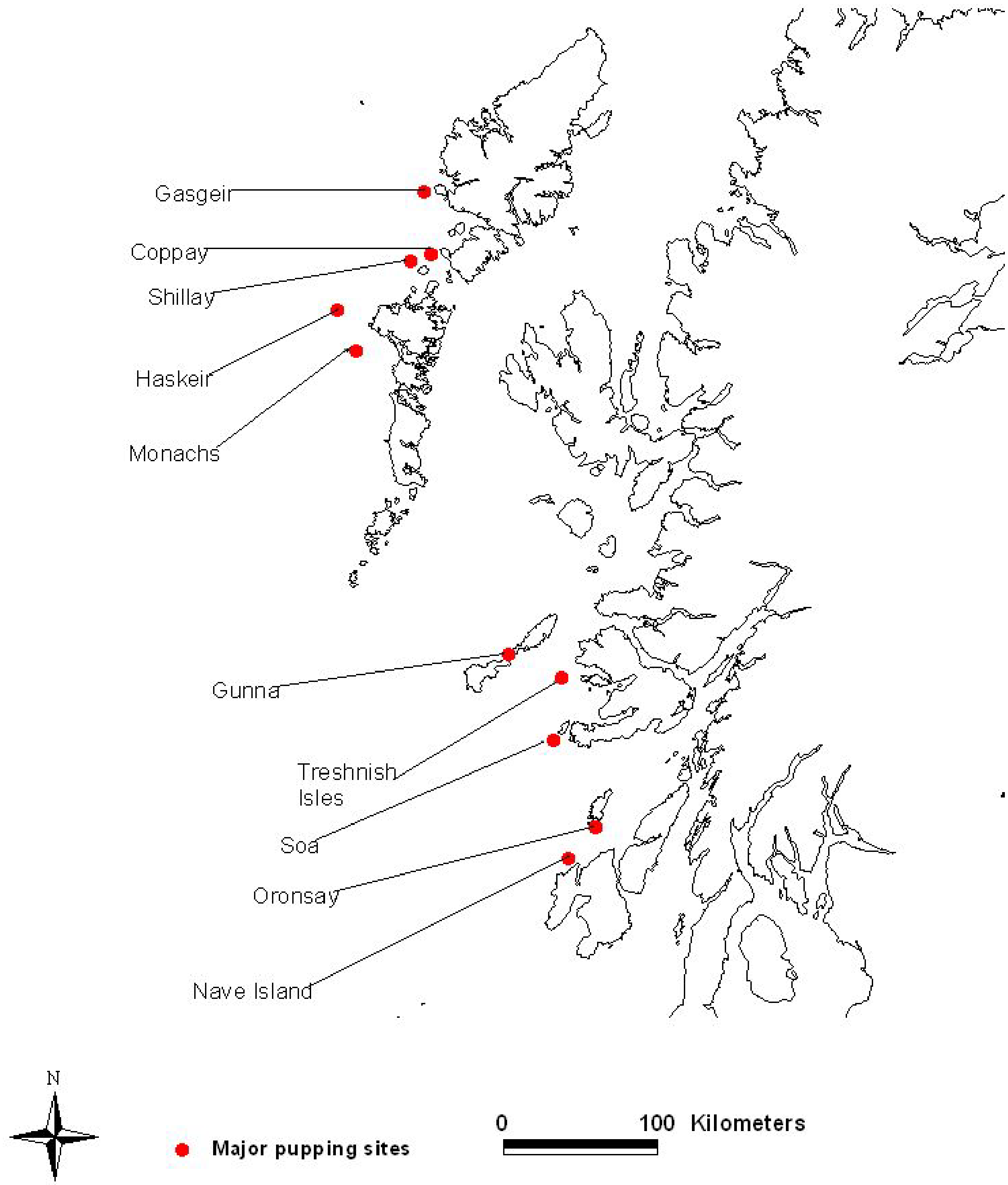

Figure 2. Major breeding colonies on the west coast of Scotland

Table 1. Estimates of grey seal population size for the Hebrides for (a) 2002 and (b) 1985 derived from the linear density dependant survival (DDS) model of Thomas & Harwood (2005). The results from the non-linear DDS model are also given to illustrate the uncertainty in population size. The model estimates include only animals associated with regularly surveyed pupping sites. The total estimates include animals associated with pupping sites that are not regularly surveyed. Estimates for sub-regions within the Inner and Outer Hebrides in 2002 were prorated according to pup counts in those areas. (Taken from Hammond and Harris 2006)

(a) 2002

2002	**Simple Linear DDS**			**Extended Non-linear DDS**		
	Model estimates	**CV**	**Total estimates**	**Model estimates**	**CV**	**Total estimates**
North Inner			297			362
South Inner			8,075			9,856
Minch			845			1,032
Inner total	8,543	0.139	9,217	10,427	0.179	11,250
North Outer			7,230			9,437
Monachs			24,742			32,296
South Outer			1,062			1,386
Outer total	31,683	0.154	33,035	41,355	0.178	43,120
Hebrides total	40,226		42,252	51,782		54,370

(b) 1985

1985	**Simple Linear DDS**			**Extended Non-linear DDS**		
	Model estimates	**CV**	**Total estimates**	**Model estimates**	**CV**	**Total estimates**
Inner total	4,662	0.145	4,662	5,776	0.148	5,776
Outer total	24,580	0.138	24,580	29,761	0.148	29,761
Hebrides total	29,242	0.141	29,242	35,537	0.148	35,537

Grey seal foraging behaviour and movements

Distribution of breeding seals is well documented, however, outwith the breeding season there is little information on the number of seals utilising different areas in different seasons. As breeding seals tend not to feed, the distribution of breeding animals may not be indicative of that of non-breeders that continue to forage or even to breeders outwith the breeding season. The summer photo-identification of grey seals compared with autumn photo-identification data of breeding seals at traditional breeding colonies have shown that seals may forage from haul-outs far from their breeding colony (SMRU unpublished data), an observation that has also been observed through telemetry studies (SMRU unpublished data). Some haul-out count data exist and an increasing amount of satellite telemetry data are becoming available from around the Britain and Ireland. During August, harbour seal (*Phoca vitulina*) surveys are carried-out by the Sea Mammal Research Unit (SMRU); these surveys provide an opportunity to record grey seal distribution, providing a valuable insight into the distribution of grey seals at this time of the year. Therefore the breeding distribution of seals may not be the best data when it comes to assessing regional and seasonal predation pressure on fish stocks.

To find out where grey seals spend their time at sea SMRU has developed Satellite Relay Data Loggers (SRDLs) (http://www.smru.st-and.ac.uk/). Data from satellite tags have revealed that individual seals often return to the same foraging areas, making many repeated movement patterns. Grey seal movements in the North Sea have been broadly categorized by McConnell (1999) into two movement types: long and distant travel (up to 2100km), and local, repeated trips to discrete offshore areas. During periods of travel, seals were observed to cover between 75 and 100 km per day. This study also revealed that 88% of trips to sea resulted in seals returning to the same haul-out from which they left, these trips were normally relatively short (mean 2.33 days) and not too distant (mean 39.8km). This led to the conclusion that the greatest conflict with fisheries may occur within the coastal zone, especially those areas near haul-out sites, rather than fisheries further offshore (Fedak 1996; McConnell et al. 1999). Satellite tracking of grey seals on the west coast of Scotland has highlighted the existence of a number of marine hot spots with many seals returning to the same locations time and time again (Matthiopoulos *et al.* 2004). For example, seals foraging from the Monachs often move out to areas around St. Kilda and the Flannan Isles to return again to the Monachs. In contrast, little travel has been observed within the Minch or off the continental shelf (McConnell 1984 & 1995). Telemetry studies have also shown that grey seals generally forage on or close to the seabed, with slow swim speeds, which imply that seals are not actively chasing down prey (Thompson, Hammond et al. 1991; Thompson and Fedak 1993; McConnell 1995; McConnell et al. 1999). This suggests that seals in these studies were targeting mainly demersal or benthic species and not pelagic species of fish.

Matthiopoulos *et al*. (2004) brought together satellite telemetry data from a number of sources to investigate the usage of available space by grey seals. As there has not been equal sampling effort throughout the areas of interest around the UK using telemetry locations from only a few individuals would give an incorrect picture of the total distribution of grey seals in each area. Therefore, Matthiopoulos *et al*. (2004) used data on population sizes at haul-out sites made on the basis of aerial surveys to generate a map of the spatial usage of the grey seal population (Figure 3.). Grey seals were found primarily to utilize shelf waters relatively close to haul-outs. This work reemphasized many of the marine hotspots previously identified and also revealed many new ones, notably areas in the Minch and Sea of the Hebrides. However, although these results currently represent the best estimates of how grey seals use the marine environment around the UK, they are neither definitive nor equally precise for all haul-outs (Matthiopoulos *et al.*, 2004).

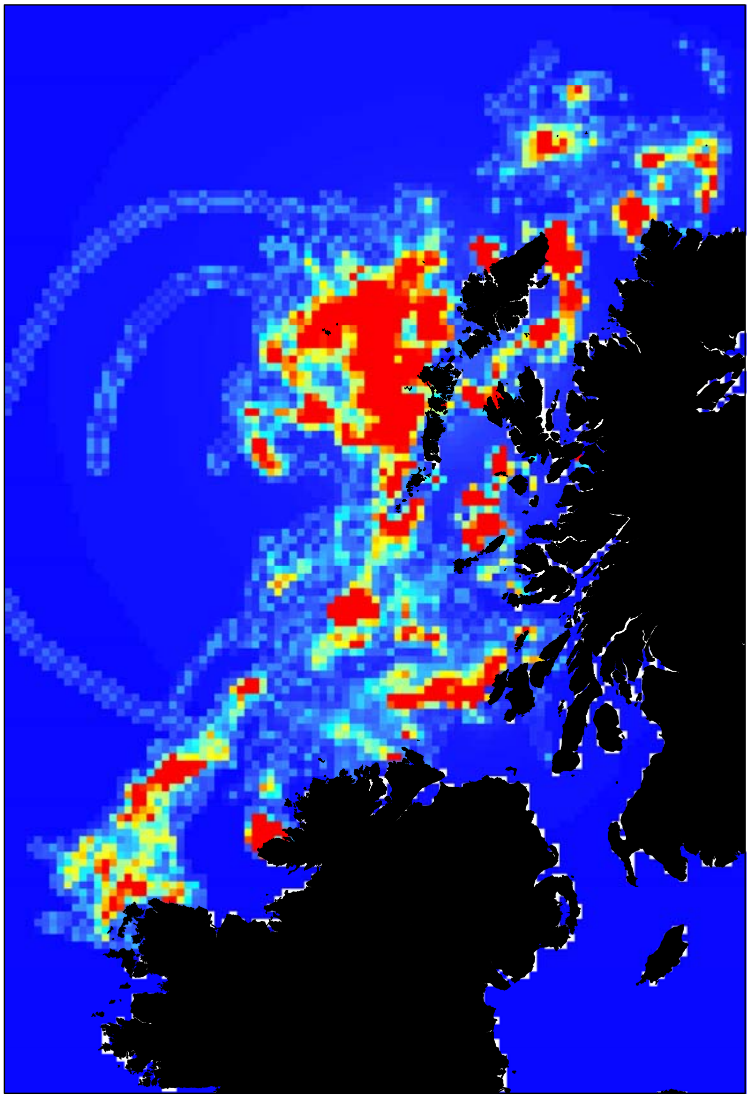

Figure 3. Spatial distribution of usage based on telemetry data from 75 individuals, haulout counts and accessibility of points in space relative to the haulout sites. Red indicates high usage and blue low usage (Matthiopoulos et al. 2004).

Grey seals and conflicts with fisheries

Grey seals, until relatively recently, were viewed as a resource and were heavily hunted around Britain. It wasn't until 1914 when the population had been reduced to a very low level that the Grey Seal Protection Act was passed (Harwood 1984). Following this, numbers began to increase and fears over what impact these numbers may have on decreasing fish stocks led to changes in the legal status of seals. By the late 1950s a Consultative Committee on Grey Seals and Fisheries was established. This paved the way for a number of culls to be approved and carried out. In 1963 it was approved that the populations of the Farnes and Orkney be reduced to three-quarters by killing moulted pups (Harwood and Greenwood 1985). Despite some culling being carried out the target numbers were never reached. Another major cull was given the go ahead in 1977 to target pups and breeding females at the Outer Hebrides in an attempt to reduce the population from 50000 to 35000 by the end of 1982. Due to logistical problems these numbers were never reached, however the presence of hunters on the islands probably caused a greater reduction in numbers than was initially thought as disturbance likely reduced pup survival and adult fecundity (Summers and Harwood 1978). Changes in public attitudes towards seals forced the culling programme to be abandoned in 1978. Conservation bodies argued that more scientific information was needed on seal numbers, distribution, diet and daily food requirements before future culls could be justified (Harwood and Greenwood 1985; Harwood 1987; Harwood and Croxall 1988).

Fishermen often accuse seals of depleting commercial fish stocks and therefore of adversely affecting their livelihood. This results in regular calls from fishermen's organisations to control the number of seals. Thus it is important to obtain up-to-date information on population size, distribution and diet to allow government to determine whether or not management action is required. The demise of western Atlantic cod was directly attributed to overfishing, seal populations contributed very little. However, the slow recovery of cod stocks may indicate that the seal population continuing to prey on depleted stocks may prevent their recovery (Mohn and Bowen 1996; Fu et al. 2001; Trzcinski et al. 2006).

When assessing the impact seals may have on fisheries it is important to have up to date and accurate figures on a number of different parameters. "The number of seal pups born plus vital parameters is used to estimate the number of grey seals, the number of seals plus their prey ration leads to estimates of prey consumption, a comparison of this consumption to the size of the prey stock leads to estimates of predation mortality, and finally the predation mortality plus a prey recruitment model leads to an estimate of impact" (Mohn & Bowen 1996). It is essential that the above process is applied within a multi species approach to attempt to account for many of the hidden intricacies of complex marine ecosystems. For example, large scale fur seal culls were carried out in South Africa to protect the local hake fishery but the decreased seal predation caused the collapse of the fishery that the cull was trying to protect. This was due to the lowered predation by seals on a sub-species of hake that predates on the commercial sub-species (Punt & Butterworth 1995). Annual grey seal breeding surveys and the increase in the deployment of satellite tags allows us to regularly update and improve our knowledge of population size and distribution. However, at present much more up to date information is needed on many of the links within the ecosystem before the true effects of any interactions can be gauged.

One of the largest consumers of fish are predatory fish and their interactions with fisheries and with seabirds and marine mammals are diverse and complex. Management of these fish can have an overwhelming effect on ecosystems, such as has been observed with the North Sea industrial fishery for sandeels. Effects on sandeels of decreases in catches of predatory fish stocks (eg. whiting) have been greater than increases in the take by seabirds, seals and the fishery (Furness 2002). A sudden increase in gadoid stocks may have the knock-on effect of devastating the sandeel stocks just as much as an increase in the take from the fishery might. For those predator species that can, this may force them to switch prey species. Seabirds that cannot switch have suffered years of low breeding success (Harris et al. 1997). When competition between fisheries and predator populations remain in such flux, ecosystems may tend to favour the generalist, with specialist populations being subjected to boom and bust cycles. Just as one population is adversely affected another may benefit – the balance, and where it should sit, is not always obvious.

Previous knowledge of the diet of grey seals off the Scottish west coast

Grey seals have often been termed opportunistic or catholic predators, preying on whichever species is locally abundant with an ability to switch to an alternative prey species when their preferred prey declines (Pierce et al. 1991(b); Fryxell et al. 1994; Furness 1996). A critical question to be posed is how will the consumption of a particular prey species vary with its availability to the predator (Harwood 1992)?

Previous information on grey seal diet in western Scotland dates back to 1985 (Hammond et al. 1994c); prior to then, information on grey seal diet was sparse and lacked seasonal and geographical coverage. For example, a study by Rae (1968, 1973) analysed stomach contents of animals, however, the sample size was small and mostly collected from by-caught animals or animals shot within the vicinity of fishing nets, whilst a study by Pierce et al. (1990) visited only the Summer Isles, on the west coast of Scotland, and collected 62 faeces between January and April 1987 and 1988. Pierce et al. (1990) analysed the data by frequency of occurrence and these results revealed a large number of Trisopterus and sandeels, followed by haddock/saithe/pollock which were not distinguished, followed by cod.

In 1985 a large number of samples were obtained from all over western Scotland (Hammond et al, 1994c). Data from this study were reanalysed in 2006, results are given in the appendix and in Hammond & Harris (2006). The main findings show that sandeels and gadoids dominated the diet, contributing approximately 43% and 32% respectively by weight. The most common gadid species were ling and cod but the dominant species varied by area and season. Sandeels were dominant in the first and third quarters, cod in the fourth and herring were important during the second quarter of the year. Flatfish, mainly megrim and plaice, contributed approximately 10% overall. Sandeels, an important component of grey seal diets elsewhere in Britain (Hammond & Grellier 2006), were found to contribute less to the overall diet and tended to be confined to the Outer Hebrides. The reason for this was attributed to the availability of the sandeels preferred seabed type. Greater numbers of cod and ling taken in the summer were thought to compensate for the observed absence in sandeel consumption seen at this time of year in other areas of Britain. Pelagic schooling fish such as herring, mackerel and horse mackerel were also found to occur more often in the summer months (Hammond et al. 1994c).

The consumption of commercially important fish species by grey seals in the North Sea in the mid-1980's was one or two orders of magnitude lower than the amount removed by the fisheries, with the exception of sandeels (Harwood and Croxall 1988). However, since then the population of grey seals has more than doubled and cod stocks, as with many other stocks, have been falling since the early 1980's and estimates for 2000 and 2001 were the lowest ever recorded (ICES 2004). The situation has clearly changed and current estimates of prey consumption are needed urgently to address policy issues related to the impact of the still increasing grey seal population on fish stocks.

The amount of food a population requires depends on how much energy each individual requires and how many individuals there are within the population. To predict the amount of energy marine mammal populations require bioenergetic models have been used (Olesiuk 1993, Mohn & Bowen 1996, Stenson et al. 1997, Nilssen et al. 2000, Winship et al. 2002, Sparling & Smout 2003, Trzcinski et al. 2006). A model by Sparling & Smout (2003) predicted the amount of energy grey seals required by quarter and by sex and age class. Errors associated with model predictions were most likely to be caused by uncertainties in the size of different components of the population, particularly estimates of the size of the male component, and estimates of metabolic rate. However it was found that uncertainty in the male component had less of an effect on overall estimates of population energy requirements suggesting that the female component of the population was the most important component in estimating population requirements in grey seals (Sparling & Smout 2003).

To simplify we take an average daily energy requirement for an 'average' grey seal, estimated as 5497 Kcal per day (Sparling and Smout 2003), this value was very similar to a previous estimate of 5530 Kcal per day (Fedak and Hiby 1985).

Grey seals consume many different species, the energy content of which differs, therefore the weight of prey required to meet energy requirements will be dependent on the species that are consumed. For example, based on annual total energy requirements, if seals consumed only oily fish such as sandeels, herring or mackerel then consumption would be between 81,000 and 141,000 tonnes. Alternatively, if these seals ate only whitefish then the annual consumption would be between 150,000 to 262,000 tonnes (SCOS 2005). However these figures are hypothetical and should be interpreted with care as diet studies have shown that rarely does diet comprise of just a few species.

Compared to the commercial landings, where the numbers of species concerned are few, the hypothetical seal consumption figures seem large and would imply an impact on commercial catches. However, for obvious reasons such 'what if' scenarios should be interpreted with care, as a component of the diet, in all areas, is made up of non-commercial species and, of the whitefish taken by seals, most are of a smaller size than those being taken by the fishery (Hammond & Fedak 1994a; Hammond et al. 1994b; Hammond et al. 1994c; Fedak 1996). Overall, therefore, it may appear that there is less of an overlap between the main commercial fisheries and seal consumption. It is possible, however, that seals, in certain areas, may have a significant local effect.

Investigating the diet of wild seals

Many studies have been carried out in recent years to investigate the diet of a range of seal species in the wild. Traditionally the method for investigating diet in free-ranging pinnipeds has been to examine stomach contents of dead animals. Seals were either killed as a direct result of the research or indirectly as a result of fishing activities or natural strandings (for example Havinga 1933; Rae 1960; Rae 1968; Rae 1973; Frost & Lowery 1980; Steward & Murie 1986; Pierce et al. 1989; Pierce & Boyle 1991; Bowen & Lawson et al. 1993; Bowen & Harrison 1996; Mikkelsen et al. 2002). A large proportion of animals had empty stomachs therefore substantial numbers were needed to be sufficient for analysis. Seals killed during the operations of fisheries often had full digestive tracts, however, the diet can be expected to be biased towards the target species of the fishery. Animals that died from natural causes, strandings, were often found with empty stomachs and also may not be representative of the whole population. Sampling from dead animals does have one important advantage over other means, that is; age, sex and general status of the seal can be determined and therefore diet analysis can be carried out for different components of the population (Bowen & Harrison 1996).

Fatty acid analysis of the blubber layer of marine mammals is a relatively new method for investigating diet and it can be used to reveal broad scale dietary information over long time scales. This approach is based on comparing fatty acid signatures in the blubber layer to fatty acid signatures present in prey species, and therefore relies on the collection of large reference collections of fatty acid signatures from prey species from each area, which as yet do not exist for most areas being studied. Analysis has been primarily qualitative although recent work has resulted in quantitative diet estimation (Bradshaw et al. 2003; Iverson et al. 2003); however full quantitative estimation of diet remains ambitious (Budge et al. 2006). Work has mainly focused on revealing changes in foraging patterns and by grouping animals that forage in similar areas by classifying their fatty acid signatures (Smith et al. 1996; Walton et al. 2000; Moller et al. 2002). For example, a study comparing the patterns of fatty acids of grey seals from two breeding colonies, one off northwest Scotland and another off southeast Scotland, found clear differences in the composition of blubber fatty acids between the two populations. The authors suggest that the most likely explanation for the observed difference is that animals associated with each colony forage in different geographical areas (Walton et al. 2000). The analysis of fatty acids may also provide clues to differences in local prey availability, predominant size classes and species abundance (Iverson et al. 1997). However as yet this method remains questionable over its ability to provide detailed fine scale compositional data that is truly quantifiable.

Analysis of stable isotopes is also a useful tool in revealing dietary patterns because the ratios of heavier versus lighter isotopes of particular elements in the tissues of predators can be traced back to those in their prey species. Drawbacks again however are that a large reference database, of stable isotopes present in prey species is needed from the area being studied. This method can be used to establish trophic relationships in an ecosystem but does not allow the identification of individual prey species or the determination of species composition in the diet and the results are difficult to quantify (Hobson et al. 1996, Niño-Torres et al. 2006).

Lavaging, emetics and enemas have been used in a few studies, but all, as do the above methods, involve seal capture, and although a successful method for elephant seals (Antonelis et al. 1987), it has been shown to be an unproductive method for grey seals (Hammond & Fedak 1994a).

Genetic analysis of faecal, stomach or intestine material can, although expensive when dealing with large sample sizes, give qualitative results on ingested prey species whether they have robust hard-parts or not, provided a large enough reference collection of prey genetic signatures is available. In diet studies where a large amount of hard-part material may be lost to digestion this method may complement morphological analysis (Barros et al. 2002; Deagle et al. 2005; Parsons et al. 2005; Symondson 2002). On its own it remains purely qualitative with no means of predicting prey size or quantities and therefore limited ability to predict the relative importance of individual prey species (ICES 2006). Serological analysis of proteins present in fecal and digestive tract material also share these limitations (Pierce et al. 1990, 1991c).

An effective method, that avoids some of the problems mentioned above and does not require animals to be captured or killed, utilises the hard remains of prey recovered from faecal samples collected from haul-out sites. Many samples can be collected in just one visit by relatively few fieldworkers, thus limiting disturbance. A large proportion of scats collected have been shown to contain prey remains (Harkonen 1987; Boyle 1990; Prime & Hammond 1990; Bowen and Harrison 1994; Hammond et al. 1994b; Hammond et al. 1994c; Tollit 1996a; Antonelis et al. 1997; Hall et al. 1998; Pierce and Santos 2003). Problems can arise from this form of study when trying to confirm the source (species) of the sample. At well-documented or monitored sites this is not a problem and where haul-outs comprise a single species and therefore samples can be assigned to species. If resources permit, molecular genetic analysis to assign species, sex and individual identity to seal faeces (Reed et al. 1997; Parsons et al. 2005). Grey seals of different ages have been shown to have different feeding habits (Mikkelsen et al. 2002) and therefore changes in haul-out behaviour with age could bias findings for a particular time and place (Tollit 1996a). Such changes have been well documented for harbour seals (Thompson 1989; Harkonen et al. 1987). Animals that frequently return to haul-outs will tend to be over represented and those that return less often, or that forage further offshore, will be under represented or not represented at all, resulting in an incomplete and potentially biased view (Bowen and Harrison 1994). However this potential spatial bias has been evaluated by Smout (2006) who used experimental and telemetry data in simulations where prey remains were returned to haul-outs in faecal material. Results indicated that for British grey seals which generally forage close to shore, these effects are not likely to be significant (Smout 2006).

A new method of faecal analysis currently being developed that does not rely on the recovery of hard-parts is near infrared spectroscopy, which theoretically has the potential to quantify seal diet. As yet this method has only been applied to captive animals fed on three different prey species and it is unknown whether this method would be as successful on predators with more complicated diets. The need for calibration through the use of captive animals and the range of prey species that may be consumed makes this a costly process in time and resources but not out of proportion with previous large-scale projects. The procedure works on the principal that organic material absorbs near infrared light at wavelengths characteristic of each type of bond when irradiated with light from this spectrum. All that is required is that faecal samples are dried and ground and once calibration equations are available for the range of possible diet components, the concentrations of different components can be determined (Kaneko et al 2006).

The cutinous beaks of cephalopods are relatively indigestible, they can often be identified to species and relationships exist between body weight and hood and rostral measurements (Clarke 1986). The otolith of teleost fish is part of the labyrinth structure situated at the back of the cranial cavity and it forms the sense organ that is responsible for detecting gravity, acceleration, retardation and hearing in fish (Harkonen 1986). There are two major otoliths within the labyrinth and because these otoliths are often robust to digestion, their shape is species-specific and their size correlates well with individual fish size they are an excellent indicator of diet composition.

As a result these structures have been widely used in the study of diets of many piscivorous animals (Harkonen 1986; Arnett et al 2001; Hull 1999; Pierce 1991c; Watt 1995).

Analyses that depend on retrieval of otoliths assume that the head of prey is not discarded. Rae (1968) observed seals around nets to occasionally discard the heads of large fish. There is no evidence to suggest that this is normally the case. Although, the occurrence of large conger eels in the diet has also led researchers to suggest that at least in the case of eels, seals are unlikely to consume the whole eel due to physical restraints, the presence of otoliths suggests heads are clearly eaten by some individuals (Hammond, Hall et al. 1994c). Recent work by the author on Scottish salmon rivers also confirms that the heads of large fish are eaten, at least some of the time (Figure 4.).

Certain prey species have delicate otoliths these may often be broken or lost altogether so using other skeletal remains can be an improvement, although difficulties incorporating these data into quantitative analysis have limited results (Browne et al. 2002). In known situations where large numbers of such otoliths may be encountered, such as, seal-salmon interactions it may be a valid improvement (Tollit et al. 2003).

Some prey species do not posses otoliths (or beaks), such as cartilaginous fish (Figure 5.) or crustaceans, therefore it is important to be able to determine whether these prey items form a significant part of the diet. A grey seal diet study in the North Sea investigated this by calculation of digestive efficiency which suggested that no major component of the diet had been missed in the study in question (Prime and Hammond 1990). Simple recording at the presence/absence level, of such structures as denticles and exoskeletons, at least allows researchers to monitor differences in their frequency of occurrence. Another potential bias is that of secondary prey ingestion. Otoliths within the stomachs of prey may also be represented within the scat sample, therefore, over representing certain prey (Arnett et al. 2001). However, simple calculations indicate that the effects on estimates of diet composition of secondary prey ingestion are very minor (P.S.Hammond pers. comm.)

Recovered partially digested remains are used to reconstruct the diet of the predator. Simple analysis of hard parts allows the frequency of prey occurrence to be revealed. However, this gives little information on the size or weight of prey consumed and leads to an overestimation of the importance of numerous small prey species and underestimates the importance of larger, less common species (Hyslop 1980). Various methods have been applied to try and quantify the relative importance of each prey species in the diet. All of which are subjected to varying levels of bias (Tollit 1996a).

The relationship between otolith size and fish weight and length are well documented (Harkonen 1986; Leopold et al. 2001), and also for cephalopod beaks (Clarke 1986). However, using measurements from partly digested fish otoliths would underestimate the size of ingested prey (Tollit 1997b). Therefore the application of correction factors to calculate undigested otolith size is necessary. This then enables diet to be presented as a percentage by weight; however, this gives no indication to the frequency of occurrence, which can be a problem when dealing with small sample sizes when a large uncommon prey item may be either over or under-represented. This uncertainty can be quantified by generating confidence intervals from computer sampling (Hammond and Rothery 1996).

As the process of digestion is not consistent or uniform, fragile items are digested quicker than more robust items therefore relationships between digested and undigested otolith size, for each major prey species, have been developed for grey seals (Prime & Hammond 1987). These relationships can be improved by creating size specific relationships. Intra-specific variation in digestion rates occurs due to differences in stomach loading (Marcus 1998) and levels of mastication so accuracy can be increased through the use of grade specific correction factors (Tollit et al. 1997b). Complete digestion also needs to be taken into account through the use of species specific number correction factors, as some will be completely lost due to digestion (Bowen 2000; Grellier et al. 2006).

Estimates of these correction factors need to be obtained through experimental investigations using captive animals in feeding experiments. While captive experiments are unlikely to completely match conditions experienced in the wild, simulating wild, natural conditions as much as possible is paramount in their success (Grellier et al. 2006). For example, it has been shown that it is important to recreate similar amounts of exercise that seals may experience in the wild (Bowen, 2000). In feeding experiments Bowen (2000) found differences in the proportion of otoliths that were completely digested between animals that were able to exercise by swimming and those that were not. Grellier & Hammond (2005) tested the use of otolith carriers in feeding experiments and found that digestion rates varied between otoliths placed in carriers and those that were not, again stressing the importance of recreating settings as close to the natural environment as possible.

Figure 4. Grey seal consuming the head of a salmon in the River Ness.

Figure 5. Grey seal feeding on a ray (a species whose otoliths are undetectable).

Sample processing

Many methods have been put forward as effective ways to isolate hard parts from faecal material. The most commonly used is that described by Treacy & Crawford (1981). Apparatus consisting of a jet spray and soft brush, to wash away soluble components, nested sieves of decreasing mesh size to collect hard parts and help separate material. This method, although effective, is extremely time consuming and great care must be taken to ensure all skeletal elements lodged in the mesh of each sieve are removed and that fragile items are not damaged (Murie & Lavigne 1986). It can also be distasteful because of the odour. Bigg and Olesiuk (1990) suggested an enclosed elutriator, apparatus to separate hard parts from soluble material, as a more effective method. Ultimately scats can be processed quicker as there is no limit to the number of elutriators, apart from resources. The equipment also benefits from less handling and exposure to odour, with less damage to skeletal structures (Bigg and Olesiuk 1990).

Another method includes the use of fine mesh bags, containing individual samples, which are then put through a washing machine cycle, a variety of cycles can be chosen depending on the machine in use. All these automated methods work well as long as the sample is easily dissolved, otherwise, the sample needs to be removed and broken up manually and the advantages are lost (SMRU unpublished data).

Aims of this project

This study focussed on assessing the diet of grey seals off western Scotland. The collection of scat samples, in each quarter of the year, over a wide geographical area of the west coast of Scotland, along with existing data from captive feeding experiments, allows us to relate prey structures recovered from faecal material to ingested prey items. It is assumed that the scats collected provide information that is representative of the diet of those seals in a particular region and season, that the frequencies observed reflect those in the diet, and that prey without otoliths or beaks do not account for a significant proportion of the diet.

Information obtained from the diet of these animals was used with estimates of population size and population energy requirements to estimate prey consumption. These quantitative data were then compared with previous diet data and existing fishery and fish stock data to assess the role grey seals play in the marine ecosystem. These results can then be used in a multi-species framework to better understand and predict changes in the ecosystem both natural and anthropogenically induced.

Specifically, the aims of this study were:

1. To sample grey seal diet at all major grey seal haul-outs along the western coast of Scotland, seasonally for one year and to record the encountered seal distribution.

2. To estimate grey seal diet composition seasonally and regionally in 2002.

3. To estimate grey seal consumption of commercial fish species in 2002.

4. To relate changes in diet composition and consumption between 1985 and 2002 to changes in abundance of commercial fish species.

2. Methods

Study area

The western coast of Scotland was divided into six regions to allow regional differences in diet composition and consumption to be assessed. These are illustrated in Figure 6. A brief description follows here.

The Inner Hebridean regions:
North Inner included the Summer Isles and the Minch.
Minch included the southern Minch, Little Minch and the northern sector of Sea of the Hebrides. This spanned from the Small Isles in the south to the Shiant islands in the north.
South Inner included the southern sector of the Sea of the Hebrides, spanning from Islay in the south to Point of Ardnamurchan in the north, including Coll and Tiree to the west.

The Outer Hebridean regions:
North Outer included the Sound of Harris the western shores of Harris and Lewis and islands to the west.
Monachs included the western sides of the Uists and offshore islands, including the north side of the sound of Barra.
South Outer included Barra and Barra Heads.

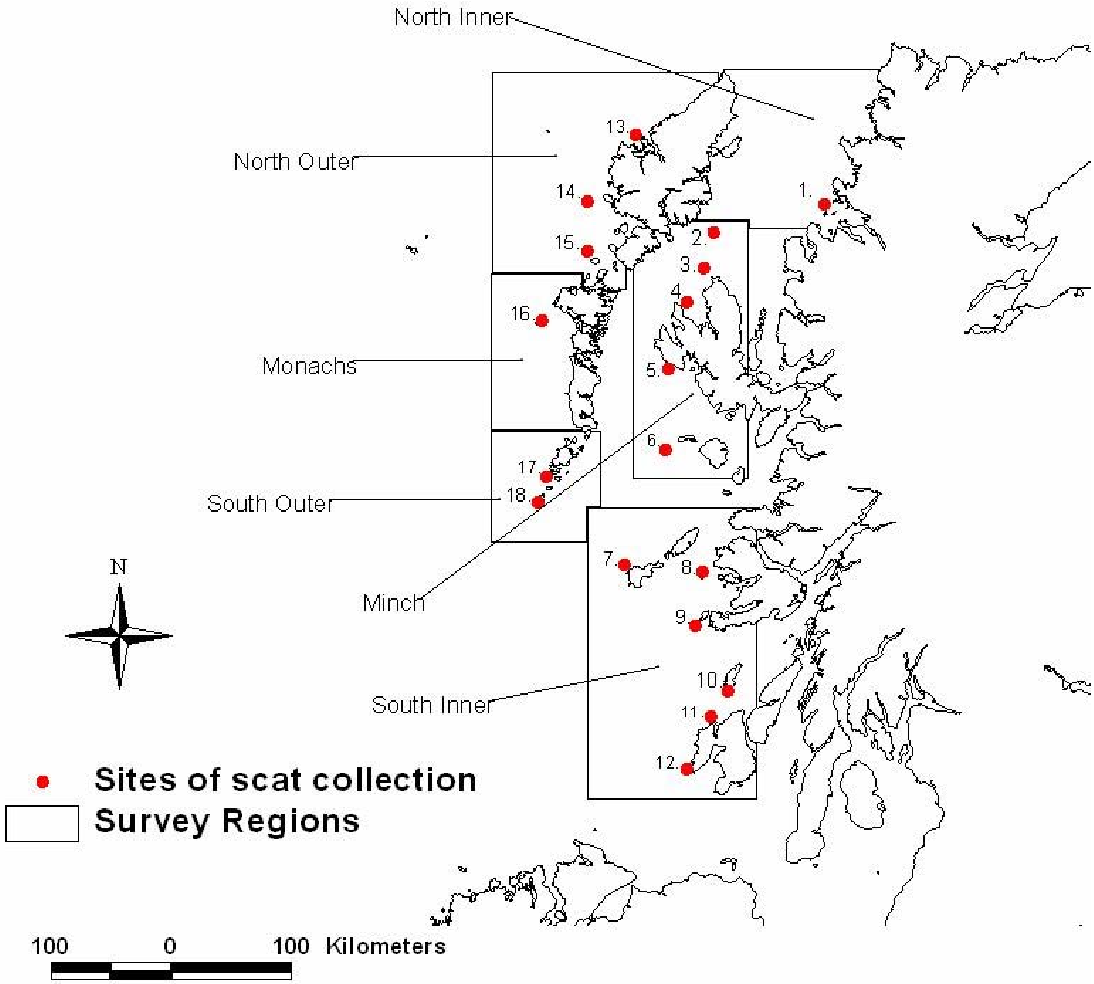

Figure 6. Survey regions and sites where scats were collected; 1. Summer Isles, 2. Shiants, 3. Fladda-Chuain, 4. Ascribs, 5. An Dubh Sgeir, 6. Oigh-Sgeir, 7. Hough Skerries, 8. Treshnish, 9. Soa, 10. Oronsay, 11. Nave Island, 12. Orsay, 13. Loch Roag, 14. Gasgeir, 15. Shillay, 16. Monachs, 17. Flodday, 18. Barra Heads.

Data Collection

Little is known about the distribution of grey seals outwith the breeding season and the breeding distribution may not be representative of foraging seals whether non-breeders or breeders. This prompted the recording of seal encounter during this study to provide an insight into possible changes in distribution that may occur over the year.

In 2002 an attempt was made to survey as much coastline as possible to locate and land at any new and all known major grey seal haul-outs in western Scotland. Species and number of seals present were recorded and any faeces were collected at least once every quarter. North Rona, a major breeding colony, was excluded from the study due to its isolated location and therefore the logistical constraints of carrying out sampling, as was St. Kilda. One flight was made to the Flannan Islands during the first survey, approximately 40km west of Lewis, but due to the location of seals and landing difficulties it was decided too dangerous to attempt to collect samples from these locations.

Surveys were either carried out by helicopter with three observers onboard scanning the coastline using x10 image stabilized binoculars and by eye, by 4m RIB with safety support from nearby yacht, or by 6m RIB working out of a safe-haven. Details of sampling trips are given in Table 2. Surveys were conducted within two hours of low water and the location, species and number of seals present, arrival time and date along with the number of samples collected were recorded. Large haul-outs were photographed to allow group size counts to be confirmed. Scats were collected from haul-outs that consisted of grey seals only so that there would be no uncertainty over the origin of the scat. All samples were placed in separate polythene bags, taking care to collect as much of the sample and as little contaminating material (eg. sand), as possible. Samples were frozen to –20°C on arrival back at the laboratory to limit the possibility of any further digestion of prey remains (Prime et al. 1987), and to limit any biological hazards associated with faecal material.

Table 2. Details of survey trips during 2002 and the season these data were allocated to

Note: In addition to these trip: two additional trips were made to the Hough skerries (South Inner) during July by a member of SMRU, and RSPB wardens regularly visited Oronsay haul-outs during the 2nd and 3rd quarters.

Dates	**Method and areas surveyed**	**Quarter**
28th February to 3rd March.	Helicopter, full unrestricted, survey of all major haul-outs along the western coasts of Scotland.	1st Quarter
5th June to 7th June.	Helicopter, restricted, survey excluding Monachs, Shiants and Oronsay due to constraints imposed by landowners/managers.	2nd Quarter
24th June to 3rd July.	4m RIB survey with support yacht excluding Summer isles, loch Roag, Ascribs, Oronsay & Orsay.	2nd Quarter
18th and 19th July	4m RIB survey with support yacht, visits made to, Minch region (Shiants, Fladda-Chuain, Canna and Oigh-sgeir) and South Inner region (Gunna, Hough skerries and Skerryvore).	2nd Quarter
19th to 29th August	4m RIB survey with support yacht excluding loch Roag, Summer isles, Ascribs and Orsay.	3rd Quarter
12th,13th and 16th September	6m RIB survey of the Monachs, Barra Heads and Gasgeir on the respective dates.	3rd Quarter
8th and 9th November	6m RIB survey of the Summer isles, Ascribs and Fladda-Chuain.	4th Quarter
16th and 17th November	6m RIB survey of the Treshnish and Soa.	4th Quarter
20th to 22nd November	Helicopter survey restricted by weather and SPA's for geese, limited cover of Monachs and South Outer.	4th Quarter

Laboratory Processing

Individual samples were thawed before washing through a nest of sieves of decreasing size; 1 mm, 600 μm and 335 μm. Not all scats were used from locations where large numbers of scats had been collected. Instead samples were processed at random until either, all had been processed, or 50 samples containing otoliths / beaks had been processed from each site. This number of samples were deemed suitable to detect seasonal / regional differences with an acceptable level of confidence (Hammond & Rothery 1996; P.S. Hammond pers comm.). Running water and a nylon brush (ie. washing up brush) were used to gently break up scats and any hard remains were removed with a pair of forceps. Various other ways of extracting hard parts from scats were investigated as discussed in the Introduction. Otoliths were dried and stored in micro-tubes that were labelled with site, date and sample number. Beaks were stored in glass vials in 75% ethanol. A note was made if any crustaceans, denticles or feathers were present.

Otoliths were identified using guides (Harkonen 1986; Leopold *et al.* 2001) and cephalopod beaks were identified using the identification guide (Clarke 1986) and assistance from Begoña Santos (Aberdeen University). Every attempt was made to identify to the species level, however sometimes it was only possible to identify to a family or higher level. Measurements, taken using digital callipers, were in millimetres to two decimal places, hood and rostral length for cephalopods, length and width for otoliths (only a length measurement was taken from sandeels). Callipers were zeroed between measurements and frequently cleaned. For very small items a dissecting microscope was used with a calibrated eyepiece graticule. Where a large number of a single prey species were present a random sub-sample was measured, either 50 measurements or 30% of the total, whichever was larger. As otoliths are subjected to varying degrees of digestion it would be unwise to apply an average single correction factor (Dellinger & Trillmich 1988). Therefore each otolith was examined to evaluate the amount of digestion that had taken place by classifying the amount of degradation to external morphological features (Tollit et al. 1997b; Leopold et al. 2001). Three categories were used: 1 – pristine, 2 – moderately digested and 3 – considerably digested. No grade was applied to squid or octopus beaks as no significant reduction due to digestion was thought to occur. However, Tollit et al. (1997b) urged caution when taking hood length measurements. Both squid and octopus in some cases were observed to be worn and fragmented at the ‘trailing edge’ of the beak (edge opposite the rostral tip), these beaks were omitted (Tollit et al. 1997b). Squid lower rostral or lower hood length was measured using a dissecting microscope with eyepiece graticule.

Analysis

Analyses were carried out following methodologies used in previous SMRU seal diet studies (Prime et al. 1987; 1990; Hammond et al. 1994a,b,c; Hall et al. 1998). In summary, partial and complete digestion were accounted for, and otolith and beak measurements were converted to estimates of prey size to allow diet composition to be assessed. Consumption estimates were calculated by converting prey in the diet to energy and scaling up to meet the energy requirements for the population in that area and then converting back to prey weight. These calculations were all performed within Fortran programs written for previous SMRU diet studies (Hammond & Rothery 1996; Hammond & Grellier 2006; Hammond & Harris 2006). Details of each step are outlined below.

Estimation of the number of grey seals using different regions in different seasons

The grey seal population, associated with regularly surveyed colonies, on the west coast of Scotland was taken to be that reported by Thomas and Harwood (2005) in their simple linear density dependent survival model. To account for colonies that are not surveyed regularly the most recent pup count was multiplied by the ratio of the estimated population size to pup count for the appropriate region from the Thomas & Harwood (2005) results. This increased estimates by approximately 5% (Hammond & Harris 2006). These regional estimates were used in the analysis to represent the distribution of seals in quarter 4.

Existing SMRU haul-out data for August were divided up into the appropriate regions summed and prorated to the size of the west coast population. These data were used to represent the summer distribution of seals, during quarters 2 and 3.

Counts recorded as part of this study from the first quarter only were summed in their appropriate regions and prorated against the west coast population estimate (Thomas & Harwood 2005) to provide population estimates for quarter 1. Table 5 in the results section shows the estimates for each quarter used in the analysis.

Diet composition

Based on new experimental data, Hammond and Grellier (2006) made a decision over which otolith or beak measurement to use for each species represented in the data. The choice of measurements for otoliths was either length preferred, width preferred, length only or width only. For octopus they were either lower hood length only or upper hood length only and for squid it was either lower rostral length only or lower hood length only.

Species and grade specific digestion coefficients, derived from feeding experiments (Grellier & Hammond 2006), were used to calculate the size of otoliths from partially digested otolith size. However, there were insufficient data to generate grade specific values in grades 1 and 2 for some species. For these cases a digestion coefficient of 1.0 was used for grade 1 and for grade 2 an estimated digestion coefficient was used from groups of species, such as flatfish or gadoids. Where no experimental data were available for a particular species or where identification had only managed to identify to a higher level, a group specific value was used (eg. flatfish or non-specific gadoid).

To estimate prey weight, published allometric relationships were applied primarily from Leopold et al. (2001) but also from other sources (Harkonen 1986, Brown & Pierce 1998, Clark 1986, Santos pers comm). For species where no relationship was available the closest matching species was used; species that fell into this category contributed very little to the overall diet. For otoliths that were categorised as unidentified gadoid, the relationship for cod was used. For unidentified flatfish the relationship for plaice was used. Analysis using other relationships revealed that the results were insensitive to these choices (Hammond & Harris 2006).

As no measurement was taken from the upper beak of squid, weights derived from squid lower beak measurements were doubled to make these data consistent with fish having two otoliths and octopus having two measurable components.

Within a single sample when otoliths from a particular species were numerous, for example as was often the case for sandeels, only a sub-sample of otoliths were measured. The size of the non-measured otoliths was assumed to be equal to the mean of the measured otoliths. In the case of broken otoliths, where it was not possible to measure either a width or length, then the size of the otolith was taken to be equal to the mean of the other otoliths of the same species in that sample, or if none were present then equal to the mean for that species in the rest of that data set.

The estimated component of each species in the diet was then adjusted by species specific recovery rates (Grellier & Hammond 2006) to account for complete digestion. The effects of applying such number correction factors are given by Grellier & Hammond (2006).

Estimated weights for each species were then summed within each region / season data set and expressed as a percentage of that data set. As no data were available for quarters 2 and 3 in the North Inner region we assumed this to be equal to the average of the adjacent quarters.

Estimating prey length

Prey lengths were estimated from equations relating otolith size to prey length from Leopold et al. (2001). Prey size classes were plotted as frequency distributions of estimated lengths for prey species that formed a major part of the diet.

Prey consumption

Estimation of prey consumption for each region / season data set was achieved by converting summed weights of each species to units of energy by multiplying weight by an average energy density value for each prey item, obtained from the literature (Murray & Burt 1977). The energy content of each species could then be expressed as a proportion of the total energy represented in the group of samples being analysed. This was then multiplied by the number of seals in that region, the average daily energy requirement of a grey seal (Sparling & Smout 2003) and the number of days in the season being analysed. To convert this energy content back to prey weight, values were divided by their species specific energy density values, providing an estimate for consumption (in kilograms) for each species within each region / season data set. These were summed across regions and seasons to provide an estimate of annual consumption for the whole study area.

Variance around obtained estimates

Estimates of variability were obtained from the Fortran diet program for estimating composition and consumption. The method by which this is achieved is laid out by Hammond and Rothery (1996), and broadly separates uncertainties into two categories; those associated with sampling error and those associated with measurement error. Sampling error is estimated using non-parametric bootstrap re-sampling where a single scat is taken as the sampling unit. Measurement error, associated with each step in the formation of estimates of composition and consumption, is estimated using parametric re-sampling of the coefficients used.

Measurement error includes: variability about estimating undigested otolith size from digested size and in accounting for complete digestion, estimates of variability here were taken from Grellier & Hammond (2006). For estimating prey size from undigested otolith size, the variability was taken from Leopold (2001). The estimate for the energy required by the population (Sparling & Smout 2003) was assumed to have a coefficient of variation of 10% (P.S. Hammond pers comm). Estimates of variability associated with the seal population estimate from Thomas & Harwood (2005) were obtained from Len Thomas (pers comm).

95% confidence intervals were taken to be the 2.5 and 97.5 percentiles of the bootstrapped distributions from a thousand replications. For the annual consumption estimate, where region / season estimates had been summed to provide an estimated annual total, results from each region

/ season bootstrapping simulation were summed and the percentiles taken from the resulting distribution.

3. Results

In 2002 at least one visit was made each quarter to all major haul-outs along the west coast of Scotland to collect scats and record the encountered seal numbers. Nine sampling trips totalling 53 days were made. The areas surveyed and counts made are given in Figure 7 – 12.

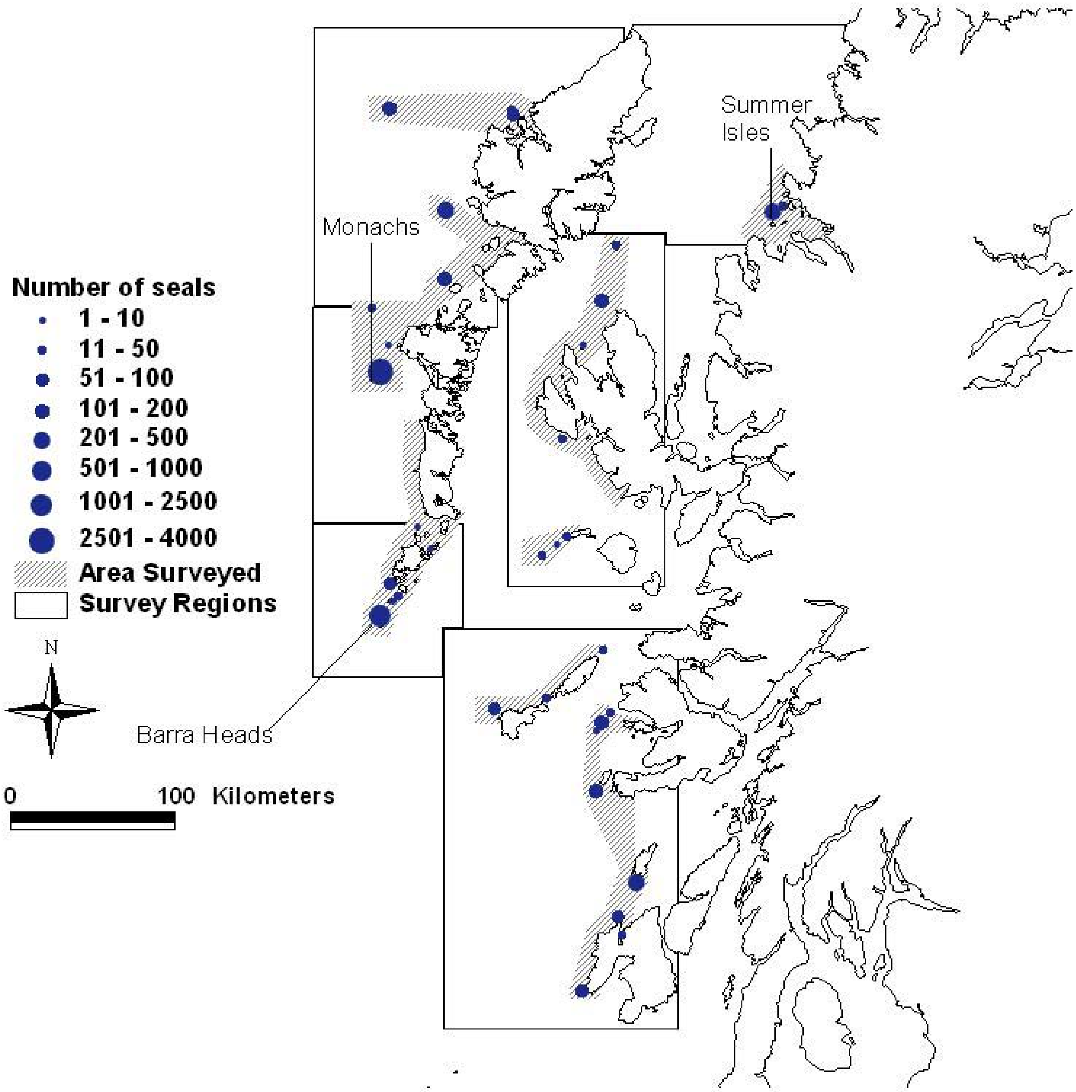

Figure 7. Area surveyed and number of grey seals counted during helicopter surveys between 28 February and 3 March 2002.

Figure 7 illustrates the distribution of seals encountered during the first survey. This was the only survey carried out in the first quarter of the year and represents a thorough sweep of all major haul-out sites. Many large haul-out groups were encountered comprising moulting animals, often above the level of the high tide mark. Large unexpected haul-outs that may represent important moulting sites, other than those at the Monachs, were observed at Glas Leac-Beg, Summer Isles and Mingulay, Barra Heads.

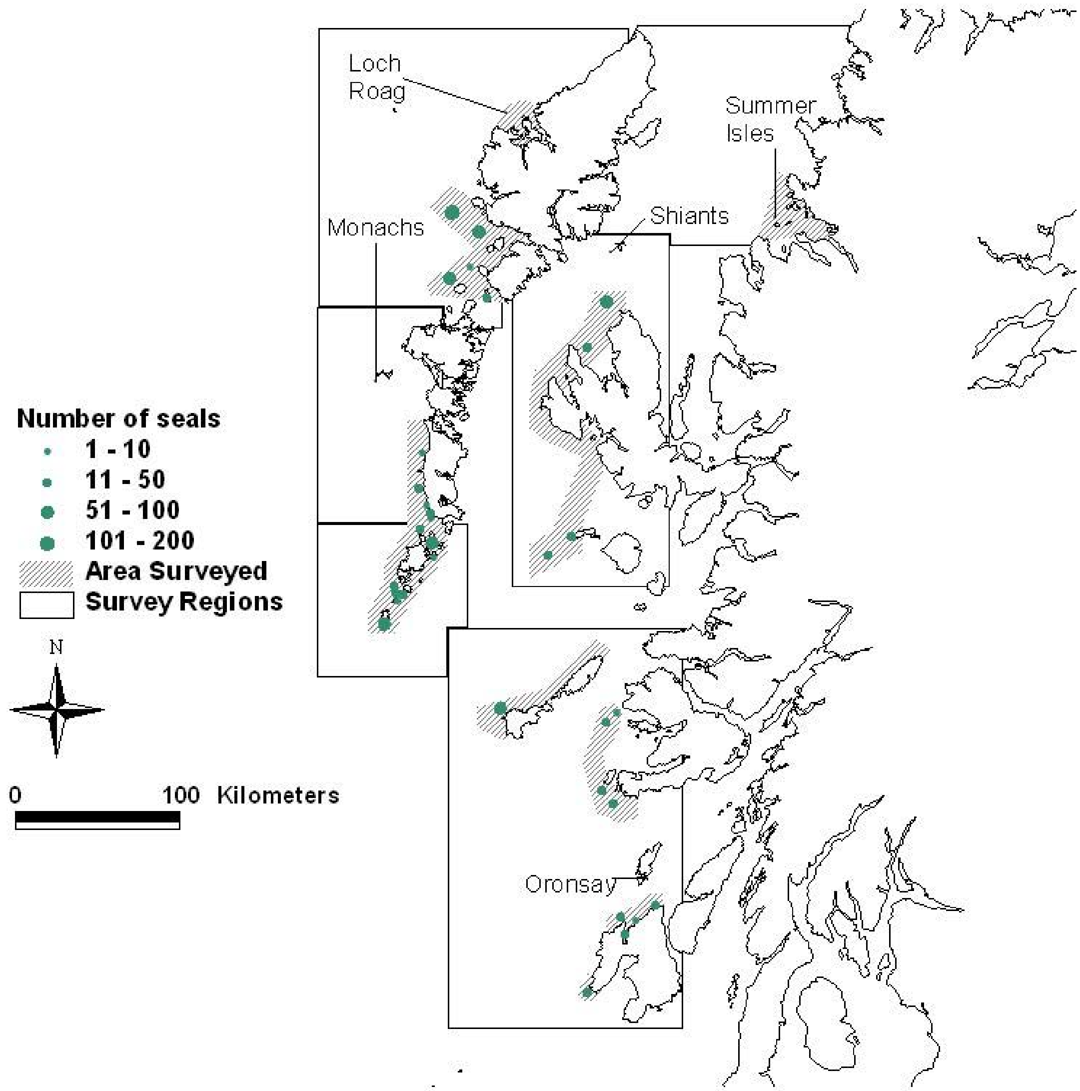

Figure 8. Area surveyed and number of grey seals counted, during helicopter surveys between 5 and 7 June 2002.

Landing restrictions due to breeding seabirds and live-stock, caused the Shiants, Monachs and Oronsay to be excluded from the helicopter survey in early June. This survey was the first of four carried out during the 2nd and 3rd quarters. Figure 8 shows the areas surveyed and number of seals counted. All seals were observed to be hauled-out in the inter-tidal zone, often on the water's edge or even partly in the water. Seals tended to form small discrete groups along the coastline. No large haul-outs comprising more than 500 seals were encountered. Notably no grey seals were recorded at the two northern most sites, the Summer Isles and Loch Roag. In comparison with the first survey far fewer seals were recorded in all areas where similar coverage was achieved.

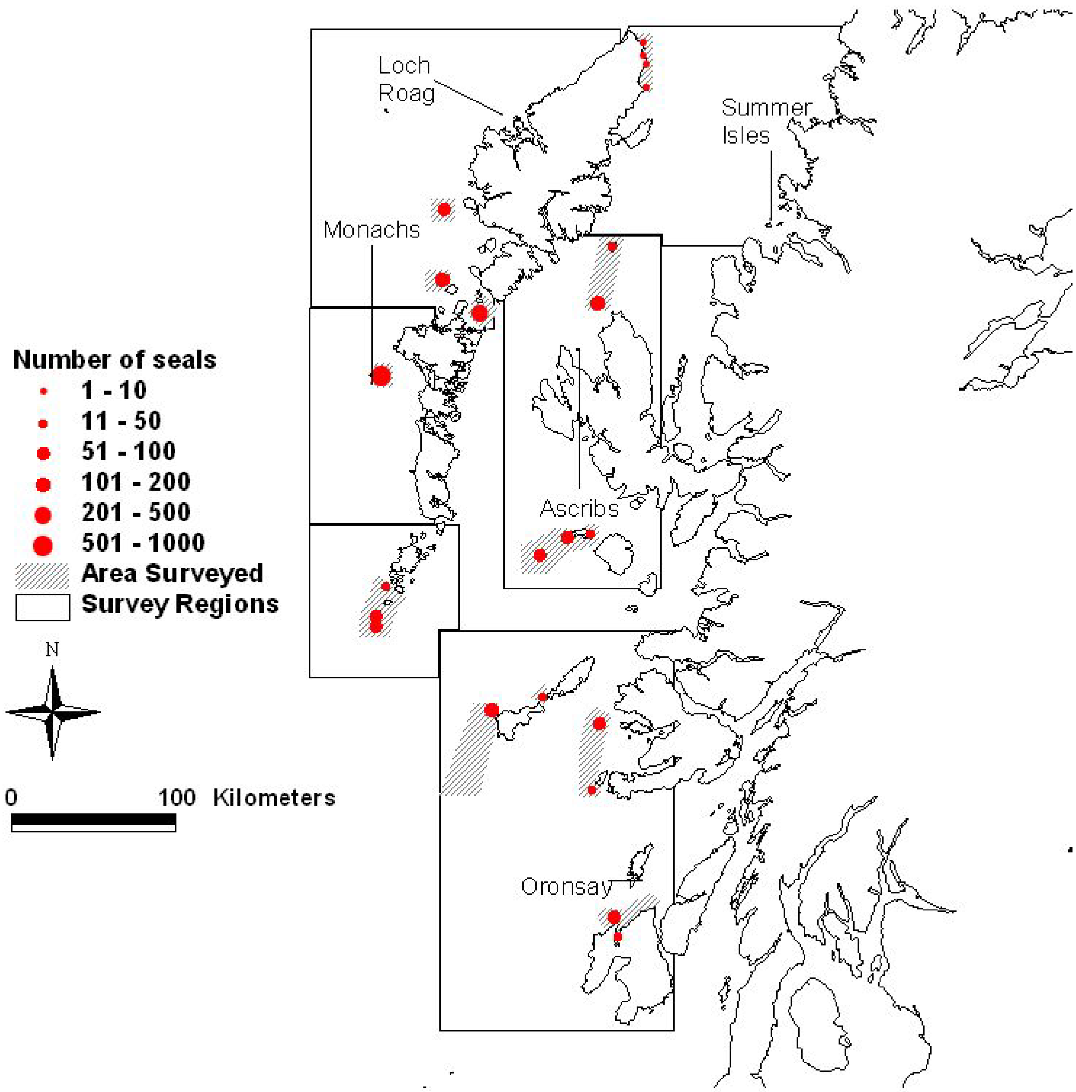

Figure 9. Area surveyed and number of grey seals counted during yacht surveys between 24 June and 3 July 2002.

The second of four surveys during quarters 2 and 3 was undertaken on the yacht "Silurian" (Figure 9.). The change in survey method, although better suited to the collection of samples from low lying inter-tidal rocks, meant that it became difficult to survey the same area in a sensible time scale. However, all major haul-outs were visited except for the Summer Isles, Loch Roag, Ascribs and Oronsay. At the Monachs only Ceann Ear was surveyed due to lack of time within the tidal window. Seals were observed to haul-out inter-tidally close to the water's edge at all sites.

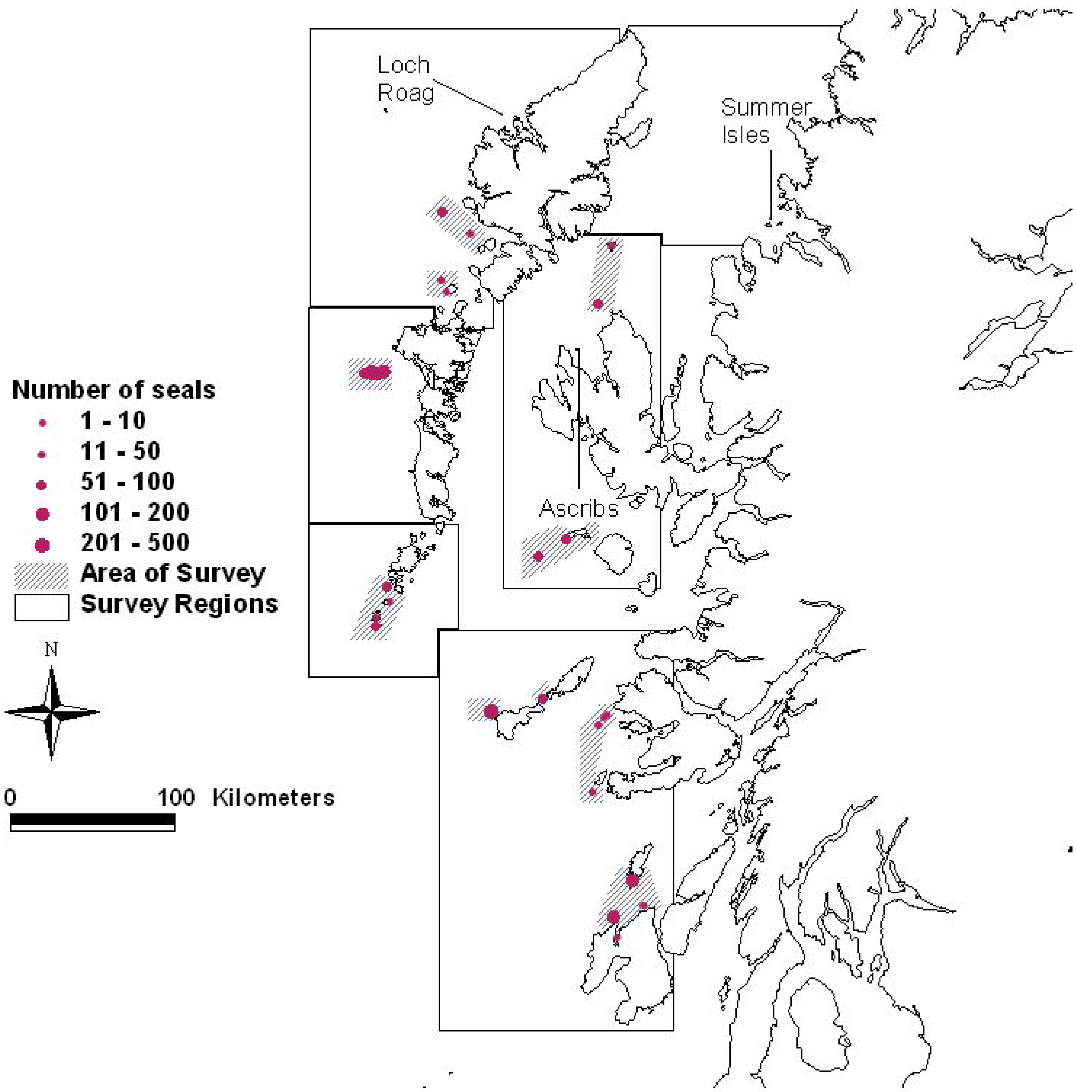

Figure 10. Area surveyed and number of grey seals counted during yacht surveys between 19 and 29 August 2002.

All major haul-outs were visited except for the Summer Isles, Loch Roag and Ascribs in the third summer survey, which was made from the yacht 'Silurian' (Figure 10). Seals were observed to haul-out inter-tidally often close to the water's edge. Grey seal distribution was similar to that observed during the third survey.

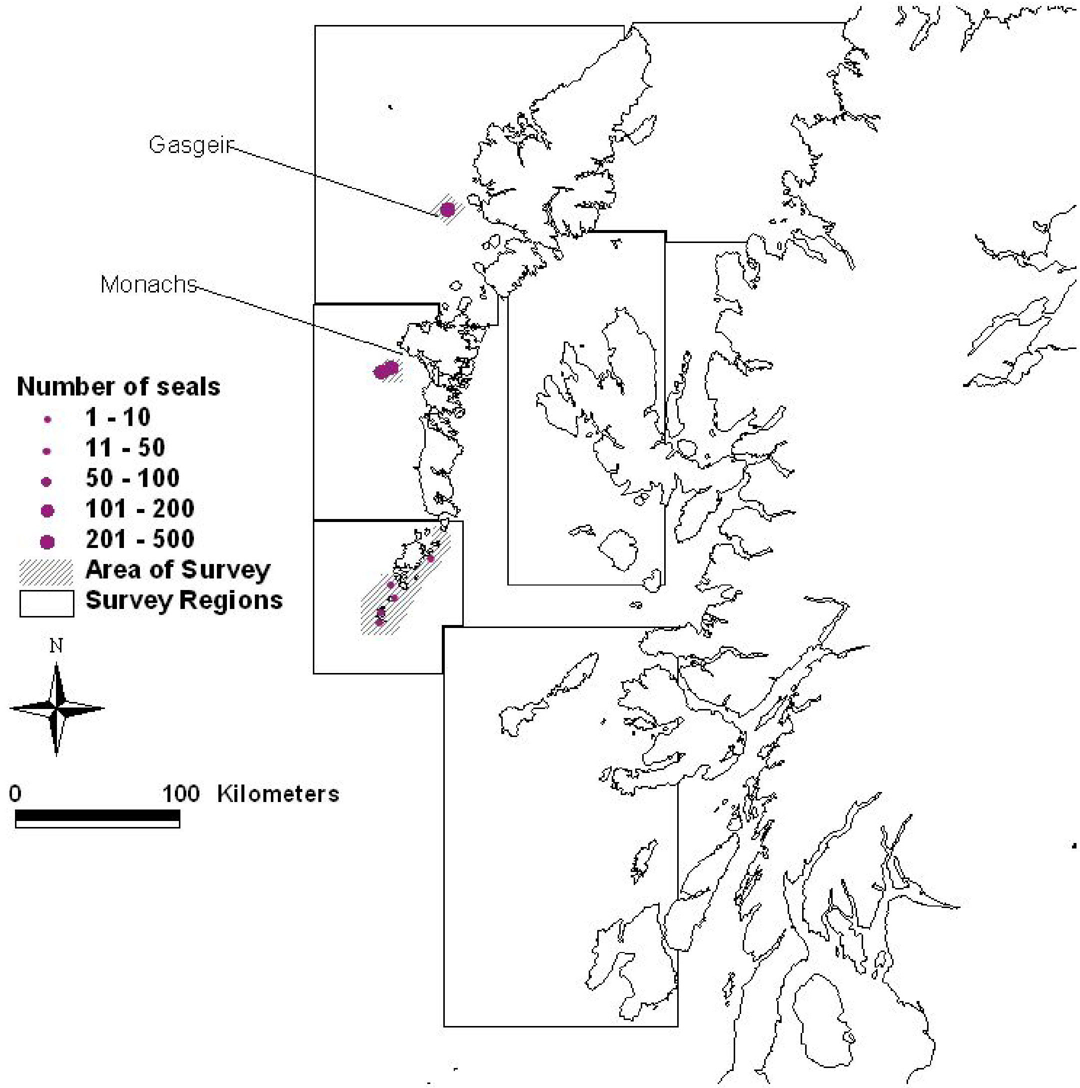

Figure 11. Area surveyed and number of grey seals counted during RIB surveys to the Monachs and elsewhere in the Outer Hebrides on 12, 13 and 16 September 2002.

The fourth summer survey was made on a rigid hulled inflatable boat to the Outer Hebrides (Figure 11). Most seals were observed hauled-out close to the water's edge, however, some animals were observed high above the inter-tidal zone, at more traditional breeding sites. This was particularly the case for Stockay, an island in the Monachs group, and to a lesser extent Gasgeir, off the Isle of Lewis.

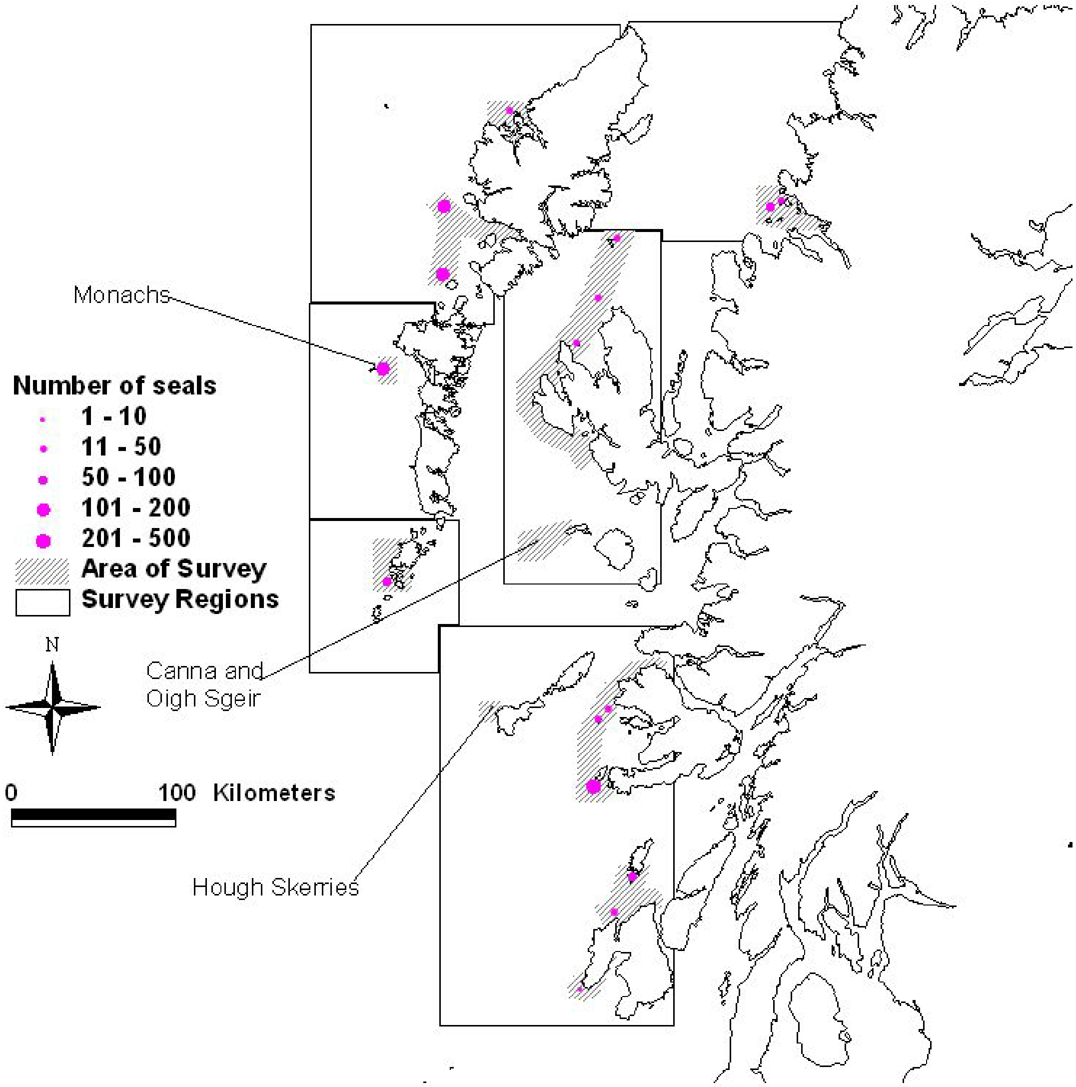

Figure 12. Area surveyed and number of grey seals counted during helicopter and RIB surveys between 8 and 22 November 2002. Note: All regions except North Inner were surveyed by helicopter between 20^{th} and 22^{nd} November, although Monachs and South Outer had reduced coverage due to SPA's for geese and bad weather respectively. North Inner was surveyed by RIB on the 8^{th} and additional RIB surveys were made to Minch and South Inner on the 9^{th} - 10^{th} and the 16^{th} - 17^{th} respectively.

The surveys in the fourth quarter were timed to coincided with the end or shortly after the end of the breeding season (Figure 12), and at many sites large numbers of weaned pups were encountered. Few adults were associated with many of the breeding colonies indicating that seals were at sea or had redistributed themselves after the end of the breeding season. Only 150 adult seals were recorded at the Monachs on the 21 November. Few adult seals were encountered throughout the survey with no grey seals recorded at Tiree's Hough skerries, Canna or nearby Oigh sgeir.

Scat collection

A total of 1589 grey seal scats was collected across the 4 quarters of the year; 1204 were processed and 19345 otoliths and beaks recovered from 49 different species. The spread of samples across time and space is shown in Table 3 and a list of identified species is given in the appendices Table ii. Samples were not evenly distributed across quarters or regions because the behaviour and distribution of seals changed through the year, making samples harder to find at certain times. For example, during the summer months seals tended to haul-out closer to the water's edge, often half in the water. They also tended to be distributed in smaller groups rather than single large haul-outs that were often encountered during the 1^{st} and 4^{th} quarters. The proportion of scats that contained hard parts varied among sites and across seasons. However, over most regions hard-parts were recovered more often from scats collected during the 1^{st} quarter. However, in the Monachs region hard-parts were consistently only recovered in approximately two thirds of samples in each quarter of the year – a relatively low return when compared to some quarter 1 values (Table 3).

Denticles were present in 5.8% of scats that were sampled, suggesting that prey items that possess these structures, such as cartilaginous fishes, are not important prey to the grey seal in this area. The most frequently encountered otoliths, by far, were sandeels (10,661 otoliths) followed by Norway pout (1,862 otoliths), poor cod (1,526), haddock (494) and sprats (426) as shown in Table 4.

Sites where scat samples were collected are given in Figure 5, coordinates for these are presented in the Appendix. Sites that were visited but did not yield any samples are too numerous to be included here, however, areas that were surveyed in each quarter are illustrated above in Figures 6 – 11.

Table 3. Number of grey seal scat samples collected, processed and the proportion that contained hard parts from the Hebrides in 2002 and the total number of hard parts (fish otoliths and cephalopod beaks) recovered. See Figure 5 for location of regions.

Region	**Quarter**	**Scats collected**	**Scats processed**	**Scats containing otoliths/beaks (proportion)**	**Otoliths/beaks recovered**
North Inner	1	102	57	51 (0.89)	1,531
North Inner	4	36	36	15 (0.42)	640
Minch	1	26	26	21 (0.81)	1,375
Minch	2+3+4	92	92	63 (0.68)	1,468
South Inner	1	83	83	70 (0.84)	1,402
South Inner	2+3	11	11	7 (0.64)	196
South Inner	4	206	125	103 (0.82)	1,597
Total Inner Hebrides		*556*	*430*	*330*	*8,209*
North Outer	1	145	78	57 (0.73)	3,087
North Outer	2+3	106	106	68 (0.64)	2,224
North Outer	4	153	153	104 (0.68)	2,247
Monachs	1	114	78	51 (0.65)	704
Monachs	2+3	155	106	70 (0.66)	913
Monachs	4	78	78	50 (0.64)	775
South Outer	1	175	68	49 (0.72)	527
South Outer	2+3	31	31	27 (0.87)	244
South Outer	4	76	76	54 (0.71)	415
Total Outer Hebrides		*1033*	*774*	*530*	*11,136*
Total Hebrides	**All**	**1589**	**1204**	**860**	**19,345**

Table 4. The number of otoliths of prey species, that contributed >5% of the diet by weight in any region/season and those for which ICES stock assessment data are available, for each region.

Species	N Inner	Minch	S Inner	N Outer	Monachs	S Outer	Total
Cod	38	46	95	75	24	26	**304**
Whiting	25	110	118	54	61	23	**391**
Haddock	108	63	68	67	113	75	**494**
Saithe	8	2	1	5	6	8	**30**
Saithe/Pollock	8	22	21	20	18	16	**105**
Ling	9	19	54	79	30	19	**210**
Rockling	13	6	31	22	15	7	**94**
Blue whiting	41	6	2	22	149	13	**233**
Poor cod	107	202	842	174	103	98	**1,526**
Norway pout	575	691	296	76	201	23	**1,862**
Plaice	3	1	3	18	28	16	**69**
Lemon sole	9	2	20	87	41	11	**170**
Megrim	0	0	0	5	0	1	**6**
Sandeel	823	1,285	798	6,119	1,205	431	**10,661**
Herring	4	15	14	90	71	15	**209**
Sprat	116	177	67	43	0	23	**426**
Dragonet	79	23	75	58	13	27	**275**
Bullrout	14	2	36	0	2	0	**54**

Diet composition

Diet composition in each region and quarter is shown in Table 5. Gadoids and sandeels, by weight, made up the highest proportions in the diet. Sandeels were particularly prevalent throughout the year in North Outer. During the first quarter they were important in the Minch, Monachs and South Outer, they were also important during the last quarter for seals at the Monachs and North Inner.

Gadoids generally had a high presence in all quarters throughout the study area. This was particularly the case for South Outer where, throughout the year, they accounted for almost half the diet. For the Outer Hebrides flatfish reached a peak in the diet during the summer months. Pelagic species increased in the diet as the year went on for North Inner, Minch and North Outer, although they were at their highest during the summer for the Monachs region.

Benthic species, including dragonet and bullrout, were important in the North and South Inner during the first and last quarters respectively. Cephalopods accounted for 5% (or almost 5%) of the diet in North Outer during the first and last quarters and also in the first quarter in the Monachs and during the last quarter for South Inner.

North Inner (Diet percentages are by weight)

In the North Inner region (Table 5a) during quarter 1 dragonet dominated the diet, accounting for over 25% of the diet, followed by sandeels (16%), cod (11%) and haddock (9%). During the last quarter sandeels accounted for the largest proportion of the diet (31%), followed by herring (18%) and cod (14%). More prey species were present in the diet during the first quarter than during the last, this however, is likely to be a result of the number of samples found in each quarter. No samples were found, in this region, during quarters 2 and 3.

Minch

Diet in the Minch (Table 5b) was dominated by sandeels during the first quarter (70%). During quarters 2, 3 and 4 combined sandeels were virtually absent and cod (19%), sprat (14%), ling (12%) and haddock (11%) made up most of the diet.

South Inner

In the South Inner region (Table 5c) sandeels formed the largest proportion of the diet during the 1st and 2nd / 3rd quarters (27% & 60% respectively) followed by cod (12% & 15% respectively); during the summer months lemon sole (10%) was also important. Cod (21%) was the most important prey during the 4th quarter followed by bullrout (11%).

North Outer

In the North Outer region (Table 5d) sandeels dominated the diet throughout the year representing 46% in quarter 1, 46% in 2/3 combined and 37% in quarter 4, followed by cod (18%) in the first quarter and herring in quarters 2+3 and 4 (13% & 18% respectively).

Monachs

In the Monachs (Table 5e), sandeels (34%) were most important during the first quarter followed by rockling (12%), herring (11%) and ling (10%). In the second and third quarters combined herring (33%) dominated the diet followed by sandeels (11%). During the last quarter sandeels (28%) again were most important followed by haddock (22%) and herring (15%).

South Outer

In the South Outer region (Table 5f) sandeels (30%) dominated the diet during the first quarter followed by herring (9%). During quarters 2+3, haddock (25%) was most important followed by plaice (15%) and sandeels (14%). Cod (20%) made up the largest proportion during the last quarter followed by haddock (15%) and sandeels (12%).

Table 5 (a – f). Hebrides 2002 regional and seasonal variation in grey seal diet expressed as percentage by weight. Listed are species contributing >5% in any quarter and species of commercial importance.

(a) North Inner

	Quarter 1		**Quarter 4**	
Species	%	95% C.I.	%	95% C.I.
Cod	**11.09**	2.73 - 21.01	**13.55**	0 - 44.59
Whiting	**1.44**	0.48 - 2.73	**0.17**	0 - 0.64
Haddock	**9.49**	2.95 - 19.24	**8.07**	0.91 - 26.69
Saithe	**0.58**	0 - 6.20		
Saithe/Pollock	**1.07**	0.06 - 13.56		
Ling	**2.65**	0.21 - 7.61	**1.57**	0 - 5.01
Rockling	**4.80**	0.21 - 12.72	**1.50**	0 - 4.92
Blue whiting	**1.38**	0.35 - 3.48		
Poor cod	**1.07**	0.45 - 1.83	**2.25**	0.04 - 7.67
Norway pout	**4.05**	1.25 - 7.40	**5.02**	0 - 18.22
Plaice	**0.61**	0 - 1.61		
Lemon sole	**1.35**	0.19 - 3.52	**0.69**	0 - 4.36
Megrim				
Sandeel	**16.29**	0.39 - 44.38	**31.40**	0 - 74.78
Herring	**0.11**	0 - 0.46	**18.43**	0 - 61.10
Sprat	**4.68**	0.65 - 13.26	**4.91**	0 - 17.33
Dragonet	**25.62**	8.65 - 45.71		
Bullrout	**4.21**	0 - 13.32	**4.50**	0 - 19.94

(b) Minch

	Quarter 1		Quarter 2+3+4	
Species	%	95% C.I.	%	95% C.I.
Cod	**6.54**	0.49 - 20.54	**18.91**	8.22 - 31.05
Whiting	**0.13**	0 - 0.39	**6.96**	0.32 - 19.44
Haddock	**0.99**	0 - 4.45	**11.02**	3.45 - 19.68
Saithe	**0.47**	0 - 7.40	**0.77**	0 - 11.50
Saithe/Pollock	**2.58**	0.26 - 26.55	**3.77**	0.27 - 32.13
Ling	**0.92**	0 - 3.90	**11.58**	4.01 - 20.47
Rockling			**2.91**	0 - 7.93
Blue whiting	**0.31**	0 - 1.18	**0.09**	0 - 0.26
Poor cod	**0.41**	0.06 - 1.21	**3.76**	1.90 - 5.89
Norway pout	**0.05**	0 - 0.17	**7.88**	2.10 - 13.84
Plaice	**0.25**	0 - 1.23		
Lemon sole	**0.21**	0 - 0.80	**0.21**	0 - 0.79
Megrim				
Sandeel	**70.40**	32.85 - 86.71	**0.07**	0 - 0.18
Herring	**6.91**	0 - 14.38	**7.42**	0 - 21.18
Sprat	**0.61**	0 - 1.92	**14.21**	3.26 - 28.70
Dragonet	**5.97**	1.59 - 14.90	**2.60**	0.21 - 6.59
Bullrout			**0.50**	0 - 1.61

(c) South Inner

	Quarter 1		Quarter 2+3		Quarter 4	
Species	%	95% C.I.	%	95% C.I.	%	95% C.I.
Cod	**11.87**	4.86 - 20.85	**14.86**	0 - 25.97	**20.58**	8.55 - 36.51
Whiting	**2.85**	1.03 - 5.20	**1.18**	0 - 19.59	**3.03**	1.67 - 4.66
Haddock	**7.17**	1.58 - 15.02			**9.23**	2.16 - 19.70
Saithe	**0.38**	0 - 7.21				
Saithe/Pollock	**1.17**	0.07 - 15.27			**1.13**	0.08 - 2.59
Ling	**9.02**	2.60 - 18.38	**1.53**	0 - 2.50	**3.45**	1.41 - 6.52
Rockling	**0.60**	0 - 1.78			**3.48**	0.66 - 7.42
Blue whiting					**0.07**	0 - 0.24
Poor cod	**6.09**	2.87 - 10.24	**1.68**	0 - 27.76	**4.75**	2.62 - 7.46
Norway pout	**0.41**	0.13 - 0.73	**2.02**	0 - 32.52	**3.01**	0.34 - 7.79
Plaice	**0.38**	0 - 1.05			**0.05**	0 - 0.18
Lemon sole	**5.56**	1.18 - 13.38	**10.09**	0 - 50.31	**0.99**	0 - 2.74
Megrim						
Sandeel	**27.28**	5.42 - 59.36	**59.57**	0.33 - 81.95	**3.91**	1.15 - 8.04
Herring	**2.94**	0.28 - 7.84			**3.51**	0.53 - 7.85
Sprat	**1.17**	0.21 - 2.91			**2.26**	0.46 - 5.87
Dragonet	**7.92**	1.70 - 17.91			**6.42**	1.61 - 14.11
Bullrout	**1.79**	0.21 - 5.28	**8.12**	0 - 55.46	**11.28**	2.85 - 22.85

(d) North Outer

	Quarter 1		Quarter 2+3		Quarter 4	
Species	%	95% C.I.	%	95% C.I.	%	95% C.I.
Cod	**18.22**	6.98 - 32.85	**6.31**	0.59 - 15.77	**6.11**	1.85 - 12.08
Whiting	**0.58**	0.13 - 1.34	**2.21**	0.39 - 5.71	**0.20**	0.05 - 0.45
Haddock	**2.27**	0.51 - 5.41	**4.94**	1.03 - 12.23	**3.24**	0.97 - 5.99
Saithe	**0.55**	0.01 - 9.20				
Saithe/Pollock	**0.97**	0.06 - 11.20	**0.51**	0 - 1.53		
Ling	**9.00**	2.97 - 17.93	**5.55**	1.77 - 11.87	**8.37**	2.82 - 15.69
Rockling	**3.19**	0.65 - 7.16	**0.03**	0 - 0.11	**0.91**	0.08 - 2.28
Blue whiting			**0.55**	0.01 - 1.60	**0.02**	0 - 0.08
Poor cod	**1.10**	0.33 - 2.34	**0.05**	0 - 0.15	**0.65**	0.30 - 1.07
Norway pout	**0.14**	0 - 0.36	**1.48**	0.12 - 4.02	**0.10**	0 - 0.26
Plaice	**0.79**	0 - 2.18	**0.37**	0 - 0.91	**1.53**	0.47 - 2.99
Lemon sole	**4.06**	1.01 - 9.93	**8.72**	2.97 - 15.39	**2.61**	0.66 - 6.31
Megrim					**0.22**	0 - 0.69
Sandeel	**45.76**	16.64 - 71.00	**45.52**	28.93 - 60.01	**37.09**	17.80 - 59.25
Herring	**2.92**	0.60 - 6.61	**13.14**	4.46 - 23.41	**18.11**	7.53 - 31.71
Sprat	**0.23**	0 - 0.73	**0.25**	0 - 0.75	**2.62**	0.83 - 5.74
Dragonet	**2.87**	0.57 - 6.76			**4.31**	0.80 - 9.20
Bullrout						

(e) Monachs

	Quarter 1		Quarter 2+3		Quarter 4	
Species	%	95% C.I.	%	95% C.I.	%	95% C.I.
Cod	**4.08**	0.18 - 10.82	**7.46**	0.86 - 16.55	**8.11**	0.55 - 18.38
Whiting	**2.24**	0.49 - 5.13	**1.10**	0.31 - 1.96	**4.09**	1.02 - 9.02
Haddock	**1.52**	0.22 - 3.63	**9.69**	1.70 - 19.72	**22.41**	6.38 - 46.72
Saithe	**0.89**	0 - 10.74	**2.02**	0.08 - 30.01		
Saithe/Pollock			**2.13**	0.12 - 29.72	**3.13**	0 - 28.27
Ling	**10.44**	2.55 - 21.80	**5.78**	0.97 - 11.59	**0.97**	0 - 2.93
Rockling	**11.73**	3.01 - 23.51	**0.85**	0 - 2.13	**0.12**	0 - 0.54
Blue whiting						
Poor cod	**1.87**	0.79 - 3.31	**0.28**	0.09 - 0.56	**0.50**	0.12 - 1.06
Norway pout	**2.89**	0.30 - 7.56	**0.94**	0.09 - 2.42	**2.63**	0.42 - 6.81
Plaice	**0.11**	0 - 0.42	**3.26**	1.06 - 5.99	**0.91**	0 - 2.42
Lemon sole	**1.74**	0 - 5.64	**4.67**	1.35 - 11.24	**1.76**	0 - 6.17
Megrim						
Sandeel	**34.18**	12.42 - 62.10	**11.38**	3.40 - 27.11	**27.89**	2.22 - 59.81
Herring	**11.29**	0 - 27.38	**32.95**	13.30 - 49.75	**15.36**	0 - 39.69
Sprat						
Dragonet	**2.97**	0.42 - 7.16	**0.46**	0 - 1.44	**0.19**	0 - 0.74
Bullrout	**2.93**	0 - 9.29				

(f) South Outer

	Quarter 1		Quarter 2+3		Quarter 4	
Species	%	95% C.I.	%	95% C.I.	%	95% C.I.
Cod	**8.01**	1.29 - 18.81	**1.57**	0 - 5.04	**19.57**	5.04 - 33.66
Whiting	**1.76**	0.58 - 3.35	**6.20**	0.91 - 12.78	**0.10**	0 - 0.36
Haddock	**8.96**	2.35 - 18.47	**24.91**	2.33 - 51.36	**15.02**	2.62 - 27.26
Saithe	**5.87**	0 - 16.73	**3.67**	0 - 51.61	**2.44**	0 - 26.76
Saithe/Pollock	**7.73**	0.35 - 19.76			**2.30**	0 - 6.11
Ling	**4.53**	0.73 - 10.60	**7.69**	0 - 21.72	**3.78**	0.89 - 7.16
Rockling	**1.48**	0 - 3.97	**2.77**	0 - 10.59	**2.55**	0 - 6.45
Blue whiting	**0.19**	0 - 0.60	**4.25**	0.71 - 9.52		
Poor cod	**1.14**	0.51 - 1.98	**1.29**	0 - 2.81	**1.95**	0.71 - 3.77
Norway pout	**0.14**	0.01 - 0.34	**0.36**	0 - 0.80	**0.73**	0 - 2.52
Plaice	**0.75**	0.00 - 2.83	**15.22**	0 - 38.76	**0.44**	0 - 1.42
Lemon sole	**1.21**	0.20 - 2.84	**4.31**	0.33 - 12.55		
Megrim	**0.38**	0 - 1.35				
Sandeel	**29.61**	10.67 - 47.28	**14.09**	2.58 - 36.96	**11.71**	2.27 - 32.43
Herring	**9.27**	1.19 - 21.89	**4.30**	0 - 16.40	**3.53**	0 - 8.29
Sprat	**0.36**	0 - 1.31	**0.27**	0 - 1.21	**4.21**	1.03 - 9.76
Dragonet	**2.04**	0 - 5.45			**7.67**	1.13 - 18.43
Bullrout						

Estimated grey seal distribution

Having an estimate of the number of seals using a region is essential in forming estimates of consumption. Table 6 shows the number of seals allocated to each region in each quarter that were used in the consumption analysis. Quarter 1 values were generated from counts of grey seals made during the survey in February/March, counts were summed within their regions and then prorated to the size of the population of grey seals on the west coast of Scotland. For quarter 2 and 3, counts of grey seals made during harbour seal surveys, by SMRU, in August were summed in their appropriate regions and prorated to the size of the population. Quarter 4 estimates were derived from Thomas & Harwood (2005) based on breeding season surveys carried out by SMRU (Table 1).

The Monachs region has the largest number of grey seals throughout the year although there are fewer seals there during the summer than at other times of the year. In quarter 2 & 3 seal numbers appear more evenly distributed than at other times with the Minch, North Outer and South Outer having approximately five or six thousand seals and South Inner nine thousand. During the last quarter the largest concentration of seals occurs at the Monachs with over 24,000 seals associated with this region, followed by the South Inner region with 8,000 seals. In contrast, the North Inner region at this time of year may have less than 300 seals. In quarter 1 over 19,000 seals may be associated with the Monachs followed by the South Outer with less than 10,000. These results show there is considerable movement of seals around the Hebrides within a single year and that certain areas are important at different times of the year (Figure 13).

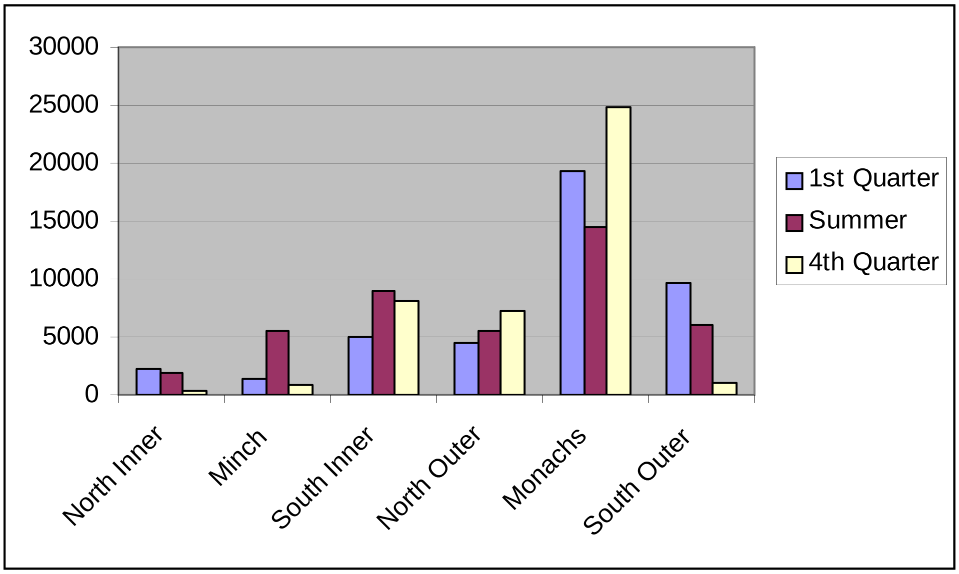

Figure 13. The regional and seasonal distribution of grey seal numbers.

Table 6. The number of grey seals, by region and season, which were used in the consumption analysis.

	Quarter 1	**Quarter 2**	**Quarter 3**	**Quarter 4**
North Inner	2318	1864	1864	297
Minch	1375	5442	5442	845
South Inner	4948	9024	9024	8075
North Outer	4534	5499	5499	7230
Monachs	19342	14405	14405	24742
South Outer	9735	6016	6016	1062

Consumption estimates

Prey consumption in 2002, based on the numbers of seals in Table 6, is given in Table 7a-f for each region / season. Those regions that have the majority of seals dominate prey consumption; the Monachs consistently had a larger population and therefore had the highest consumption (Table 7e).

As no composition data were available for North Inner during quarters 2 & 3, consumption values from the preceding and following quarters (1 and 4) were converted to per capita values per day, the average of these two values was then multiplied by the number of seals and days in quarters 2 and 3.

Overall consumption of sandeels in 2002 accounted for the largest dietary component, by far, at approximately 20800 tonnes. This was followed by herring (9789), haddock (7952), cod (7565) and ling (4449). The most important flatfish were lemon sole at 2880 tonnes and plaice at 1660 tonnes (Table 8).

Converting total consumption figures to per capita values allow comparisons to be made on changes in seal diet between 2002 and 1985, irrespective of population size (Table 9). Values for 1985 were reproduced from Hammond & Harris (2006).

Comparing the per capita diet of seals on the west coast of Scotland between 1985 and 2002 indicated that there were changes in consumption of the main prey species found in the 1985 diet. The amount of sandeels consumed fell by more than a third and consumption of ling almost halved. A significant increase in herring and haddock consumption likely compensated for some of this change. There was little change in the contribution of cod, whiting and plaice. Other increases occurred in the consumption of lemon sole, rockling, dragonet, bullrout, sprat and blue whiting (a species not detected in 1985). Another significant change in the diet was the almost complete absence of megrim in 2002. In 1985 it was the fourth largest component and accounted for almost 7% of the diet.

Table 7. Amount of prey consumed (in tonnes) by grey seals in different regions and seasons in the Hebrides in 2002. Total consumption values are given for reference only. Listed are species contributing >5% in any quarter and species of commercial importance. For region / season population sizes please refer to Table 6.

(a) North Inner

	Quarter 1 (n=51)		**Quarter 4** (n=15)	
Species		95% C.I.		95% C.I.
Cod	**130.4**	28.5 - 289.3	**17.2**	0.0 - 73.0
Whiting	**17.0**	5.2 - 36.7	**0.2**	0.0 - 1.0
Haddock	**111.6**	31.7 - 259.4	**10.2**	1.1 - 41.0
Saithe	**6.8**	0.0 - 76.5		
Saithe/Pollock	**12.5**	0.6 - 153.0		
Ling	**31.2**	2.2 - 98.8	**2.0**	0.0 - 8.3
Rockling	**56.4**	2.6 - 162.0	**1.9**	0.0 - 8.0
Blue whiting	**16.3**	3.8 - 43.9		
Poor cod	**12.5**	5.0 - 23.2	**2.8**	0.1 - 10.9
Norway pout	**47.6**	13.1 - 95.1	**6.4**	0.0 - 27.2
Plaice	**7.2**	0.0 - 21.2		
Lemon sole	**12**	1.9 - 42.9	**0.9**	0.0 - 6.5
Megrim				
Sandeel	**191.5**	5.5 - 497.9	**39.7**	0.0 - 94.2
Herring	**1.3**	0.0 - 5.4	**23.3**	0.0 - 72.0
Sprat	**55.0**	6.9 - 162.5	**6.2**	0.0 - 25.1
Dragonet	**301.2**	90.2 - 570.8		
Bullrout	**49.6**	0.0 - 176.4	**5.7**	0.0 - 29.3
Total	**1175.8**		**126.6**	

(b)Minch

	Quarter 1 (n=21)		**Quarter 2+3** (n=63*)		**Quarter 4** (n=63*)	
Species		95% C.I.		95% C.I.		95% C.I.
Cod	**35.5**	2.4 - 131.7	**1030.5**	395.7 - 1860.1	**80.0**	30.7 - 144.4
Whiting	**0.7**	0.0 - 2.5	**379.2**	16.0 - 1160.0	**29.4**	1.2 - 90.1
Haddock	**5.4**	0.0 - 28.7	**600.7**	171.7 - 1215.7	**46.6**	13.3 - 94.4
Saithe	**2.6**	0.0 - 46.6	**41.8**	0.0 - 684.3	**3.2**	0.0 - 53.1
Saithe/Pollock	**14.0**	1.4 - 161.3	**205.8**	13.6 - 1851.4	**16.0**	1.1 - 143.7
Ling	**5.0**	0.0 - 26.5	**631.2**	203.4 - 1281.6	**49.0**	15.8 - 99.5
Rockling			**158.6**	0.0 - 467.6	**12.3**	0.0 - 36.3
Blue whiting	**1.7**	0.0 - 7.1	**4.8**	0.0 - 15.9	**0.4**	0.0 - 1.2
Poor cod	**2.2**	0.3 - 7.3	**204.8**	94.0 - 360.7	**15.9**	7.3 - 28.0
Norway pout	**0.3**	0.0 - 1.1	**429.5**	104.4 - 826.7	**33.3**	8.1 - 64.2
Plaice	**1.4**	0.0 - 7.9				
Lemon sole	**1.1**	0.0 - 5.0	**11.7**	0.0 - 48.2	**0.9**	0.0 - 3.8
Megrim						
Sandeel	**382.6**	195.4 - 528.1	**3.8**	0.0 - 10.5	**0.3**	0.0 - 0.8
Herring	**37.5**	0.0 - 84.5	**404.6**	0.0 - 1088.8	**31.4**	0.0 - 84.5
Sprat	**3.3**	0.0 - 11.9	**774.7**	187.2 - 1674.4	**60.1**	14.5 - 130.0
Dragonet	**32.4**	8.0 - 97.2	**141.7**	11.5 - 393.0	**11.0**	0.9 - 30.5
Bullrout			**27.2**	0.0 - 94.9	**2.1**	0.0 - 7.4
Total	**543.4**		**5874.8**			

*- Scats were pooled in quarters 2, 3 & 4.

(c) South Inner

	Quarter 1 (n=70)		**Quarter 2+3** (n=7)		**Quarter 4** (n=103)	
Species		95% C.I.		95% C.I.		95% C.I.
Cod	**289.3**	103.7 - 569.2	**1169.5**	0.0 - 2210.8	**904.4**	310.2 - 1846.7
Whiting	**69.4**	23.0 - 147.4	**93.2**	0.0 - 1834.2	**133.0**	57.4 - 238.9
Haddock	**174.7**	34.6 - 422.5			**405.6**	78.6 - 969.3
Saithe	**9.2**	0.0 - 183.3				
Saithe/Pollock	**28.6**	1.5 - 399.2			**49.5**	3.4 - 447.9
Ling	**220.0**	63.1 - 495.3	**120.5**	0.0 - 206.4	**151.5**	50.7 - 310.4
Rockling	**14.6**	0.0 - 50.1			**153.0**	26.3 - 380.8
Blue whiting	-				**2.9**	0.0 - 11.5
Poor cod	**148.5**	58.4 - 282.6	**132.3**	0.0 - 2475.9	**208.6**	95.8 - 344.9
Norway pout	**10.0**	2.9 - 20.9	**158.9**	0.0 - 2880.3	**132.4**	12.2 - 325.8
Plaice	**9.2**	0.0 - 27.0			**2.3**	0.0 - 8.2
Lemon sole	**135.5**	27.0 - 356.0	**793.7**	0.0 - 5225.2	**43.6**	0.0 - 156.7
Megrim						
Sandeel	**665.0**	133.4 - 1336.8	**4687.2**	29.8 - 6766.3	**172.0**	38.9 - 473.0
Herring	**71.7**	6.4 - 196.9			**154.2**	26.5 - 339.1
Sprat	**28.4**	4.5 - 76.1			**99.4**	20.0 - 275.5
Dragonet	**193.0**	37.3 - 508.7			**282.1**	68.5 - 614.1
Bullrout	**43.6**	4.7 - 143.8	**638.8**	0.0 - 5688.6	**495.9**	99.8 - 1087.7
Total	**2437.6**		**7868.2**		**4394.0**	

(d) North Outer

	Quarter 1 (n=57)		**Quarter 2+3** (n=68)		**Quarter 4** (n=104)	
Species		95% C.I.		95% C.I.		95% C.I.
Cod	**381.2**	127.4 - 842.0	**301.3**	28.4 - 863.8	**188.2**	49.2 - 412.0
Whiting	**12.1**	2.5 - 32.6	**105.5**	15.3 - 288.1	**6.3**	1.3 - 14.9
Haddock	**47.4**	10.3 - 133.9	**235.6**	43.5 - 620.5	**99.8**	27.4 - 201.5
Saithe	**11.4**	0.2 - 204.4				
Saithe/Pollock	**20.4**	1.1 - 287.1	**24.3**	0.0 - 393.7		
Ling	**188.3**	58.1 - 474.4	**264.8**	58.4 - 619.9	**257.7**	73.7 - 545.2
Rockling	**66.8**	12.5 - 168.0	**1.3**	0.0 - 5.2	**27.9**	2.0 - 74.8
Blue whiting			**26.4**	0.5 - 101.7	**0.7**	0.0 - 2.6
Poor cod	**23.1**	6.4 - 55.3	**2.6**	0.0 - 8.4	**20.1**	8.2 - 35.7
Norway pout	**2.8**	0.0 - 8.7	**70.5**	5.9 - 221.2	**3.2**	0.0 - 8.2
Plaice	**16.4**	0.0 - 51.6	**17.8**	0.0 - 46.2	**47.0**	12.9 - 98.9
Lemon sole	**84.9**	19.9 - 243.4	**416.2**	106.7 - 1073.8	**80.5**	18.3 - 208.7
Megrim					**6.8**	0.0 - 21.7
Sandeel	**957.5**	364.7 - 1555.0	**2171.5**	1032.7 - 3496.3	**1141.8**	468.2 - 1994.9
Herring	**61.2**	11.0 - 153.8	**626.9**	184.0 - 1358.9	**557.5**	193.8 - 1011.5
Sprat	**4.8**	0.0 - 17.2	**11.8**	0.0 - 38.9	**80.6**	23.3 - 186.9
Dragonet	**60.1**	10.9 - 158.4			**132.6**	23.3 - 320.8
Bullrout						
Total	**2092.6**		**4770.8**		**3078.9**	

(e) Monachs

	Quarter 1 (n=51)		**Quarter 2+3** (n=70)		**Quarter 4** (n=50)	
Species		95% C.I.		95% C.I.		95% C.I.
Cod	**356.1**	14.5 - 1055.5	**947.9**	106.1 - 2376.6	**931.6**	65.3 - 2358.7
Whiting	**195.1**	37.6 - 504.7	**139.7**	38.6 - 290.9	**470.1**	98.1 - 1230.5
Haddock	**132.4**	17.7 - 353.8	**1231.4**	205.0 - 2909.3	**2575.6**	564.0 - 6615.1
Saithe	**77.6**	0.0 - 148.4	**256.7**	9.1 - 3929.2		
Saithe/Pollock			**271.3**	16.8 - 3838.5	**359.9**	0.0 - 3202.3
Ling	**911.0**	207.3 - 2190.0	**734.8**	112.6 - 1675.0	**111.2**	0.0 - 362.0
Rockling	**1023.6**	252.6 - 2287.7	**108.3**	0.0 - 309.5	**14.3**	0.0 - 66.7
Blue whiting			**410.2**	133.7 - 907.3	**22.8**	0.0 - 71.4
Poor cod	**163.1**	58.5 - 339.4	**35.4**	10.4 - 76.6	**57.2**	12.4 - 136.7
Norway pout	**252.6**	27.2 - 771.2	**119.9**	10.7 - 323.9	**302.6**	39.9 - 890.1
Plaice	**9.5**	0.0 - 37.2	**414.9**	137.8 - 876.0	**104.1**	0.0 - 305.3
Lemon sole	**151.6**	0.0 - 586.4	**593.5**	166.2 - 1575.4	**202.4**	0.0 - 774.9
Megrim						
Sandeel	**2982.8**	1081.6 - 5438.1	**1446.0**	427.9 - 3661.6	**3205.5**	233.1 - 6637.1
Herring	**985.3**	0.0 - 2503.6	**4188.0**	1883.1 - 6455.8	**1765.6**	0.0 - 4252.2
Sprat						
Dragonet	**258.8**	36.6 - 706.9	**59.0**	0.0 - 201.5	**22.3**	0.0 - 90.0
Bullrout	**256.0**	0.0 - 863.1				
Total	**8726.3**		**12708.2**		**11493.8**	

(f) South Outer

	Quarter 1 (n=49)		**Quarter 2+3** (n=27)		**Quarter 4** (n=54)	
Species		95% C.I.		95% C.I.		95% C.I.
Cod	**375.8**	34.0 - 909.1	**101.5**	0.0 - 356.8	**112.3**	25.0 - 219.7
Whiting	**82.4**	14.1 - 172.1	**402.3**	62.9 - 937.3	**0.6**	0.0 - 2.2
Haddock	**420.3**	68.7 - 965.0	**1614.6**	140.9 - 3611.7	**86.2**	12.6 - 174.2
Saithe	**275.5**	0.0 - 2986.3	**238.1**	0.0 - 3480.6	**14.0**	0.0 - 163.2
Saithe/Pollock	**362.7**	11.0 - 3599.5				
Ling	**212.4**	17.4 - 540.8	**498.7**	0.0 - 1603.0	**21.7**	5.0 - 43.0
Rockling	**69.4**	0.0 - 231.1	**179.4**	0.0 - 763.7	**14.7**	0.0 - 39.4
Blue whiting	**8.7**	0.0 - 31.6	**275.5**	46.2 - 676.0		
Poor cod	**53.5**	11.8 - 109.7	**83.4**	0.0 - 196.1	**11.2**	3.7 - 23.7
Norway pout	**6.5**	0.3 - 16.7	**23.1**	0.0 - 58.4	**4.2**	0.0 - 14.9
Plaice	**35.0**	0.0 - 126.5	**987.0**	0.0 - 2838.5	**2.5**	0.0 - 8.5
Lemon sole	**56.6**	7.6 - 161.0	**279.3**	23.3 - 853.9		
Megrim	**17.8**	0.0 - 67.4				
Sandeel	**1389.0**	291.3 - 2559.6	**913.7**	192.2 - 2307.8	**67.2**	12.7 - 163.1
Herring	**434.7**	53.3 - 1023.2	**278.6**	0.0 - 1031.4	**20.2**	0.0 - 45.6
Sprat	**16.9**	0.0 - 69.6	**17.6**	0.0 - 79.1	**24.1**	6.0 - 53.6
Dragonet	**95.5**	0.0 - 272.0			**44.0**	6.6 - 110.5
Bullrout						
Total	**4691.5**		**6483.1**		**573.7**	

Table 8. Estimate of the amount (in tonnes) of prey consumed by grey seals in the Hebrides in 2002, in rank order, only species contributing >5% in any quarter and species of commercial importance are shown.

Species	Total consumption	95% C.I.		
Sandeel	**20820**	**12268**	**-**	**25443**
Herring	**9789**	**5542**	**-**	**12782**
Haddock	**7952**	**4616**	**-**	**15026**
Cod	**7565**	**4504**	**-**	**9625**
Ling	**4449**	**2789**	**-**	**6244**
Lemon sole	**2880**	**1564**	**-**	**7558**
Saithe + Pollock	**2317**	**1415**	**-**	**11283**
Whiting	**2151**	**1191**	**-**	**3991**
Rockling	**1960**	**919**	**-**	**3328**
Dragonet	**1876**	**1038**	**-**	**2414**
Norway pout	**1682**	**848**	**-**	**4510**
Plaice	**1660**	**472**	**-**	**3529**
Bullrout	**1595**	**426**	**-**	**6769**
Sprat	**1266**	**507**	**-**	**2148**
Poor cod	**1205**	**835**	**-**	**3617**
Blue whiting	**784**	**347**	**-**	**1407**
Megrim	**25**	**0**	**-**	**77**

Table 9. Average per capita consumption rates in the Hebrides during 2002, presented with 1985 figures from Hammond & Harris (2006)

Species	Kg consumed per seal day		Kg consumed per seal year	
	2002	**1985**	**2002**	**1985**
Sandeels	1.35	2.10	493	765
Herring	0.63	0.26	232	94
Haddock	0.52	0.14	188	52
Cod	0.49	0.50	179	184
Ling	0.29	0.56	105	206
Lemon sole	0.19	0.02	68	6
Saithe + Pollock	0.15	0.28	55	104
Whiting	0.14	0.13	51	47
Rocking	0.13	0.03	46	10
Dragonet	0.12	0.02	44	7
Norway pout	0.11	0.18	40	67
Plaice	0.11	0.11	39	40
Bullrout	0.10	0.00	38	2
Sprat	0.08	0.00	30	0
Poor cod	0.08	0.05	29	19
Blue whiting	0.05	0.00	19	0
Megrim	0.00	0.35	1	128

Size of prey consumed by grey seals

For the main prey species, estimates of prey length are shown in Figures 14 – 18. As the frequency histograms are plots of estimates, care needs to be taken when interpreting the tails of these distributions, as they are likely the product of sampling error. In addition, prey whose otoliths are completely digested are likely smaller than those whose otoliths were recovered; these prey are not represented in the length data shown.

The distributions of prey lengths show that seals predated on mainly small fish. Most cod consumed were less than 50 cm with the mode at 35 – 40cm, these fish therefore, would be mostly immature. Distribution of haddock lengths indicates that the majority were between 24 – 36cm, with the mode at 30 – 32cm. For whiting, most were 20 – 28 cm, with the mode at 24 – 26cm. For sandeels most were 16 – 24 cm, with the mode at 18 – 20cm, most herring were between 25 – 45 cm, with the mode at 35 – 40cm, indicating that almost all sandeels and herring consumed would have been mature.

Consumption compared with stock biomass and fishery catch

West of Scotland grey seal consumption in 2002 was compared with total stock biomass (TSB) and fishery catches in the area. Table 10 shows estimates of total stock biomass in ICES Division VIa for species assessed by ICES Working Groups (WG), compared with estimates of consumption and catch for assessed species (http://www.ices.dk/products/CMdocs/2005/ACFM/ACFM0105.pdf).

As no final analytical estimate was produced by ICES for many of the fish stocks it is not possible to compare consumption with all commercially important prey species in 2002. The exceptions are haddock, saithe and herring where higher levels of confidence exist in estimates. Of these species haddock showed the highest level of consumption relative to stock size at just over 9%. Consumption of saithe and herring relative to stock size are lower, less than 4%.

Comparing consumption with catch of the main commercial species off the west coast of Scotland shows that for many species grey seal consumption was significant relative to fishery catch. For cod and whiting the high level of consumption relative to catch is due to large restrictions placed on fisheries in 2002 in the form of quotas to limit the catch of cod and whiting. For haddock and herring, where restrictions were not so great, consumption is still high at almost

50% and 30% of the fishery catch. This is not the case for saithe and megrim where consumption relative to catch is much smaller.

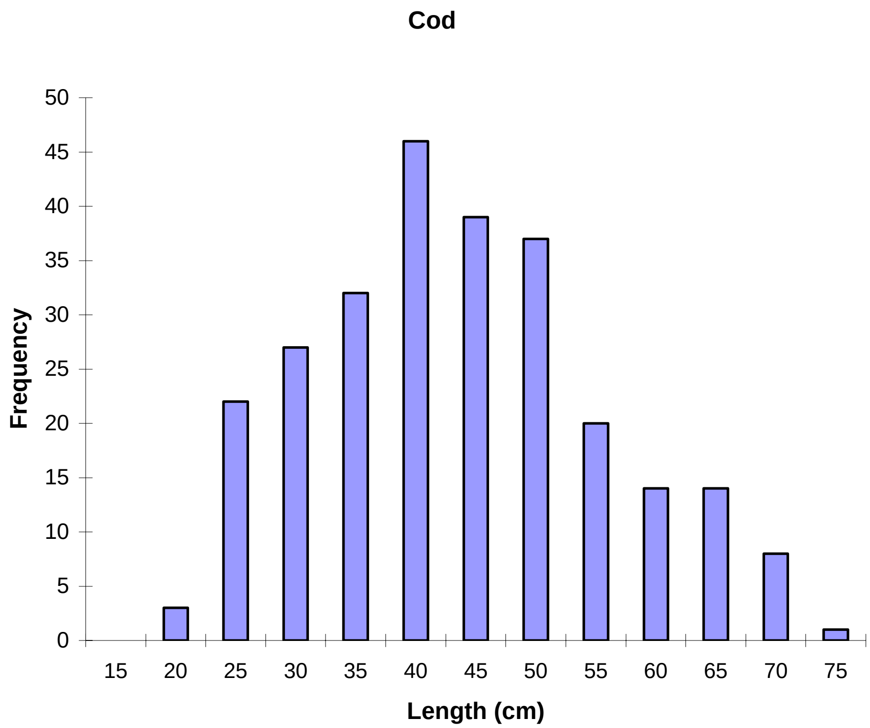

Figure 14. Distribution of estimated cod lengths in the diet in 2002

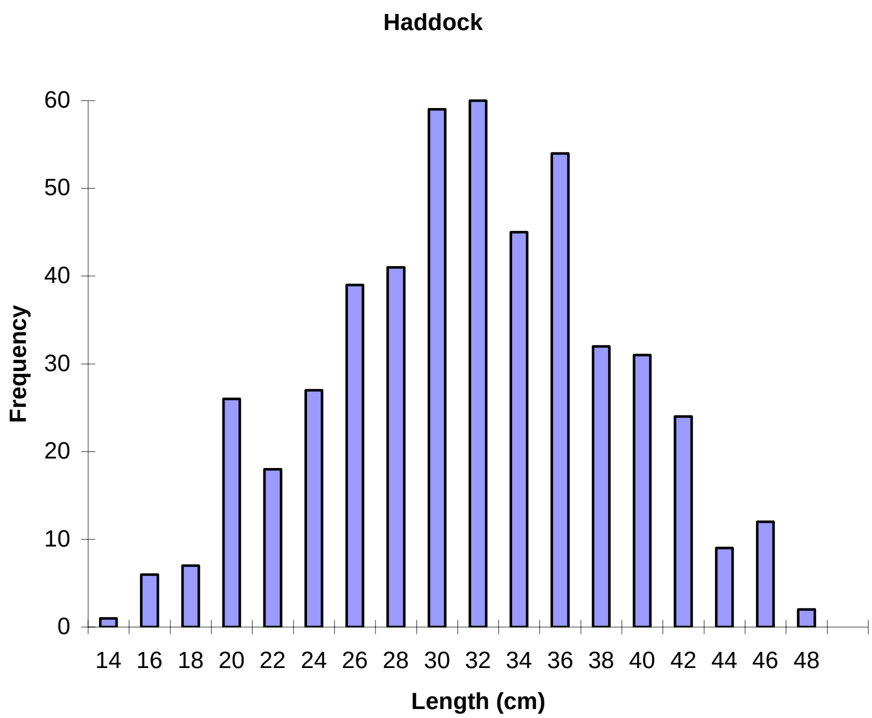

Figure 15. Distribution of estimated haddock lengths in the diet in 2002

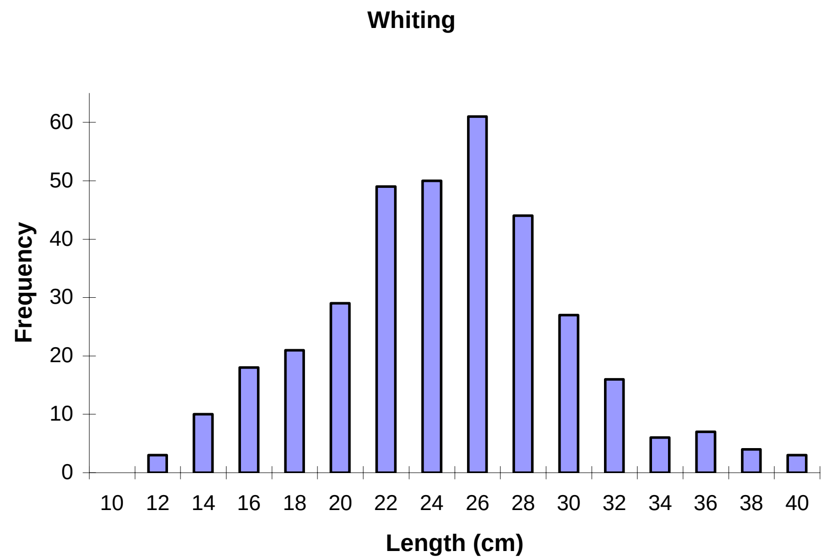

Figure 16. Distribution of estimated whiting lengths in the diet in 2002

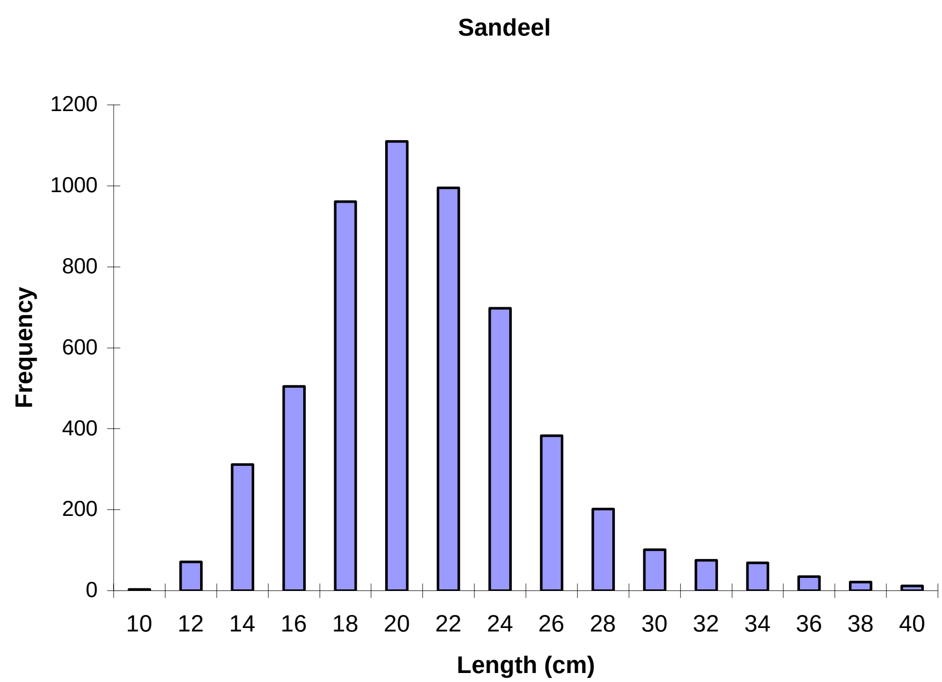

Figure 17. Distribution of estimated sandeel lengths in the diet in 2002

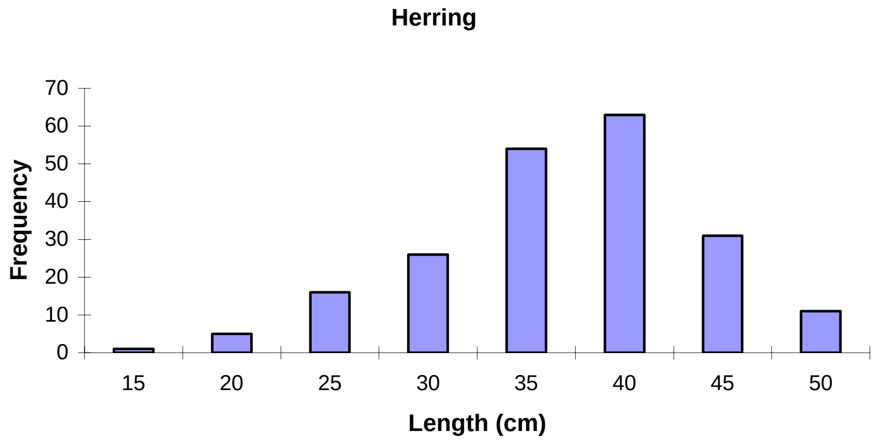

Figure 18. Distribution of estimated herring lengths in the diet in 2002

Table 10. For 2002: estimated total stock biomass (TSB) and estimated grey seal consumption in the Hebrides area compared to fishery catch in ICES Division VIa for species assessed by ICES WG.

Estimates for cod, whiting and haddock TSB are the result of exploratory assessments by the ICES Northern Shelf Demersal Stock Assessment WG 2004 (http://www.ices.dk/products/CMdocs/2005/ACFM/ACFM0105.pdf). The WG was not able to conclude a final analytical estimate for cod and whiting therefore the values given are uncertain and are purely illustrative of stock trends.

Estimates of saithe TSB are of the stock assessments for Sub-Area IV and Division VIa combined from the ICES WG on the Assessment of Demersal Stocks in the North Sea and Skagerrak 2004 (http://www.ices.dk/products/CMdocs/2005/ACFM/ACFM0705.pdf).

Estimates of herring TSB are from assessments of the ICES Herring Assessment WG for the Area South of 62°N in 2005 (http://www.ices.dk/products/CMdocs/2005/ACFM/ACFM1605.pdf).

Estimates of megrim TSB are from an exploratory assessment of the ICES North Shelf Demersal Stock Assessment WG 2004, the estimates are uncertain and therefore are only presented to illustrate stock trends (http://www.ices.dk/products/CMdocs/2005/ACFM/ACFM0105.pdf).

Error associated with TSB estimates are not available from ICES WG reports. The level of restrictions placed on what fisheries are allowed to land, in the form of quotas, will be discussed later. Estimated 95% confidence intervals for prey consumption are given in Table 8.

Species	**Estimated TSB (tonnes)**	**Estimated consumption (tonnes)**	**Consumption as a % of TSB**	**Fishery catch (tonnes)**	**Consumption as a % of catch**
Cod	**11,000***	7,565	N/a	2,400	**315.2**
Whiting	**13,000***	2,151	N/a	3,900	**55.2**
Haddock	**87,000**	7,952	**9.1**	16,000	**49.7**
Saithe (NS+VIa)	**730,000**	2,901	**0.4**	122,000	**2.4**
Herring	**272,000**	9,789	**3.6**	32,000	**30.6**
Megrim	**7,600***	25	N/a	1,800	**1.4**

* - High level of uncertainty.

Comparison of consumption with stock and catch between 1985 and 2002

Table 11 shows the relative change in estimated TSB and catch between 1985 and 2002 on the west coast of Scotland, which shows clearly the decline in the estimated abundance of some of the commercially valuable species and the declines in fishery catches as enforced by reduced quotas. The change in consumption relative to TSB and to catch between these years demonstrates how important grey seal consumption has become in the face of these very large decreases in some stocks. Where consumption relative to total stock biomass was high in 1985 these further increases could now cause serious concern for fishery managers. The cod stock in this region for instance has decreased by almost three quarters and the fishery catch has been reduced by 91%. However, over the same time period, consumption relative to stock size has increased by more than 50% and as a result consumption relative to fishery catch has increased by almost three times. For cod, at least, consumption has significantly increased relative to the stock and catches between 1985 and 2002. In Table 11 megrim represents the only decline in overall consumption between the two years.

Table 11. Relative change between 1985 and 2002 in estimated TSB, consumption relative to TSB, catch/landings, and consumption relative to catch/landings. Changes in TSB are presented as percentages because absolute estimates of TSB are unreliable but the relative difference between them is more reliable. This is especially the case for cod, whiting and megrim. The figures in Table 11 should therefore be regarded as illustrative rather than definitive.

Species	Change in estimated TSB (%)	Change in consumption relative to TSB (%)	Change in catch (%)	Change in consumption relative to catch (%)
Cod	-74	+55.8	-91.1	+295.2
Whiting	-72	+13.5	-83.7	+49.3
Haddock	-17	+7.7	-61.9	+46.1
Saithe (NS+VIa)	+3	+0.1	-46.0	+1.4
Herring	-24	+2.8	-17.9	+23.6
Megrim	-37	-31.7	-18.2	-167.6

4. Discussion

Grey seal distribution and abundance in 2002

During 2002 the west coast of Scotland was successfully sampled in each quarter of the year. Coverage, however, between quarters was not even, partly due to logistical constraints, restrictions imposed by landowners/managers and severe weather, all of which played a significant role in shaping each survey. This clearly limits the ability to make comparisons between surveys on seal abundance and distribution, as will the decision to survey areas around known haul-outs rather than entire coastlines. For many haul-outs only one count is available for a given period in the year, and, as it is known that the number of seals that haul-out can fluctuate widely over the low tide window and over consecutive days (pers obs), it would therefore be unwise to draw any firm conclusions on seal abundance and distribution. Due to changes in seal behaviour through the year it was necessary to change the mode of transport to enable appropriate access of haul-outs - from the use of a helicopter to boats. During summer months grey seals were observed to haul-out in smaller groups right on the waterline, occasionally half in the water often spread over many off lying skerries. At this time of the year the most effective way of covering many of the west coast locations was by small boat. This method also reduced disturbance to breeding seabirds - a requirement made by many land managers in the area. In contrast many locations were inaccessible by boat during the first and last quarters of the year due to their exposed locations and constant swell preventing any landing from the sea. Access at these times was only effectively possible by helicopter. Seals at these times would often be observed high above the water level, often forming large groups, promoting the use of a helicopter where a pilot would usually only need to land once to allow access to the entire haul-out. This change in survey method, although essential to optimise scat collection, further limits the ability to make comparisons on seal abundance and distribution between surveys. However it is clear from this study that the largest haul-outs occurred during quarter 1, a finding that is consistent with moult behaviour. This period also represented the easiest time of year to find scats and these scats were generally more likely to contain hard-parts than at other times of the year. This may indicate a period of increased foraging by grey seals between breeding and the moult or shorter foraging trips. Although due to the lack of telemetry data at this time of the year, as tags are shed at this time of year, it is difficult to draw conclusions on foraging behaviour.

At present the only comprehensive data on grey seal distribution on land in this area comes from surveys carried out by SMRU in August and of the distribution of breeding animals in October and November (SCOS 2005). These provide estimates of animal abundance in very different ways; the latter generates abundance estimates from models using data on pup production (Thomas & Harwood 2005) and does not consider the distribution of foraging animals. From satellite telemetry data we know that at least some animals will travel hundreds of kilometres to traditional breeding colonies, where most of the time is spent out of water, only to immediately return to their haul-outs to resume foraging bouts, as little as three weeks later (SMRU unpublished data). This implies that some seals at least feed very little, if at all, in the region they choose to breed in. As yet it is unknown how prevalent this behaviour may be, although it indicates that perhaps caution should be taken when using breeding distributions in seal diet studies – especially where marked regional and seasonal differences occur in the diet. This study begins to provide much needed distribution data at other times of the year, notable the first quarter and an insight into immediate post breeding distribution – which, when more information becomes available, may provide a more accurate picture of foraging during quarter 4.

Assessing grey seal diet from scat analysis

The use of hard parts, recovered from scats, to reconstruct the diet of grey seals makes several assumptions. It is important to take these into account to limit any biases they may cause (DaSilva & Neilsen 1985; Murie & Lavigne 1986; Jobling & Breiby 1986; Jobling 1987; Pierce & Boyle 1991). Firstly we assume that scats collected contain information that is representative of the population being studied so that the observed data reflect the prey consumed by the population. To take account of any regional and seasonal differences in the diet it is important that sufficient samples are collected seasonally from each region to prevent any bias as a result of this. This was achieved for most regions (Table 3). In converting recovered otoliths and beaks to estimates of diet composition it is important to account for partial and complete digestion to limit any associated bias. The methods used here use comprehensive and robust estimates of digestion coefficients and recovery rates (Grellier et al. 2006), along with the latest allometric equations from the literature to relate otolith size to prey size (Leopold et al. 2001; Harkonen 1986; Brown & Pierce 1998; Clark 1986; Santos *pers comms*).

In extrapolating composition data to estimates of consumption it is essential that an accurate estimate of the size of the population is available. Considerable uncertainty exists over the size of the British grey seal population (SCOS 2005). Various models have been put forward to recreate the natural processes that go on within the dynamics of this population in an attempt to provide an accurate estimate of population size. Models presented to SCOS in 2005 allowed the growth of the population to be limited by forms of density dependence by either decreasing fecundity or decreasing juvenile survival. For each mechanism the rate of decrease in fecundity or survival was modelled using a linear function or a non-linear function (Thomas & Harwood 2005). Each model fitted the data equally well and was regarded by SCOS to be equally robust. In this study the simple linear density dependent survival model was used over other models; it provided the smallest population estimate. If other models submitted to SCOS in 2005 were used then consumption values would be much larger - in the case of the next largest estimate the extended non-linear density dependent survival model, approximately 30% larger (SCOS 2005). Therefore, reducing the uncertainty over which population model to use would help reduce the largest potential source of bias in the consumption results. Therefore consumption estimates presented here potentially represent underestimates of true prey consumption.

Improved data on the seasonal distribution of seals could further reduce bias in consumption estimates, especially where there are large seasonal and regional differences in diet composition or if large shifts in the distribution of seals take place over the course of a year. As yet we know little of the distribution of seals outwith the breeding season and although values were generated for use in this study, they are not robust. They do, however, provide some insight. The alternative of using the distribution of breeding animals to estimate consumption is less ideal as the breeding distribution is unlikely to represent that of foraging animals. The pupping and mating process for grey seals generally takes less than one month but it is the distribution of animals for the remaining 11 months that is important in assessing diet.

In this study, an attempt was made to produce consumption estimates based on the seasonal distribution of seals. If the breeding distribution (quarter 4) had been taken to represent the distribution over the entire year, then results for total consumption would have differed by an estimated 20% increase in the consumption of herring, 2% increase in the consumption of sandeels, a 20% decrease in the consumption of haddock and a 6% decrease in the consumption of cod. Although these changes in consumption of some species appear large, they are all well within 95% confidence intervals of the estimates.

A further source of bias in estimating consumption is the use of an annual average energy requirement (Sparling & Smout 2003) and not seasonal values for energy requirement. At the time the consumption figures were estimated these values were not available. It is likely that grey seal energy requirements may be higher during the summer months and lower during the winter months due to pupping and moulting. This would lead to a slight increase in prey consumption during quarters 2 & 3 and a slight decrease in quarters 1 & 4. From the diet composition results, this would have little effect on the main gadoids; cod, haddock and whiting, but estimated consumption of herring, sprat, flatfish, Norway pout and blue whiting would likely increase and estimated consumption of sandeel, rockling, dragonet, bullrout, cephalopods and poor cod would decrease.

There are three further sources of bias that needed to be accounted for. Firstly we assumed that scats that are defecated at sea are the same, in prey content, as those that are defecated at haul-out sites. In evaluating this potential source of bias, Smout (2006) brought together, in a modelling framework, prey distributions, seal telemetry data and passage rates of prey remains through seal guts. She concluded that, at least in the case of grey seals around Britain, very little if any bias is expected from sampling at haul-out sites.

Secondly, we assumed that the heads of prey are not discarded by seals and that prey such as cartilaginous fish do not make up a significant part of the diet. The latter was evaluated by recording the presence of denticles, structures that members of the shark and ray family have that are not readily digested. In this study denticles were recorded in 5.8% of samples, suggesting that these species did not make up a significant part of the diet on the west coast of Scotland. With respect to fish heads, it is not possible to say what proportion of seals in the wild discard the heads of prey. Fishermen that use fixed nets often claim that ‘rogue’ seals remove only part of the fish from their nets or are often seen to discard the heads of large fish that have been removed from the net. This implies that scat analysis would be biased towards smaller fish, if heads were only discarded from larger fish. However feeding behaviour around fishing nets is probably not representative of the population as a whole. Observations made by the author, of seals predating on large salmonids (n=31) in Scottish rivers and estuaries would suggest that the head is often consumed and is usually the first part of the fish to be eaten. However during these observations seals spent between 5 – 30 minutes tearing prey into smaller portions, which makes it impossible to say that during this messy process the whole prey is consumed. Underwater observations in captivity suggest that parts of large fish that are dropped during the processes of feeding are later recovered and eaten by seals (SMRU unpublished data). The recovery of many large prey otoliths from scats indicates that the heads of large prey are often eaten.

Thirdly, it is important to consider secondary prey ingestion (Arnett et al. 2001), accounting for otoliths that may be present in the stomachs of prey. Large fish consume smaller fish and it is possible that some of the otoliths recovered from seal scats are actually from the stomachs of larger fish. However, based on the number of otoliths recovered from scats and the observed stomach contents of large fish, simple calculations indicate that even in extreme circumstances, secondary prey is likely to contribute far less than 1% of diet composition (Hammond *pers comm*).

Remains of crustacea present in scat samples are possibly the result of secondary prey ingestion. There is little evidence that grey seals eat crustaceans, although some authors have hypothesised that they may form part of the diet of immature seals (Prime & Hammond 1990). In the case of commercially important species, underwater filming of grey seal behaviour around creel pots revealed that the filmed individuals that had learnt to raid pots were doing so only for the bait, leaving crab and lobster alone.

Diet of grey seals off Western Scotland

From the results, it is clear that seals on the west coast of Scotland have a truly catholic diet with seasonal and regional differences. In 2002, 49 prey species or family groups were recorded, including at least 4 different squid species and the lesser octopus (list of the recorded species is given in the appendices Table ii). Thirty-four species or family groups were recorded in 1985. However, it is possible that species that were rarely encountered may have been recorded as unidentified and, in the case of cephalopods, that they were completely ignored. Species that were recorded in 1985, but not in 2002, included hooknose, conger eel, turbot and goldsinny. Species recorded in 2002, but not in 1985, included dab, long rough dab, brill, grey gurnard, solenette, blue whiting, sprat, greater forkbeard and halibut. The greater number of recorded species in 2002 may represent a more varied diet than in 1985, perhaps in response to reduced stocks of preferred prey. However, because it is impossible to say how many ‘minor’ species may have been recorded as unidentified, especially in 1985, it is difficult to draw conclusions about differences in species diversity of diets in 1985 and 2002.

Gadoids remain important prey species in all regions and seasons in western Scotland as they were in 1985 (see appendices, Table iii – vi, for results from 1985, Hammond & Harris 2006). This mirrors a similar finding in the North Sea study (Hammond & Grellier 2006). The importance of gadoids and sandeels was also apparent in a study by Pierce et al. (1990), which was carried out in the North Inner region between 1986-1988. The occurrence of sandeels in the diet decreased from 1985. This decrease was balanced by an increase in gadoids and a large increase in herring. A decrease in sandeels was also recorded in the North Sea, which was balanced by an increase in gadoids and benthic species (Hammond & Grellier 2006).

Whereas gadoids west of Scotland formed a consistent contribution to the diet throughout the year, sandeels were more variable. Although important in all regions sandeels, appeared in the diet in some quarters but not others, for example accounting for 60-70% by weight of the diet in one quarter and being negligible in the following quarter. Large quarterly fluctuations were also apparent in 1985 although it is difficult to compare regional differences directly to 2002 as fewer but larger regions were used to analysis the 1985 study. At times where sandeels formed a minimal contribution to the diet, gadoids often formed the largest contribution to the diet. Sandeels, despite being preferred prey, appear not be accessible in all regions throughout the year and at these time it is likely seals switch prey. The varied appearance of sandeels in the diet is likely due to seasonal changes in their behaviour, survey trawls and acoustic surveys reveal that populations can undergo large annual fluctuations (Greenstreet et al. 2005). However, in some regions sandeels consistently make up a high proportion of the diet throughout the year, for example North Outer in 1985. This was attributed to the region North Outer containing areas of preferred habitat for sandeels (Hammond et al. 1994c).

Flatfish were more prevalent in the Outer Hebrides than in the Inner Hebrides in both years, especially so during summer 2002. Pelagic schooling fish in the diet were mainly confined to the Inner Hebrides in 1985 and to quarter 2. In 2002 more pelagic species were recorded in the diet, they made up a larger percentage of the diet by weight during the last quarter of the year and were important prey in most regions. The exceptions were in the Monach Isles, where they formed their largest percentage during the summer, and the southern regions where they never reached more than 10% in either region or any quarter. This suggests that pelagic species were more important to grey seals in the northern and central regions and generally later in the year.

Benthic species also increased in importance in 2002, when they were most prevalent during the winter months and especially so for the North Inner and South Inner regions, where they accounted for almost 30% of the diet during this period. In 1985 overall they formed less than 1% of the diet. The importance of cephalopods was not estimated for the 1985 diet, however, in 2002 they accounted for almost 5% of the diet during either quarter 1 or quarter 4 for regions North Inner, South Inner, and the Monach Isles and for North Outer they made up almost 5% throughout the winter. No indication of salmonids was found in either the 1985 or 2002 study.

Therefore, in comparison with findings of the 1985 study, there appears to be little change in species composition within the diet, at least for the major species, with sandeels and gadoids still forming the majority of the diet. Notable differences occurred in the presence of pelagic species, especially herring, increasing considerably in the diet in 2002. Sprat and blue whiting, species that were not recorded in the 1985 diet, were detected throughout the study area in 2002, although they occurred most frequently in the Outer Hebrides during the summer. Sandeels and ling formed the largest component of the diet by weight in 1985 but the importance of both these prey declined in 2002. Species that increased in importance included lemon sole, rockling, bullrout and dragonet, while megrim, which contributed approximately 7% of the diet in 1985, was rarely detected in 2002.

Despite these changes in the proportions each species contributed to the diet in 1985 and 2002 it is clear that sandeels and gadoids, and now herring, are the main prey for grey seals in this area. The importance of sandeels and gadoids in the diet are consistent with other diet studies from other regions (Mikkelsen et al. 2002, Bowen & Harrison 1994, Hammond & Grellier 2006). Although herring contributed to the 1985 diet it did not form a significant component. This agrees with a study from a region of the Norwegian Sea which showed that even though herring was likely to be highly available to grey seals, they did not make a large contribution to the diet (Touminen et al. 2005) suggesting that high availability of a species does not necessarily drive prey choice and, that at least in this area, herring was not preferred prey. However, other studies have shown herring as important and also dominating the diet in some areas (Bowen et al. 1993, Lundstrom et al. 2006). The estimated length of herring from the west coast of Scotland in 2002 was consistently higher than in 1985 and in the North Sea (Hammond & Grellier 2006) and those recorded from commercial catch market sampling (Anne McLay *pers. comm*). This suggests that further work should be undertaken to confirm estimates of herring size; any change could reduce the contribution of herring to the diet in this study.

When comparing the diet of seals on the west coast with the diet of seals in the North Sea (Hammond & Grellier 2006) some similar patterns were evident. Regional and seasonal differences existed although core species remained the same with their proportions fluctuating. In both areas sandeels and gadoids could be considered the preferred prey in both 1985 and 2002. Some regions of the North Sea showed a decrease in sandeel importance as seen on the west and the central North Sea sites showed a 5-fold decrease in the importance of cod. Haddock greatly increased, as did benthic species. The importance of pelagic species in the diet from west of Scotland was not reflected in the North Sea diet; however, there are many similarities in the diet between the two regions and some of the trends between 1985 and 2002 are reflected here too.

In the southern North Sea there was a decrease in the sandeel component and an increase in the proportion by weight of benthic species in the diet similar to that observed for some regions west of Scotland. Regional variations resulted in an overall decrease in the importance of sandeels from both west of Scotland and the North Sea. Increases in the importance of benthic species was recorded in both areas, as was a large increase in the importance of haddock.

A major difference, over this time period, between these two areas has been the rate of growth in the grey seal population. Between 1985 and 2002, the overall North Sea population has increased 3-fold, much larger than the increase observed on the west coast of Scotland. This three-fold increase in the North Sea has driven a substantial increase in the consumption of prey species from an estimated 39,000 tonnes in 1985 to 116,000 tonnes in 2002 (Hammond & Grellier 2006), compared with 53,000 tonnes increasing to 77,000 tonnes for the west coast. It is clear that predation pressure has increased at a much higher rate in the North Sea.

Prey consumption

Consumption estimates of prey species by seals are of considerable importance in understanding the role seals play within the ecosystem. Prey consumption is driven by diet composition and the abundance of seals. Grey seals can be described as central place foragers more often foraging close to a haul-out as shown by telemetry studies (McConnell *et al.* 1999). However seals can switch haul-outs and utilise other areas therefore are more flexible than traditional central placed foragers. This may usually mean that predation pressure is likely to be concentrated to certain regions, often relatively close inshore. Where seals in these areas increase to sufficient levels of abundance and diet includes 'critical' species, seals may have considerable effects on local prey populations and local catches (Butler et al. 2006).

Consumption estimates for cod were highest during quarter 4 at the Monach Isles, and also, the South Inner region. As the number of seals in the South Inner region is relatively small (Figure 13), this could indicate an area of higher cod abundance during quarter 4 or an area where grey seals are exerting higher predation pressure. For the remaining major prey species, the Monach Isles clearly have the highest consumption values, more haddock by far were consumed here in quarter 4, more sandeels mainly during quarter 1 & 4 and most herring during the summer than any other region. These estimates are clearly a result of the high seal abundance at the Monachs. It is difficult to make comparisons with 1985, as less information is available on the distribution of seals. However the largest breeding colony in 1985 was at the Monachs (SCOS 2005) and therefore at least during quarter 4 we can assume that consumption estimates were likely highest here, the same as in 2002. When one region contributes so much to estimates of consumption it is important that sufficient samples are collected and that confidence intervals accurately portray any uncertainty (see Table 7e).

Therefore, findings of this study show that grey seals on the west coast of Scotland consume large quantities of sandeels, herring and gadoids, despite considerable declines in some of these species. Predation pressure by grey seals is likely to be highest relatively close to haul-outs and be dependent on prey composition and stock size. Clearly predation pressure on some species is seasonal; for example consumption of herring is highest during the summer from the Monach Isles region. This is possibly an effect of seasonal movements of prey species as stocks move closer to or away from these central placed foragers, or possibly a decrease in the abundance of a preferred prey species.

Although absolute estimates of stock size are uncertain or, for some species, not available the trend for the above stocks is more certain. From 1985 to 2002 herring and haddock stocks remained relatively healthy and per capita consumption of these species increased considerably. For stocks showing the greatest signs of decline, cod and whiting, per capita consumption remained surprisingly constant between 1985 and 2002. Stock estimates for sandeels and ling are not produced for these species, but considerable declines in per capita consumption of these species may indicate declines in these stocks, a shift in their distribution, or just an increase in an alternative preferred prey species resulting in the observed differences in seal consumption.

According to ICES, fish stocks in ICES division VIa for cod and whiting have undergone a large decrease in their populations since 1985 and were at historically low levels in 2002 (ICES 2004). The grey seal population during this period increased by almost 1.5 times (SCOS 2005). Despite this, these prey species continued to contribute a similar proportion to the diet per capita. Stocks of herring and haddock also declined, although the stocks are thought to be much larger than those of cod and whiting and maintain a relatively healthy status. Sandeels are notoriously difficult to survey with any accuracy and assessments are not attempted in division VIa; they are not discussed here. Since 1985, fishery surveys have recorded a dramatic increase in the abundance of blue whiting (ICES 2004b) and this is reflected here by the occurrence of this species in the diet of grey seals on the west coast of Scotland when it was not detected in the 1985 diet.

Comparisons made between the sizes of fish consumed between the two years reveals that for many species they were either the same size or slightly larger in 2002 (See appendices Table vii for 1985 results). For cod the mean length in 1985 was 37.7cm and in 2002 it was 41.2cm, for whiting mean length was 22.2cm in 1985 and 23.7cm in 2002 and for sandeels it was 20.6cm in 1985 and 20.5cm in 2002. However for haddock and herring the differences were much larger with the majority of haddock in 1985 being <24cm whilst in 2002 the majority were >24cm. Haddock become mature at between 30 – 40cm, therefore approximately half of the haddock consumed in 2002 would have been mature. For herring almost all the fish were <34cm in 1985 however in 2002 almost half were >34cm. These are large for herring as they rarely exceed 40cm, and it is likely that most would have been mature (Muus et al. 1999). Apart from sandeels, it appears that seals were consuming mainly immature fish in 1985, but this has changed in 2002, at least for haddock and herring.

Comparing overall consumption in the North Sea with total stock biomass revealed that consumption relative to stock size in the North Sea is still low for most species less than 1%. The exception was cod, which was subjected to the highest level of predation pressure with annual consumption at 3.7% of the stock in this area (Hammond & Grellier 2006). This is in contrast with results for the west of Scotland where rates of consumption relative to TSB are very much higher. It is unwise to estimate, other than crudely, how much higher as estimates of stock biomass are far more uncertain here (Table 11). It is clear though that predation pressure is likely to be far higher in 2002 than it was in 1985 west of Scotland and that it is likely to have a significant effect on some stocks there.

Per capita consumption of the main species in the North Sea between 1985 and 2002 followed similar trends to those west of Scotland with the exception of cod, the consumption of which decreased by 30% in the North Sea, whilst remaining at a similar level to 1985 on the west coast, therefore maintaining a high level of predation pressure on cod stocks west of Scotland. Per capita sandeel consumption decreased by 15% in the North Sea but decreased even more west of Scotland. Whiting remained the same in the North Sea as it did on the west coast, but haddock consumption quadrupled, an increase that was similarly reflected west of Scotland. As with per capita consumption rates many of the fish stocks demonstrated similar trends between the two areas (ICES 2004).

Per capita consumption of cod decreased in both sea areas (albeit a very slight decrease west of Scotland); however the decrease in stocks was more substantial. Whiting consumption, although not as high as some other gadoid species, has remained relatively constant but stocks have also decreased considerably. Haddock stocks in both sea areas have remained at relatively high levels and consumption in both areas has increased considerably. Sandeel per capita consumption also decreased in both sea areas as did ling, an important prey species especially west of Scotland. These decreases in the main prey species of 1985, especially sandeels, and increases in other species such as herring, benthic species and certain gadoids may be evidence of prey switching, possibly away from preferred species. There may be considerable physiological consequences involved in prey switching, such as the possibility of fish-induced anaemia (Thompson *et al.* 1997), potentially reducing fecundity rates in seals and therefore having a limiting effect on population growth. It may also result in increasing predation on 'critical' species and therefore reduce the rate at which species are able to recover from overexploitation.

Concluding remarks

It is apparent that grey seals on the west coast of Scotland continue to consume large amounts of sandeels and gadoids, which, possibly together with herring, can be considered to be preferred prey. A decline in the per capita consumption of the main 1985 prey species, sandeels and ling, was compensated for by higher consumption of herring and haddock. However, due to the increase in the size of the seal population between the two studies, overall consumption has significantly increased for many prey species despite large declines in some of the fish stocks. This is particularly the case for cod and whiting where declines have let to large reductions in catch quotas, resulting in much friction between industry and management, at a time when estimates of overall grey seal consumption of these 'critical' species has increased. It is clear that in 1985 when the seal population was smaller and fish stocks were larger, predation pressure by seals was much less. The situation has now changed and grey seal predation may represent significant pressure on dwindling stocks. However, grey seal pup production has stabilised in recent years (SCOS 2005) and although the population in this sea area is likely to continue to increase for some time, the population is now thought to be close to its current carrying capacity, therefore, prey consumption on the west coast is unlikely to significantly increase over future years.

At the moment it is not possible to assess fully the impact grey seals have on fish stocks or whether a reduction in the size of the seal population would result in an increase in commercial fish stocks. The lack of information in other areas of the marine ecosystem, for example consumption estimates for other predators, needs to be addressed before drawing any firm conclusions. Large populations of cetaceans exist around Britain, for example an estimated 231,000 harbour porpoise can be found in the North Sea alone (SCANS-II September Report available at http://biology.st-andrews.ac.uk/scans2). Important populations of harbour seals, large seabird populations and predatory fish populations all consume large quantities of commercial species. Until consumption rates from these species can be quantified, it is hard to place grey seal predation pressure in context. The northeast Atlantic is home to very larger populations of harp and hooded seals that are occasionally seen around Scotland and it is unknown what proportion of their diets may come from these waters. Reducing grey seal numbers in an attempt to provide more fish for commercial fisheries could result in an increase in other important predators using the area and resources therefore resulting in little, if any, benefit to the fishery; in extreme cases this could even result in reduced catches (Punt & Butterworth 1995).

Future work

A large number of otoliths and beaks from a wide range of species were collected by SMRU in 2002. Some of these hard parts should be used to form a centralised reference collection that would provide an important teaching aid and help improve consistency between studies in the grading of digested otoliths.

The large size of most of the west of Scotland herring needs to be investigated; do larger than average herring exist west of Scotland? If not it is important that whatever is causing this anomaly be identified. Work to address this is currently underway.

Considerable uncertainly exists over which grey seal population model to use in estimating grey seal population size. SCOS highlighted the need to reduce this uncertainty (SCOS 2005) and work at SMRU is ongoing and annually reviewed by SCOS. Limited information is available on the seasonal distribution of seals around Britain and although annual surveys for harbour seals are conducted during August, which provides information on grey seal distribution at this time of the year, surveys should be carried out to quantify grey seal distribution at other times of the year. This would improve regional and total estimates of consumption allowing improved assessments of regional predation pressure on prey stocks and provide insight into predator prey interactions, providing suitable information is available on prey abundance and seasonal movements.

Certain stock assessments suffer from a lack of robustness, such as the west of Scotland cod and whiting stock assessments, we are therefore unable to make comparisons between TSB and consumption. Stock assessments are more confident for other regions (ICES 2004); improvements in stock assessments west of Scotland need to be made before comparisons can be made.

The energy density values for prey were taken from Murray & Burt (1977) who used fillets rather than whole fish. The seasonal energy content of whole fish should be reassessed in the near future to help improve estimates of consumption.

Large populations of harbour seals are also found on the west coast of Scotland, counts of seals hauled-out in this region have been around 13,000 (SCOS 2005). It is uncertain what proportion may be in the water at the time these counts are carried out, but an estimated 40% of seals are likely not to be counted in this way (Duck et al. 2005). The limited amount of diet data available for harbour seals from the Inner Hebrides has suggested that they eat broadly similar species to grey seals, in particular gadoids and pelagic species (Pierce et al. 2003). The diet of harbour seals from a wide geographic area west of Scotland should be assessed as a priority.

Data from this study should be used in multi-species models to better understand ecosystem function. This would enable us to begin to answer such questions as, do grey seals limit the ability of 'critical' species, such as cod, to recover from overexploitation, or do reduced populations of preferred prey limit grey seal population growth. Alternatively questions could be asked such as – are seals better adapted to predate on fish stocks at lower abundance levels than other species that are not equally adapted or are unable to switch prey, therefore resulting in greatly reduced fecundity rates? Such species may include breeding seabirds.

As many commercial fish stocks remain at such 'critical' levels and grey seal populations continue to increase, grey seal diet should be assessed again in the relatively near future.

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Appendix 1

Table i. Latitude and longitude of sites where samples were collected and region allocation.

Region	Location	Lat.	Long.
Minch	An Dubh Sgeir	57.202	6.403
Minch	Ascribs	57.353	6.311
Minch	Fladda-chuain	57.446	6.262
Minch	Shiants	57.541	6.262
Minch	Oigh-sgeir	56.582	6.408
North Inner	Tanera Beg	58.006	5.267
North Inner	Sgeirean Glasa	57.578	5.262
North Inner	Glas-leac Beag	57.591	5.305
Monachs	Ceann Ear	57.314	7.366
Monachs	Stockay	57.321	7.35
Monachs	Shivinish	57.313	7.381
Monachs	Ceann Iar	57.315	7.394
North Outer	Shillay, SoH	57.481	7.153
North Outer	Gaskgeir	57.59	7.173
North Outer	Floday, Loch Roag	58.16	6.544
South Outer	Curachan	56.582	7.213
South Outer	Flodday, Vatersay	56.537	7.341
South Outer	Mingulay	56.488	7.383
South Outer	Berneray	56.471	7.381
South Inner	Hough skerries	56.314	7.007
South Inner	Lunga	56.293	6.254
South Inner	North Treshnish	56.311	6.228
South Inner	Soa, Iona	56.171	6.273
South Inner	Oronsay	56.003	6.144
South Inner	Nave Is.	55.538	6.206
South Inner	Loch Gruinart	55.516	6.189
South Inner	Orsay	55.409	6.31

Table ii. Species recorded during assessments of grey seal diet, west of Scotland in 1985 & 2002 (+ Species recorded during study).

Common_name	Latin_name	1985	2002
Cod	Gadus morhua	+	+
Whiting	Merlangius merlangus	+	+
Haddock	Merlanogrammus aeglefinus	+	+
Saithe	Pollachius virens	+	+
Pollack	Pollachius pollachius	+	+
Pout Whiting or Bib	Trisopterus luscus	+	+
Poor Cod	Trisopterus minutus	+	+
Norway Pout	Trisopterus esmarkii	+	+
Ling	Molva molva	+	+
Plaice	Pleuronectes platessa	+	+
Lemon sole	Microstomus kitt	+	+
Mackerel	Scomber scombrus	+	+
Herring	Clupea harengus	+	+
Rockling	(none specific)	+	+
Sandeel	(none specific)	+	+
Dover Sole	Solea solea		+
Sprat	Sprattus sprattus		+
Hooknose or Pogge	Agonus cataphractus	+	
Flounder or Butt	Platichthys flesus		+
Dragonet	Callionnymus lyra	+	+
Conger eel	Conger conger	+	
Dab	Limanda limanda		+
Megrim or Whiff	Lepidorhombus whiffiagonis	+	+
Bullrout	Myoxocephalus scorpius	+	+
Horse Mackerel or Scad	Trachurus trachurus	+	+
Brill	Scophtalmus rhombus		+
Sea Scorpion	Taurulus bubalis	+	+
Lesser Weever	Trachinus vipera		+
Greater weever	Trachinus draco	+	
Butterfish	Pholis gunnellus		+
Turbot	Scophthalmus maximus	+	
Witch	Glyoptocephalus cynoglossus	+	+
Goldsinny	Ctenolabrus rupestris	+	
Eelpout	Zoarces vivaparus	+	+
Ballan wrasse	Labrus bergylta	+	+
Cuckoo wrasse	Labrus mixtus	+	+
Norwegian topknot	Phrynorhombus norvegicus	+	+
Topknot	Zeugopterus punctatus	+	+
Goby	(none specific)		+
Octopus	Eledone cirrosa		+
Long rough dab	Hippoglossoides platessoides		+
Argentine	Argentina sphyraena		+
Tadpole-fish	Raniceps raninus	+	+
Grey gurnard	Eutrigla gurnardus		+
Silvery Pout	Gadiculus argenteus	+	+
Solenette	Buglossidium luteum		+
Hake	Merluccius merluccius	+	+
Blue Whiting	Micromesistius poutassou		+
Greater Forkbeard	Phycis blennoides		+
Halibut	Hippoglossus hippoglossus		+
Loligo	Loligo forbesi		+
Stout bobtail squid	Rossia sp.		+
Ommastrephidae	(unknown) Ommastrephidae		+
Sepiolids	Sepiolids		+

Table iii. Taken from Hammond & Harris (2006). Number of grey seal scat samples (containing hard parts that were processed) collected from the Hebrides in 1985 and the total number of hard parts (fish otoliths and cephalopod beaks) recovered.

Region	**Quarter**	**Scats**	**Hard parts recovered**
Hebrides	1	194	5,770
Hebrides	2	23	837
Hebrides	3	80	3,239
Hebrides	4	130	1,867
TOTAL	**All**	**427**	**11,713**

Table iv. Taken from Hammond & Harris (2006). Seasonal variation in grey seal diet (expressed as percentage by weight) in the Hebrides in 1985. Listed are species contributing >5% in any quarter and species of commercial importance.

	Q1		**Q2**		**Q3**		**Q4**	
Species	**%**	95% C.I.	**%**	95% C.I.	**%**	95% C.I.	**%**	95% C.I.
Cod	**5.37**	2.21 - 9.97	**10.08**	1.65 - 24.03	**4.97**	1.94 - 10.53	**18.07**	7.73 28.56
Whiting	**2.7**	0.77 - 5.64	**1.1**	0.13 - 2.93	**5.12**	2.35 - 8.75	**1.78**	0.34 3.42
Haddock	**3.25**	1.17 - 6.60	**1.22**	0 - 4.02	**3.6**	0.39 - 8.13	**3.32**	0.24 7.28
Saithe	**1.86**	0.20 - 21.69	**6.93**	0 - 48.31	**1.28**	0.12 - 11.55	**3.67**	0.4 41.38
Pollock	**1.2**	0.13 - 3.07	**1.09**	0 - 3.21	**1.16**	0 - 3.37	**4.81**	0.5 12.46
Ling	**7.23**	2.93 - 12.80	**13.93**	1.55 - 31.59	**6.3**	2.28 - 12.97	**16.42**	6.54 25.27
Norway pout	**0.54**	0.19 - 1.00	**4.27**	1.15 - 7.96	**3.58**	1.45 - 6.26	**5.73**	1.17 12.26
Plaice	**2.51**	0.62 - 5.56	**3.9**	0.56 - 10.17	**1.89**	0.48 - 4.28	**0.74**	0.07 1.75
Megrim	**6.44**	1.64 - 13.57	**7.91**	1.82 - 16.17	**2.78**	0.88 - 5.79	**10.1**	2.71 20.62
Sandeel	**60.47**	35.81 - 79.25	**30.1**	11.05 - 55.7	**62.5**	41.61 - 79.58	**20.65**	3.64 44.66
Herring	**0.78**	0 - 2.39	**15.18**	0 - 43.9	**2.29**	0.47 - 5.08	**2.44**	0.46 5.43

Table v. Taken from Hammond & Harris (2006). Estimates of the amount of prey consumed (in tonnes) by grey seals in the Hebrides in each quarter of 1985. Listed are species contributing >5% in any quarter and species of commercial importance.

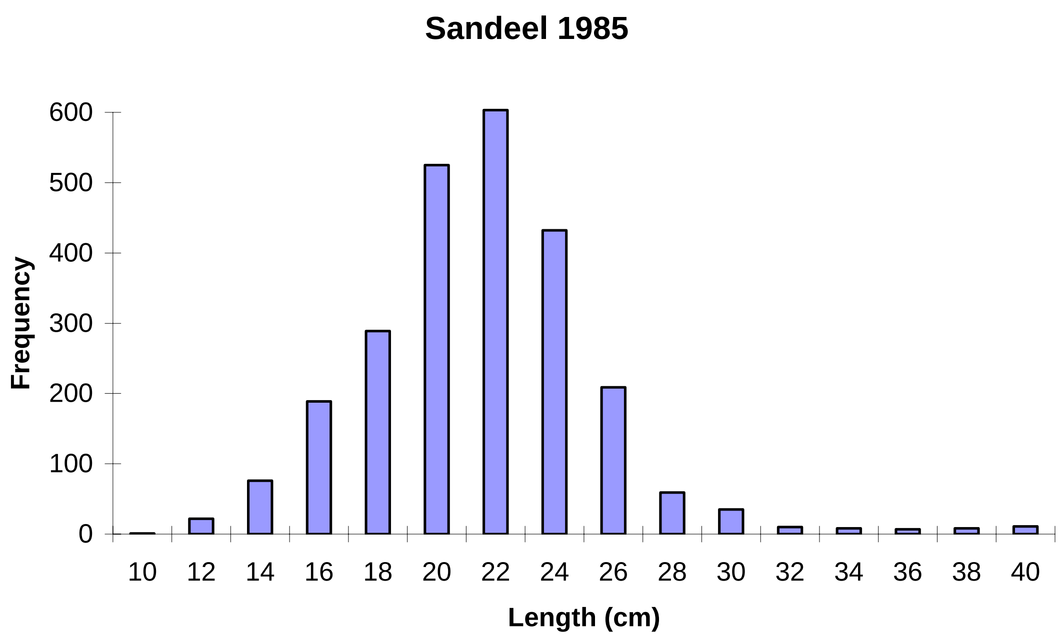
Species	**Q1**	95% C.I.	**Q2**	95% C.I.	**Q3**	95% C.I.	**Q4**	95% C.I.
Cod	**669**	238 - 1,425	**1,329**	223 - 3,542	**613**	223 - 1,401	**2,762**	1,035 - 5,038
Whiting	**337**	87 - 817	**146**	17 - 475	**631**	251 - 1,218	**273**	56 - 575
Haddock	**406**	130 - 910	**161**	0 - 614	**445**	47 - 1,102	**507**	35 - 1,183
Saithe	**232**	24 - 2,864	**914**	0 - 7,889	**159**	15 - 1,499	**561**	59 - 6,897
Pollock	**150**	15 - 440	**144**	0 - 469	**143**	0 - 444	**735**	75 - 2,024
Ling	**901**	322 - 1,769	**1,837**	187 - 5,122	**778**	269 - 1,788	**2,509**	905 - 4,559
Norway pout	**67**	21 - 138	**563**	139 - 1,243	**442**	164 - 876	**875**	170 - 1,871
Plaice	**313**	68 - 783	**514**	77 - 1,513	**233**	61 - 602	**114**	11 - 274
Megrim	**803**	193 - 2,028	**1,043**	240 - 2,446	**343**	104 - 777	**1,544**	365 - 3,551
Sandeel	**7,537**	4,417 - 11,090	**3,969**	1,444 - 7,731	**7,716**	5,031 - 11,150	**3,156**	568 - 6,531
Herring	**97**	0 - 318	**2,002**	0 - 5,307	**283**	55 - 653	**373**	73 - 909

Table vi. Taken from Hammond & Harris (2006). Estimates of the amount of prey consumed (in tonnes) by grey seals in the Hebrides area in 1985, listed in rank order. Given are species contributing >5% in any quarter and species of commercial importance.

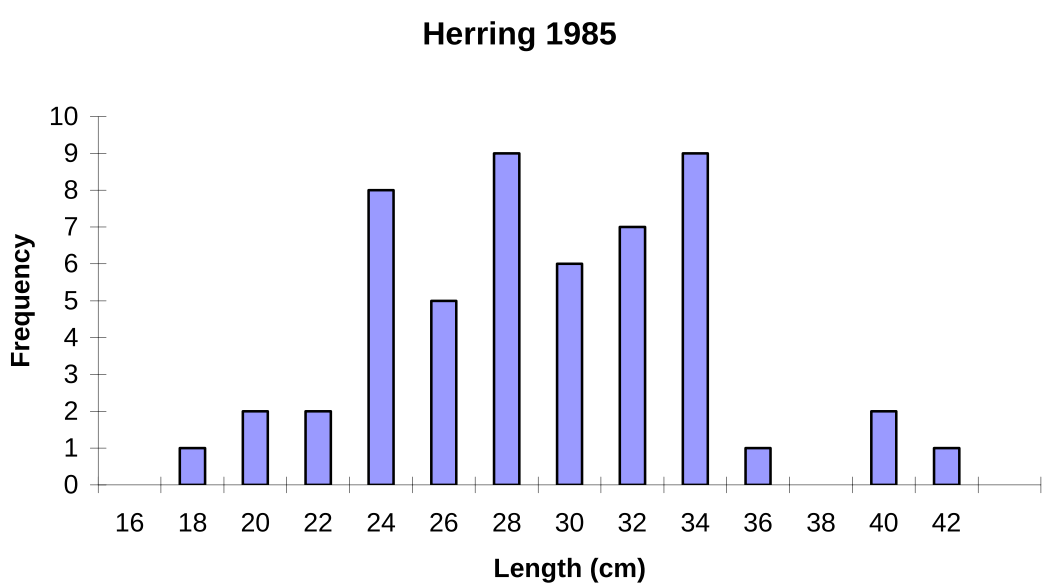
Species	**Total Consumption**	95% C.I.
Sandeel	**22,377**	16,187 - 29,201
Ling	**6,025**	3,199 - 9,943
Cod	**5,372**	3,023 - 8,831
Megrim	**3,733**	1,913 - 6,310
Herring	**2,755**	486 - 6,105
Norway pout	**1,947**	867 - 3,108
Saithe	**1,866**	540 - 12,284
Haddock	**1,519**	716 - 2,689
Whiting	**1,386**	765 - 2,148
Plaice	**1,174**	528 - 2,323
Pollock	**1,172**	377 - 2,533
All species	**53,277**	**45,546 - 64,724**

Figure vii. Taken from Hammond & Harris (2006). Frequency distributions of estimated fish length for (a) sandeel, (b) herring, (c) cod, (d) whiting and (e) haddock consumed by grey seals in the Hebrides in 1985

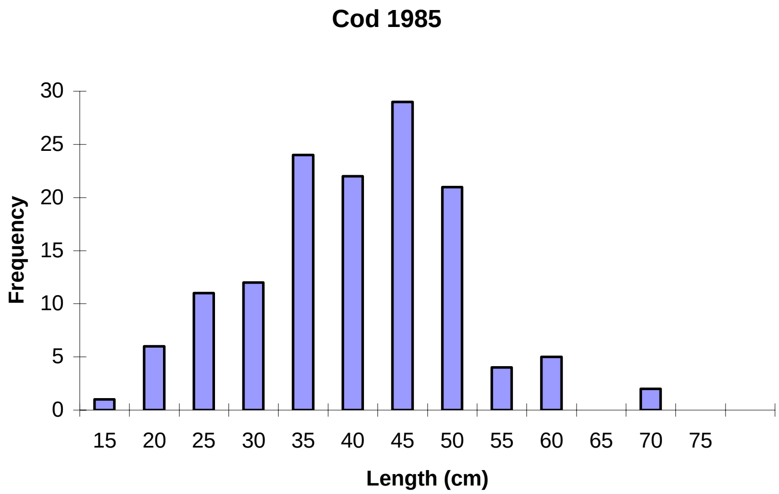
(a) Sandeel



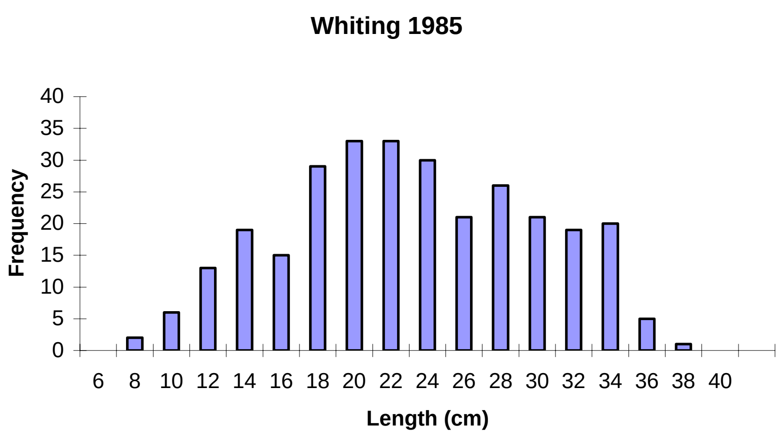
(b) Herring



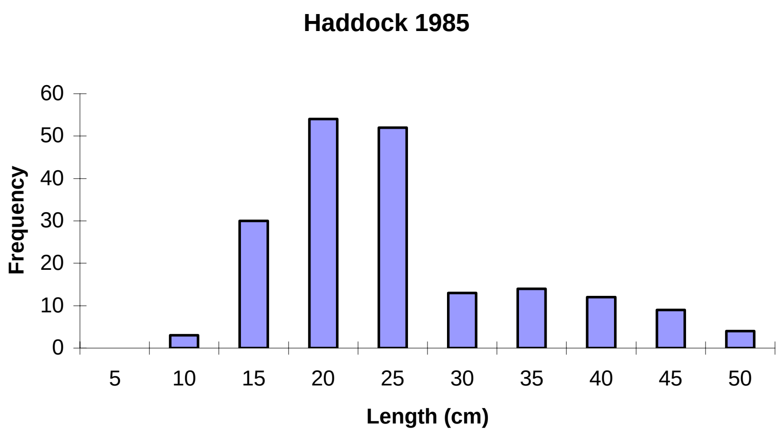
(c) Cod



(d) Whiting



(e) Haddock


Haddock 1985
Frequency
60
50
40
30
20
10
0
5
10
15
20
25
30
35
40
45
50
Length (cm)