THE DIET AND FEEDING ECOLOGY OF HARBOUR SEALS AROUND BRITAIN

Lindsay J. Wilson

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at the
University of St Andrews**

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The diet and feeding ecology of harbour seals around Britain

Lindsay J. Wilson

This thesis is submitted in partial fulfilment for the degree of PhD
at the
University of St Andrews

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CONTRIBUTIONS TO THE DATA CHAPTERS

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Kate Grellier (SMRU), Chapter 2.

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ABSTRACT

Since 2000, there has been a marked decline in the number of harbour seals in some regions around Britain; one possible contributing cause is competition for prey with sympatric grey seals. To explore one important aspect of this interaction, in this thesis the diet of harbour seals is estimated using analysis of hard prey remains recovered from faeces and compared with equivalent results for grey seals. To estimate coefficients to account for partial and complete digestion of hard prey remains, 100 whole prey feeding trials were conducted with six harbour seals and 18 prey species. Differences were found among prey species and between harbour and grey seals highlighting the importance of applying predator- and prey-specific digestion correction factors when reconstructing diet. In a comprehensive exploration of the diet of harbour seals around Britain, sandeel and flatfish dominated in the North Sea and large gadoids dominated on the Scottish west coast with seasonal pulses of pelagic prey. Variation in diet was linked to regional and seasonal differences in prey distribution and abundance. Sex-specific variation in harbour seal diet was examined in four regions. The main difference detected was in The Wash, where female diet quality was significantly higher than males in winter, which appeared to be driven by greater consumption of pelagic prey by female seals associated with seasonal energetic requirements of their annual life cycle. Comparison of the diet of harbour and grey seals revealed regional differences in diet composition, diversity and quality between the two species. However, there was no consistent pattern in this variation in relation to regional variation in harbour and grey seal population trajectories and no clear evidence for interspecific competition for prey. Future work should focus on an integrated investigation of prey abundance and distribution, and seal diet and foraging behaviour/distribution.

Chapter 1

GENERAL INTRODUCTION

1.1 Introduction

Foraging theory states that predators forage in such a way as to maximize their net energy intake. In other words, individuals should attempt to consume prey that will maximise calorific intake whilst minimizing their energy expenditure searching and capturing the prey (Ydenberg *et al.*, 1994; Houston, 1995). Prey in the marine environment are often patchily distributed and, due in part to its dynamic nature, may vary widely in abundance and distribution between years; marine predators must therefore be able to respond effectively to both temporal and geographical changes in prey abundance. Foraging theory also predicts that predators should respond to changes in prey abundance and distribution in a manner that maximises efficiency (energy gain over energy expenditure), net rate of energy intake, or average rate of delivery of energy to offspring (Ydenberg *et al.*, 1994; Houston, 1995). The success or failure of individuals to respond to variations in food availability and effectively reconcile their energetic balance can have significant effects on the life history of individuals affecting both survival and reproductive success and consequently can influence the dynamics of populations (Coulson *et al.*, 2000). For example, food intake by females can affect birth mass (*e.g.*, Lunn *et al.*, 1994) and maternal size and age can affect the growth and development of offspring (*e.g.*, Arnborn *et al.*, 1997; Pomeroy *et al.*, 1999).

It is generally accepted that top predators in marine ecosystems are responsive to changes in their environment and that measurements of these responses can be used to inform management (Timoshenko, 1995; Boyd *et al.*, 2006). In many communities, diet (along with reproductive success and population size) of higher predators has been used as an index to monitor ecosystem structure and dynamics at lower levels (*e.g.*, Monaghan, 1996; Reid and Croxall, 2001). Changes in the dominant prey types as a consequence of natural (*e.g.*, climate) or anthropogenic (*e.g.*, fishing) ecosystem regulation can have large effects throughout the ecosystem. For example, recruitment of sandeel (*Ammodytidae*) stocks in the North Sea is negatively correlated with high winter sea temperatures (Arnott and Ruxton, 2002). Furthermore, in the 1990s the North Sea sandeel fishery was the single largest fishery in the region (ICES, 2004). In 2004, seabird populations experienced the worst breeding season on record and this has been linked to lack of suitable food *i.e.*, sandeel (Harris *et al.*, 2004; Mavor *et al.*, 2005). At the same time fishery landings were <50% of the average indicating repeated recruitment failure (ICES, 2004). Although the specific mechanism behind the 2002-2004 sandeel recruitment failure (ICES, 2006) in the North Sea remains uncertain, it is clear that the abundance of this important species is affected by climate-driven bottom-up control (Arnott and Ruxton, 2002) and fishery driven top-down control (ICES, 2004). Where an ecosystem is dominated by a single keystone prey species, such as the sandeel in the North Sea (Furness, 2003; Frederiksen *et al.*, 2006) or Antarctic krill (*Euphausia superba*) in the Southern Ocean (Croxall *et al.*, 1999; Reid *et al.*, 2005), the consequences of change in trophic interactions are considered more overt and in more complex ecosystems the effects of changes in resource may be more difficult to detect.

Warm blooded predators are generally located near the top of marine food webs and marine mammals as major consumers within their environment are likely to have an important role in determining the structure of marine food webs (Katona and Whitehead, 1988; Bowen, 1997; Pauly *et al.*, 1998). In some areas, because of their body size and abundance, marine mammals may have a significant influence on the structure and function of their constituent communities and, as such, dietary studies have ecological significance through investigation of their biology and role in marine ecosystems. Marine mammals may also have economic significance via the quantification of marine mammal-fisheries interactions (*e.g.*, Northridge, 1984; Harwood and Croxall, 1988).

Diet is often dynamic and varies as different individuals and species experience the environment on different spatial and temporal scales (Levin, 1992). In pinnipeds, diet is known to respond in non-linear ways to intrinsic and extrinsic factors such as; sex, age, condition, season, geographic location, prey abundance, distribution and energy content (reviewed in Bowen and Siniff, 1999; Bowen *et al.*, 2002). Prey distribution and abundance is considered the primary driver for seasonal and geographic variation in pinniped diets including; Steller sea lions, *Eumetopias jubatus* (Sinclair and Zeppelin, 2002), harbour seals, *Phoca vitulina* (Thompson *et al.*, 1996b) and grey seals, *Halichoerus grypus* (Bowen and Harrison, 1994). Longitudinal studies have described inter-annual variability in diet as a function of prey availability in Antarctic fur seals, *Arctocephalus gazella* (Reid and Arnould, 1996; Lea *et al.*, 2002), grey seals (Walton and Pomeroy, 2003; Bowen and Harrison, 2007) and harbour seals (Bowen and Harrison, 1996; Thompson *et al.*, 1996b). Sex and age specific seasonal changes in diet have also been documented *e.g.,* grey seals and Steller sea lions (Beck *et al.*, 2005; Beck *et al.*, 2007; Trites and Calkins, 2009) and the physiological constraints of body size on oxygen storage and utilisation is expected to influence dive depth and duration in pinnipeds and consequently foraging options (Boyd and Croxall, 1996).

Diet may also vary depending on a predator's preference for certain prey types and evidence of selective predation; that is, the representation of prey species in the diet that is disproportionate to their abundance has been found in grey seals (Bowen and Harrison, 2007), harp seals, *Phoca groenlandica* (Lawson *et al.*, 1998) and harbour seals (Tollit *et al.*, 1997a). However, selective predation is difficult to infer due to the difficulties in estimating both diet and prey species abundance. Seals therefore tend to be considered generalist predators, consuming a variety of prey species (*e.g.*, Andersen *et al.*, 2004; Bowen and Harrison, 2007) though a few key species may dominate (*e.g.*, Tollit and Thompson, 1996). They frequently share the same habitats as other marine generalist predators and, consequently, are potentially competing for the same food resources.

The understanding of key ecological concepts such as competition also hinges on the ability to measure what prey species that potentially competing predators select, and why. Theoretical studies have grouped competition into two main categories: interference and exploitation competition (Ricklefs, 1973). Interference competition is when a species improves its competitive position by eating, killing, intimidating or otherwise interfering with its competitors, while exploitation competition exists when an individual or species utilises a limiting resource and denies its use to another individual or species (Ricklefs, 1973). When food becomes limiting and there are multiple predators exploiting the same resource, competition for prey will intensify. This may occur within a species (intra-specific competition) or across species (inter-specific competition).

Direct competition for food resources is difficult to demonstrate. However diet studies have been used to identify trophic overlap between sympatric predators, including harbour seals and great cormorants, *Phalacrocorax carbo* (Andersen *et al.*, 2007) and harbour seals and grey seals (Bowen *et al.*, 2003). However, diet studies used in isolation may misrepresent behaviour. For example, the diet of adult Weddell seals (*Leptonychotes wedellii*) and emperor penguins (*Aptenodytes forsteri*) appear to overlap, yet there is little trophic overlap due to geographical and seasonal differences in habitat use (Burns and Kooyman, 2001). Modification of resource use and niche exploitation is a common response to interspecific competition, as seen in sympatric jackals: black-backed jackal, *Canis mesomelas* and side-striped jackal, *Canis adustus* (Loveridge and Macdonald, 2003). However, at the theoretical extreme, species' exclusion from contested habitat can occur (Kruuk *et al.*, 1994).

1.2 Seals around Britain

Two species of seal live in the waters around Britain: harbour seals and grey seals. Circumpolar in their distribution in the Northern Hemisphere, harbour seals are divided into five sub-species and the European population represents one sub-species (*Phoca vitulina vitulina*). Grey seals occur only in the North Atlantic, Barents and Baltic Seas and are mainly concentrated on the east coast of Canada and the United States of America and in north-west Europe.

The harbour seal and grey seal are sympatric through much of their range around Britain; however, the two species have different haul-out and at-sea movement strategies. Grey seals are the larger, more numerous predator and it is possible that harbour and grey seals compete for food; however, there is insufficient diet information for harbour seals even to allow accurate comparisons of diet. No new data have been collected on grey seal diet since 2002 (Hammond and Grellier, 2006; Hammond and Harris, 2006), and fine-scale measures of species distribution and abundance throughout the year have not been examined for many years. The lack of any recent diet information for harbour seals at a time when sea bird populations are showing repeated breeding failures due to poor food years (Regehr and Montevecchi, 1997; Wanless *et al.*, 2005) makes diet a clear priority for investigation.

Systematic investigation of pinniped diet in the UK has historically focused on grey seals due, in part, to their larger numbers and their role as potentially significant consumers of commercially exploited fish species (Harwood and Croxall, 1988; Hammond and Grellier, 2006; Hammond and Harris, 2006). To date, the diet of harbour seals has only been studied in a few areas (Thompson *et al.*, 1996b; Tollit and Thompson, 1996; Hall *et al.*, 1998; Brown *et al.*, 2001; Pierce and Santos, 2003; Sharples *et al.*, 2009).

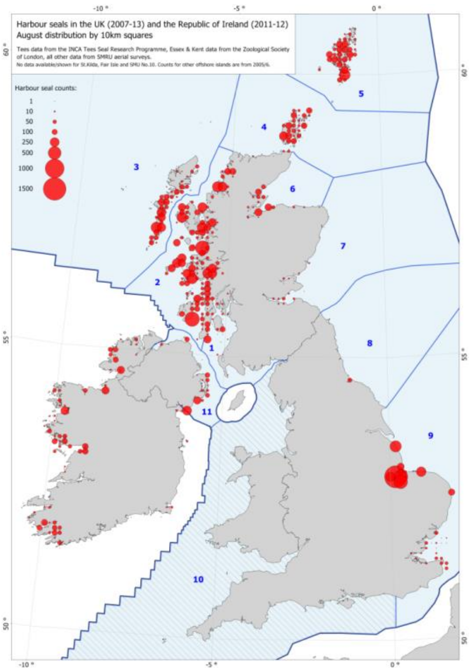
1.2.1.1 Abundance and distribution: harbour and grey seals

Approximately 30% of European harbour seals are found around Britain, a decline from approximately 40% in 2002 (SCOS, 2013). Harbour seals are widespread around the coast of Scotland and in southeast England they are concentrated in the major estuaries of the Thames, The Wash, Firth of Tay and Moray Firth (Figure 1.1). Approximately 28% of the world's grey seals breed in the UK and 88% breed at colonies in Scotland (SCOS, 2013). The main breeding colonies in Scotland are in Orkney and the Outer Hebrides, with further colonies in Shetland and along the north and east coasts of mainland Britain (Figure 1.1). The population estimate for harbour seals in the UK in 2010 was 36,050 (approximate CI 29,500-48,050) and the total UK grey seal population estimate at the start of the 2010 breeding season was estimated to have been 111,300 (95% CI 90,100-137,700, SCOS, 2011).

There has been a marked decline in harbour seals around Scotland over the last 10 years (Lonergan *et al.*, 2007; SCOS, 2013) with potentially serious implications for the conservation and management of the species. The most recent counts (SCOS, 2013) indicate that the Firth of Tay population has declined by 85%, the Orkney population by 75% and the Shetland population by 30% since 2000. Harbour seals in the Moray Firth are now stable following a period of decline (at 60-70% of previous counts) and populations in the Inner and Outer Hebrides remain stable (SCOS, 2013).

Significant declines in harbour seal numbers have also occurred previously in The Wash, England linked to the 1988 and 2002 phocine distemper virus (PDV) epidemics (52% and 22% decline, respectively), but PDV had limited impact elsewhere in the UK (SCOS, 2013). Counts from 2002 to 2008 did not indicate a recovery in The Wash population and the lack of recovery of the English east coast harbour seal populations contrasted with the rapid growth in numbers in the Wadden Sea, the nearest European population (SCOS, 2013). However, counts increased by 40% from 2008 to 2010 and the number of seals counted in 2012 was higher than the pre-2002 epidemic count (SCOS, 2013). The decline in harbour seal numbers over the last decade is in contrast to the grey seal population trends. In the North Sea the grey seal population continues to increase, however, in the Northern Isles and the Inner and Outer Hebrides the populations remain stable (Duck and Morris, 2013).

A)



B)

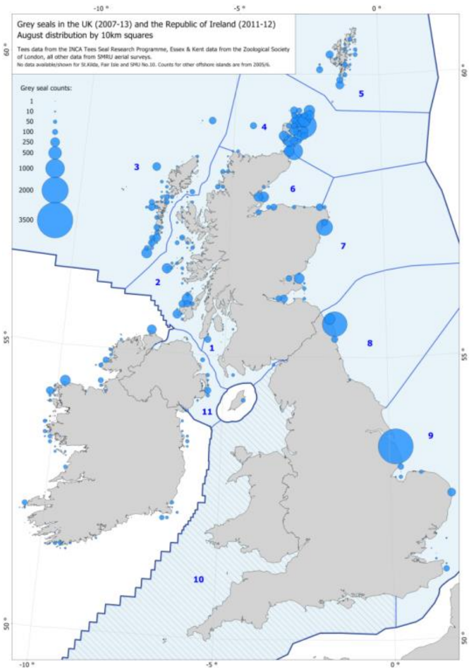


Figure 1.1: Number and distribution of A) harbour seals and B) grey seals around the British Isles, from surveys carried out in August between 2007 and 2013. The geographic regions are: 1) SW Scotland, 2) W Scotland, 3) Western Isles, 4) N Coast & Orkney, 5) Shetland, 6) Moray Firth, 7) E Scotland, 8) NE England, 9) SE England, 10) W England & Wales, 11) Northern Ireland. Reproduced from Duck and Morris (2014).

The decline in numbers of harbour seals around Scotland is expected to be the result of reduced fecundity or reduced survival of one or more components of the population, and a number of projects have commenced to identify which factors are causing the change in fecundity or survival (SCOS, 2009; Hall and Kershaw, 2012). The regions in which harbour seal numbers have declined are characterized by different habitats and it is possible that different factors may be responsible for the declines in different regions. The absence of any apparent mass mortality events indicates that the cause of the decline is not a major disease event such as PDV. Increases in mortality due to chronic disease, shooting, toxic algae, nutritional stress, predation and competition for prey with grey seals, other marine predators and fisheries are all potential factors under consideration (SCOS, 2009; Hall and Kershaw, 2012).

1.2.1.2 Diet and foraging ecology: harbour seals

The diet of harbour seals has been described at a range of temporal and regional scales in the UK and Ireland but has not been studied as comprehensively as for grey seals. Early studies of harbour seal diet focused on the collection of seal stomachs and digestive tracts to estimate the diet of seals around Scotland. Many carcases were collected from or near salmon fishing nets or from the east coast of Scotland from which 80% of the Scottish Salmon catch was derived (Rae, 1973) and may explain the high proportion of Atlantic salmon (*Salmo salar*) described in the diet. Other prey included; whiting (*Merlangius merlangus)*, saithe (*Pollachius virens)*, herring (*Clupea harengus*) and flatfishes (mainly plaice *Pleuronectes platessa*) as well as salmon and more estuarine species such as the viviparous blenny (*Blennioidei*, Rae, 1968). A follow up study in 1967-1971 revealed a marked increase in clupeids and a slight increase in small gadoids though this change in diet was believed to reflect the larger numbers of seals obtained in the winter on the west coast and poorer sampling from the Firth of Tay and east coast sites (Rae, 1973).

More recent studies using hard prey remains recovered from faeces (scats) have shown strong seasonal peaks in the contribution of prey species and considerable variation across the regions where harbour seal diet has been studied. For example, sandeels peaked in the winter and spring diet in the late 1990s in south-east Scotland (Sharples *et al.*, 2009), in the summer in Orkney and the Moray Firth in the late 1980s and early 1990s respectively (Pierce *et al.*, 1990a; Tollit and Thompson, 1996) and in spring and early summer mid-1990s in Shetland (Brown and Pierce, 1998). Strong seasonality was also observed in the diet of south-eastern North Sea harbour seals with sandeels dominating in summer (Hall *et al.*, 1998). However, on the west coast of Scotland, sandeels were a very minor part of the diet throughout the year (Pierce and Santos, 2003).

At times when sandeels were not prevalent; salmonids dominated the diet of south-east Scotland seals (Sharples *et al.*, 2009), whereas gadoids and/or clupeids dominated in the Moray Firth in winter (Tollit and Thompson, 1996). Clupeids also tended to be far more frequent in scats collected during Orkney winters (Pierce *et al.*, 1990a) and gadids dominated the winter diet and pelagic fish the autumn diet in Shetland (Brown and Pierce, 1998). In the south-eastern North Sea, whiting and bib (*Trisopterus luscus)* dominated in winter (Hall *et al.*, 1998).

Synchronised regional assessments of diet have revealed differences in the key prey in the Moray Firth, where flatfish dominated the diet, and Orkney, where gadoids were dominated in the mid-1980s (Pierce *et al.*, 1990a). On the west coast of Scotland, diet differences were detected at a smaller spatial scale between the islands of Mull and Skye with variation in the numerical importance of *Trisopterus* species (Pierce and Santos, 2003). The overall relative unimportance of sandeels in the diet of harbour seals on the west coast of Scotland identified by Pierce & Santos (2003) is in marked contrast to most other areas of Britain (*e.g.*, Tollit and Thompson, 1996; Hall *et al.*, 1998; Sharples *et al.*, 2009).

Inter-annual estimates of harbour seal diet have revealed variation in the proportion of clupeids in the winter diet of Moray Firth harbour seals (Tollit and Thompson, 1996). In the mid-1980s, the diet of Moray Firth harbour seals was dominated by flatfish (Pierce *et al.*, 1990a); however, in 1989-1992 key prey reported were sandeels, lesser octopus (*Eledone cirrhosa*), whiting, flounder (*Platichthys flesus*) and cod (*Gadus morhua*, Tollit and Thompson, 1996). Substantial interannual variation in the contributions of pelagic and gadoid fish has also been identified in the summer diet of harbour seals in Shetland (Brown and Pierce, 1998).

Harbour seal distribution at sea tends to be coastal. Foraging trips are typically short distance (11-100 km) and short duration (1-6 days *e.g.*, Thompson *et al.*, 1996a; Cunningham *et al.*, 2009; Sharples *et al.*, 2012). Differences in foraging trip parameters across different regions have been found, which are expected to reflect the local habitat conditions; however, they do not seem to be influenced by individual level factors, such as size, sex and body condition (Sharples *et al.*, 2012).

1.2.1.3 Diet and foraging ecology: grey seals

To date, dietary analysis in Britain has primarily focused on the diet of grey seals to inform seal management policy in relation to the impact on declining fish stocks (Hammond and Prime, 1990; Prime and Hammond, 1990; Hammond *et al.*, 1994a; Hammond *et al.*, 1994c; Hammond and Grellier, 2006; Hammond and Harris, 2006).

Marked changes have been documented in the diet of grey seals in the North Sea between 1985 and 2002 (Hammond and Grellier, 2006) but there was limited evidence for change on Scotland's west coast (Hammond and Harris, 2006).

In the northern North Sea (Orkney, Shetland and the Moray Firth), sandeels dominated the diet in all regions and seasons in 2002 and in 1985 (Hammond and Grellier, 2006). Cod was also a common prey item. However, the proportions of these two prey species did change from 1985 to 2002. The proportion of sandeels in the diet decreased but the proportion of gadoids increased in 2002 (Hammond and Grellier, 2006).

In the central North Sea, there was more sandeel and fewer gadoids in the diet in 2002 (Hammond and Grellier, 2006). In the southern North Sea diet changed from sandeels, cod and sole (*Solea solea*) in 1985, to species such as the short-spined seascorpion (*Myoxoxephalus scorpius*) and dragonet (*Callionymus lyra*) in 2002. Sandeels and gadoids showed some seasonal importance (Hammond and Grellier, 2006).

The size of prey species consumed in 2002 across all areas of the North Sea was significantly smaller than of those consumed in 1985 (Hammond and Grellier, 2006). An increase in annual consumption from 39,000 tonnes in 1985 to 116,000 tonnes in 2002 reflected an almost threefold increase in grey seal population size (Hammond and Grellier, 2006).

The main species in the diet of grey seals in the northern Inner Hebrides in 2002 were dragonet, sandeel, cod and haddock (*Melanogrammus aeglefinus*). In the Minch, sandeel dominated in January-March, and cod, haddock, ling (*Molva molva*) and sprat (*Sprattus sprattus*) in the rest of the year (Hammond and Harris, 2006). In the southern Inner Hebrides, sandeel and cod were the main prey. In the northern Outer Hebrides sandeel was the dominant prey in all seasons while herring, cod and ling had seasonal importance. In the southern Outer Hebrides, sandeel and gadoids (particularly haddock) were dominant with seasonal peaks of plaice (Hammond and Harris, 2006). In the Monarch Isles sandeel and herring were the predominant prey species (October-March and April-September, respectively). Estimated annual consumption of prey by grey seals in the Hebrides area increased between 1985 and 2002 from 53,000 tonnes to 77,000 tonnes (Hammond and Harris, 2006), also reflecting the increase in grey seal population size over that time.

In summary, sandeel and gadoid fish were the dominant prey species for grey seals in most regions with seasonal increases in pelagic fish, flatfish and benthic species. Substantial changes in diet were observed in only a few regions between 1985 and 2002, however, over all regions the size of prey ingested in 2002 was smaller.

The movements of grey seals are highly variable, though two general patterns have been described: long, distant travel and repeated localised trips from haul-out sites to discrete offshore areas (McConnell *et al.*, 1999). Dives are primarily to the sea bed (Thompson *et al.*, 1991a; McConnell *et al.*, 1999) and foraging trips generally more off shore than those undertaken by harbour seals (*e.g.*, McConnell *et al.*, 1999; Matthiopoulos *et al.*, 2004; Sharples *et al.*, 2012).

1.3 Methods for studying the diet of seals

1.3.1 Diet determination: prey hard structure analysis

The recovery, identification and quantification of identifiable prey hard parts from stomachs, intestines and faeces has been used for many years to estimate diet (*e.g.*, Rae, 1968; 1973; Prime and Hammond, 1985; Antonelis *et al.*, 1987; Bowen and Harrison, 1996; Hall *et al.*, 1998; Pierce *et al.*, 2004). Stomach content analysis relies of the retrieval of prey hard parts from the stomach and digestive tract of dead animals. Active collection of animals has ethical and conservation problems and by-caught animal diet will likely be biased towards the species being fished. Furthermore, dead stranded animals may not be representative of the population and are uncommonly reported for collection. Stomach content analysis does have the benefit of recording the animal species, sex and age; however, retention time in the gut varies for different prey remains and gastrointestinal tracts are often empty reducing their value for analyses. There is, however, a much greater chance of obtaining prey remains by stomach flushing and rectal enema (reviewed in Tollit *et al.*, 2010). There are unquantified biases for incomplete recovery of contents from stomach flushing and also animal welfare issues because animals are typically restrained during both procedures.

Scat (faecal) analysis is routinely used to estimate the diet composition of free-ranging seals (Bowen and Harrison, 1994; Hammond *et al.*, 1994c; Hammond *et al.*, 1994a; Tollit and Thompson, 1996; Hall *et al.*, 1998; Trites *et al.*, 2007a), although its use is limited with some species of otariid because many hard remains are regurgitated (Gales and Cheal, 1992). This is the method by which diet is estimated in this thesis.

The advantages of scat analysis are that samples can be collected from haul-out or breeding sites with relative ease, involving a short period of disturbance for the animals (Kucey and Trites, 2006). However, the age and sex of the source animal will usually be unknown and sometimes the species of the defecating animal will also be unknown, for example at mixed species haul-out sites. Information relating to the species and sex of the defecator is however readily available through the use of novel molecular techniques (Reed *et al.*, 1997; Matejusová *et al.*, 2013).

Scats typically represent recent feeding and, as such, are useful for diet determination of coastal species but should be used with caution for more wide ranging species. The approximate time for prey remains to pass through the gut of pinnipeds is one or two days (Grellier and Hammond, 2006) this potentially biases the diet estimate to the prey most recently consumed prior to returning to land from a foraging trip. This is however considered unlikely to significantly bias the results for harbour and grey seals around Scotland (Smout, 2006).

Sampling bias can occur where scat collection itself is not representative of the demographic, temporal and geographical variability in diets, and this could occur where the number of scats collected is low. Low sample sizes will also result in a lack of precision in final estimates. A minimum sample size of 59 scats was considered sufficient for Steller sea lion diets containing 12 or more prey species (Trites and Joy, 2005). Another potential source of bias is associated not with the scat sampling regime onshore, but with the distribution of seal foraging locations at sea, if faecal matter associated with distant foraging trips is more likely to be deposited at sea than faecal matter associated with near-shore foraging. The potential for such a bias can be determined through an integrated analysis of forage trip durations, foraging location and prey passage time information (Smout, 2006).

The retrieval of hard parts from the scat is straightforward and well tested using nested sieves (*e.g.*, Tollit and Thompson, 1996; Hall *et al.*, 1998) or washing machines (Orr *et al.*, 2003). Hard parts from individual scats are retained for identification and measurement. Fish otoliths and cephalopod beaks are most frequently used because they can readily be identified to species from reference collections and because strong relationships exist between their size and fish/cephalopod size (Clarke, 1986; Härkönen, 1986; Leopold *et al.*, 2001). Other identifiable bones have also been used as diagnostic structures to estimate diet (Tollit *et al.*, 2004b) but this approach does not necessarily improve estimates (Arnett, 2001). In some studies, the minimum number of individuals (White, 1953; Ringrose, 1993; Tollit *et al.*, 2003) has been calculated to estimate the number of prey items eaten from prey structures by avoiding counting the same prey more than once. Otoliths are the most commonly used structure to determine fish species and size and are used in this study. When using sagittal otoliths, which are paired in fish, it can be assumed that the number of fish is half the number of sagittal otoliths. Enhancements can be made through determination of left, or right sides and consideration of size range. Unbroken otolith length and width is commonly used to determine fish size, while rostral length is used to estimate the body length of cephalopods.

A potential bias for reconstructing diet composition from hard parts is the ability to represent prey items with no diagnostic hard parts (*e.g.*, cartilaginous fish, Pierce *et al.*, 1993) or whose hard parts are not consumed (*e.g.*, seals are known to tear the heads off fish which are too large to swallow whole, Bowen and Harrison, 1994). However, for grey seals in the North Sea Prime and Hammond's (1990) calculation of digestive efficiency suggests that scat analysis does not cause a major component of the diet to be missed .

For accurate quantification of diet composition, partial and complete erosion of structures during digestion must be taken into account (Bowen, 2000; Grellier and Hammond, 2006). Numerical correction factors (NCFs) take into account interspecific differences in otolith/beak complete digestion, reducing bias in favour of species with large and robust hard parts. Captive feeding studies are used to derive NCFs by comparing known numbers of prey consumed with estimates derived from diet reconstruction using counts of structures which survive digestion (Tollit *et al.*, 1997b; Bowen, 2000; Grellier and Hammond, 2006; Tollit *et al.*, 2007). NCFs are available for some prey of a number of pinniped species including harbour and grey seals (reviewed in Bowen, 2000).

The passage of prey remains through the digestive tract typically takes 1-3 days (Grellier and Hammond, 2006), although cephalopod beaks can be retained in the gastrointestinal tract for longer (Tollit *et al.*, 2003). Digestion coefficients (DCs) account for bias as a result of size underestimation where hard parts have been partial digested. The application of DCs is required for estimation of the size of fish from diagnostic structures where allometric relationships occur between hard part size and prey size. For many species a simple linear regression describes the relationship between otolith length and fish length. Application of regressions to derive fish weight introduces random and systematic errors, typically estimated using bootstrap techniques (Hammond and Rothery, 1996; Pierce, 2007).

Prey biomass, estimated from prey hard remains combines information on the number and size of prey eaten and is considered the most appropriate method to illustrate differences in diet composition (Pierce *et al.*, 1991a; Hammond *et al.*, 1994a). Together with energy density values for prey species, it also provides one of the best means to determine which prey satisfy the energy requirements of seals (Lavigne *et al.*, 1985). Errors in the estimation of seals diet arise from natural 'sampling error', variation in the amount of different fish consumed and 'measurement error', associated with estimating fish weight from partially digested otoliths. Hammond and Rothery (1996) estimated the bias and variance around estimates of grey seal diet using a Monte Carlo re-sampling method. In their simulations, for large samples (>100 scats) the majority of variability resulted from measurement error, not sampling error and more than 90% of the total measurement error resulted from the calculation of undigested otolith size from partially digested otolith size. Critical to reducing variability in the estimation of prey contribution to diet are, therefore, a sufficient number of samples and good digestion coefficients (Hammond and Rothery, 1996).

1.3.2 Diet determination: molecular identification of prey remains

In recent years there have been considerable advances in molecular techniques for the identification of prey. Fatty Acids (FAs) can be used as trophic tracers because: only a limited number of FAs can be biosynthesized by animals, they are generally not degraded during digestion and are taken up by tissues in their original form; adipose storage in animal bodies is usually in reservoirs which can be substantial (reviewed in Tollit *et al.*, 2010). Fatty Acid Signature Analysis can be used to determine prey qualitatively and quantitatively by examination of the FAs that are deposited in predator adipose tissue with little modification and in a predictable way (Iverson *et al.*, 2004; Iverson, 2009). FA analysis requires the collection of high lipid samples (blubber biopsy or milk samples) that can be collected from animals either remotely (*e.g.*, Hooker *et al.*, 2001) or while under restraint (*e.g.*, Lea *et al.*, 2002). Depending upon the temporal nature and life history strategy of the species of interest, the FA composition may reflect diet over days or months.

Examination of differences in FA signatures can reveal spatial or temporal variations in diet (Iverson *et al.*, 1997a; Iverson *et al.*, 1997b; Walton *et al.*, 2000). Identification of specific combinations of FAs can be used to identify particular prey species or taxa (*e.g.*, Thiemann *et al.*, 2007) and, when compared with a representative prey fatty acid and lipid content library, a multivariate optimization model can predict the relative proportion of prey species in the diet (Quantitative Fatty Acid Signature Analysis (QFASA), Iverson *et al.*, 2004). The most important issue to account for when predicting diet using QFASA is predator metabolism (Nordstrom *et al.*, 2008).The deposition of FAs in a predator is currently accounted for by Calibration Coefficients (CCs), which have been estimated for a small number of pinniped species fed a long-term diet of herring. Research suggests that predator species-specific CCs should be used where possible (*e.g.*, Nordstrom *et al.*, 2008). QFASA typically uses a restricted subset of prey FA signatures to match diet; however, the choice of prey FA subset may influence the models discrimination between prey species (Nordstrom *et al.*, 2008). Very short term (pulsed) feeding events has been inconsistently detected using QFASA (Hoberecht, 2006) and as such this method is considered to best reflect diet over weeks to months in pinnipeds (Beck *et al.*, 2005; Hoberecht, 2006).

Trophic studies for marine mammals using stable isotopes provide information on food assimilation and integration over a relatively long time span. Isotopic distributions provide the basis for tracing the origins of elements and molecules spatially through trophic interactions. Relatively consistent changes in isotopic ratios support isotopic discrimination between predator and prey up the food chain, stable nitrogen isotope values ($\delta^{15}N$) can be used to predict the trophic position of organisms if baseline food web values are known (*e.g.*, Hobson and Welch, 1992) while stable carbon isotope measurements ($\delta^{13}C$) have been used to provide spatial information by latitude (*e.g.*, Hobson, 2005). However, stable isotope analysis provides relatively coarse information on diet and discrimination of diet composition is extremely limited; for this, baseline isotope values are required for all potential prey in the food web and isotopic factors between diet and tissue sampled are required, as well as information on turnover rate.

The application of molecular techniques to identify prey species from DNA (Jarman *et al.*, 2002; Casper *et al.*, 2007b) is a relatively recent advance in diet studies. As a prey detection technique it has obvious advantages where prey are soft bodied and not represented by hard parts (Olesiuk *et al.*, 1990), if only fleshy parts of large prey are consumed (*e.g.*, the bellies of salmon) or if the hard parts of prey are regurgitated (*e.g.*, cephalopod beaks, Bigg and Fawcett, 1985). Captive feeding studies suggest that detection of prey in faecal matter is more representative of recent feeding and not a composite of meals over many days (Deagle *et al.*, 2005) and concurrent comparison of scat analysis and prey DNA remains in scats have been used to improve the prey biomass and consumption estimates for Steller sea lions (Tollit *et al.*, 2009). Quantitative PCR techniques have been developed to estimate relative quantities of target species. However, the technique is costly and it is typically used to answer very specific questions, such as the contribution of salmonids in a predator's diet (Deagle and Tollit, 2007). Validation of DNA studies is not as advanced as the more established QFASA method and further testing is warranted however, the method overall is promising.

1.4 Ecosystem features and resource diversity around Britain

The species of fish and size of fish available to seals is subject to both environmental and anthropogenic influences. Around Britain, the habitat available to seals and their prey is varied, ranging from the relatively shallow and sandy North Sea to the east to the geomorphological complex Inner seas and Atlantic Ocean off the west coast of Scotland with fjords, reefs, muddy sand and numerous islands. To the north of mainland Scotland, Orkney and Shetland straddle the boundary of the North Sea and Atlantic Ocean.

1.4.1 The North Sea including Orkney and Shetland

The North Sea is shallow (<50 m) in the south with a deeper central part (50-100 m, ICES, 2008a). Sand and finer muds in deeper waters dominate the southern and more central coastal regions, with sands becoming coarser further west. Around Orkney and Shetland coarse sand and gravel dominate (ICES, 2008a). Water circulation in the North Sea is generally an anticlockwise gyre driven mainly by windforcing. The main warm water inflow is from the North Atlantic entering around Orkney and Shetland in the north (ICES, 2008a) and via the Channel in the south (Hughes and Lavin, 2005). Changes in zooplankton and fish distributions have been linked to the strength of these inflows (ICES, 2008a).

Dominant commercial species in the fish community of the North Sea are herring and horse mackerel (*Trachurus trachurus,* mainly in summer), cod, haddock, whiting and saithe, common dab (*Limanda limanda*), plaice, long rough dab (*Hippoglossoides platessoides*), lemon sole (*Microstomus kitt*) and sole, sandeels and Norway pout (*Trisopterus esmarkii*). Other important pelagic fish species in the North Sea ecosystem are sprat and blue whiting (*Micromesistius poutassou*).

Fine scale assessments of fish communities were conducted in the Moray Firth 1992-94 by Greenstreet et al. (1998). Fifty-three species of fish were identified but only six (sandeel, sprat, herring, dab, lemon sole and plaice) accounted for 96 % of the total assemblage biomass (Greenstreet *et al.*, 1998). The two most abundant gadoid fish were whiting and haddock (Greenstreet *et al.*, 1998). At a larger scale, Callaway *et al.*, (2002) reported on the diversity and community structure of fish in the North Sea from groundfish surveys conducted in 2000 with 2m beam and otter trawls. Species such as sandeel and gobies (*Gobiidae*), which are sampled poorly by trawls, were not described. In the northern North Sea in relatively shallow waters (50-100m), haddock, whiting, herring, dab, and plaice were dominant, while at depths of 100-200m, Norway pout dominated (Callaway *et al.*, 2002). In the shallower waters of the southern North Sea (<50 m), fish communities were made up of small species more characteristic of inshore waters; solenette (*Buglossidium luteum*), dab, and dragonet, plaice, sole and whiting (Callaway *et al.*, 2002).

All commercially exploited stocks of round fish and flatfish species in the North Sea have at some time been exposed to high levels of fishing mortality (ICES, 2012).

Although the main commercial stocks are generally considered to be depleted, there are recent signs of recovery (*e.g.*, ICES, 2011b; 2013; 2014b).

During the past 30 years, the abundance of large fish has decreased in the North Sea and numbers of small fish significantly increased (Daan *et al.*, 2005; Marty *et al.*, 2014), although Norway pout does not follow this trend (Marty *et al.*, 2014). The increase in the number of small fish is an indirect effect of overexploitation of the large predatory fish species (ICES, 2008b). Smaller body size in fish has also been linked to warming sea temperatures (Daufresne *et al.*, 2009) *e.g.*; six of eight commercial fish species have reduced in body size over the last 40 years coinciding with a 1-2 °C increase in water temperature in the North Sea (Baudron *et al.*, 2014).

The deepening of fish assemblages by approximately 3.6m decade^{-1}, the northward shift in mean latitude of abundant thermal specialists and a southward shift of small southerly species with a northern range boundary in the North Sea has also been attributed to warmer sea temperatures (Dulvy *et al.*, 2008). The size structure on the west of Scotland has also changed over time, with a decrease in the relative abundance of large fish and an increase in smaller fish. Blanchard *et al.*, (2005) suggest that fishing has had a stronger effect on the changes in size structure than changes in temperature.

Warmer sea temperatures are also affecting zooplankton; warmer water species are becoming more dominant. Beaugrand (2003) showed a clear association between increased abundance of warmer water zooplankton and a reduction in cod recruitment. Furthermore, there has been an increase in fish species with typically more 'southern' distributions (*e.g.*, red mullet *Mullus surmuletus*, anchovy *Engraulidae* species and pilchard *Clupea pilchardus*) in the northern North Sea and this is probably a response to the increased water temperatures (Beare *et al.*, 2004)

1.4.2 West of Scotland

The shelf area on the west coast of Scotland contains mixed substrates, generally with soft sediments (sand and mud) in the western part and tending towards rockier areas in the eastern part (ICES, 2011a). The water circulation is dominated by the pole-ward flowing slope current which introduces warmer water from the south and is strongest in summer (ICES, 2011a).

Descriptions of the dominant fish west of Scotland are only available from the 1980s (Gordon and De Silva, 1980; Gordon, 1981): whiting, sprat, hake (*Merluccius merluccius*) and haddock. West of the Hebrides in deeper water (>100 m) and in northern Scotland, haddock, poor cod (*Trisopterus minutus*), Norway pout, whiting and grey gurnard (*Eutrigla gurnardus*) dominated. While along the shelf edge (300-450 m), silvery pout (*Gadiculus argenteus*), blue mouth redfish (*Helicolenus dactylopterus*) and hollowsnout rattail (*Coelorinchus caelorhincus*) were dominant (Gordon and De Silva, 1980; Gordon, 1981).

Variation in the temperature and salinity of the North Sea and west coast of Scotland generally reflects the influence of the North Atlantic Oscillation (NAO) on water movements from the Atlantic into these areas. Long term coastal monitoring of Scottish waters has revealed a general trend of increasing sea surface temperature since 1980 at a rate of around 0.5°C per decade (FRS, 2004).

On the west coast of Scotland there are commercial fisheries for: cod, haddock, whiting, hake, herring, lemon sole, plaice and witch (*Glyptocephalus cynoglossus*, ICES, 2011a). Migratory species such as mackerel (*Scomber scombrus*), horse mackerel and blue whiting are exploited while using the area for spring spawning before migrating north out of the region. The herring stock is composed of two groups, which spawn in either spring or autumn, and the autumn spawners are dominant (Hatfield and Simmonds, 2002). Sandeel, sprat and Norway pout are major forage fish with currently no major industrial exploitation (ICES, 2011a).

1.5 Thesis aims

Marine mammals as higher predators are major consumers within their ecosystem and as such most likely have a key role in determining food web structure (Bowen, 1997). Information about the diets of marine mammals is therefore important for understanding trophic interactions and community structure as well as the role of anthropogenic and natural environmental change on ecosystems (Bowen, 1997; Tollit *et al.*, 2010). As well as being important for understanding the role of marine mammals dietary information is also considered important for informing the conservation and management of species (Bowen, 1997; Tollit *et al.*, 2010).

The role of harbour seals in the marine community around Britain has not been assessed to the same extent as the role of grey seals. Therefore knowledge of their role as predators in our coastal waters remains relatively poor. Filling information gaps about the current diet of harbour seals, variation in harbour seal diet and similarities with the diet of grey seals will provide important contextual evidence for understanding if diet is influencing the divergent population trends of this species around Britain.

The work described in the following chapters is intended to improve current knowledge of the diet of harbour seals and inform the wider research programme into the decline of this species around Britain. In Chapter 2, I describe feeding experiments conducted with harbour seals to estimate digestion correction factors (DCFs) for the most common prey species consumed around Britain. Without harbour seal and prey specific robust DCFs that take into account the partial and complete digestion of prey remains, the diet of harbour seals around Britain cannot be estimated accurately. Based on the limited assessment of Tollit *et al.* (1997b) and more extensive work of (Grellier and Hammond, 2006) I expected to find harbour seal and prey specific differences in the partial and complete digestion of hard prey remains through my experimental work. To estimate harbour seal diet as accurately as possible for this study and to allow direct comparison with grey seal diet estimates my first goal was to generate robust DCFs which are described in the following chapter.

In Chapter 3, I examine regional and seasonal variation in the diet of harbour seals around Scotland and in The Wash, England from scats collected over a 12 month period. Understanding prey consumption and the profitability of different prey are essential for understanding marine mammal - prey interactions and their influence on the marine ecosystem and so I used three metrics to study the diet: diversity, composition and quality. I also compared the diet in 2010/11 to previous studies where possible to look for variation in diet that may indicate foraging niche change, which may be a consequence of changes in the available prey base.

The quality and/or quantity of prey available to seals have the potential to influence the status of local populations. The decline of Steller sea lions in the Gulf of Alaska and the Aleutian Islands was strongly linked to changes in the available prey base. Diet switching from fatty fishes such as herring, sand lance (*Ammodytes hexapterus*) and smelt (Osmeridae) to walleye pollock (*Theragra chalcogramma*) and other gadid species (Emlen, 1966) and very low diversity of diet, typically dominated by pollock (Emlen, 1966), are two significant dietary differences believed to have influenced the population declines (Merrick and Calkins, 1996; Merrick *et al.*, 1997; Rosen and Trites, 2000; Trites and Donnelly, 2003; Winship and Trites, 2003). Captive feeding studies support these findings revealing that sea lions would have to eat 35-80% more pollock than herring to maintain similar net energy intakes, implying serious consequences for animals relying heavily on pollock (Rosen and Trites, 2000).

The diets of declining Steller sea lion populations were considered to be 'nutritionally inadequate' due to poor nutrition caused by sub-optimal quantity or quality of prey available (reviewed in Trites and Donnelly, 2003). Nutritional stress can affect population success through reduced birth rates, growth inhibition, starvation, disease susceptibility, increased juvenile mortality and behaviour modifications (*e.g.*, extended foraging trips/bouts, Trites and Donnelly, 2003). However, the evidence supporting the links between the Steller sea lion decline and nutritional stress have recently been called into question in Biological Opinion (BiOp) reports published by the National Marine Fishery Service (NMFS, NOAA Fisheries, 2010; NOAA Fisheries, 2014) and NOAA commissioned, Center for Independent Experts (CIE) independent peer reviews of the 2010 BiOp (Bowen, 2012; Stewart, 2012; Stokes, 2012). However, this conclusion is not supported across all the academic community working on the Steller sea lion decline. Nutritional stress has been one of the most difficult hypotheses to test; yet for some it remains the central leading hypothesis regarding the impact of fisheries and the lack of recovery in the western stock of Steller sea lions (*e.g.*, Trites *et al.*, 2007a; Rosen, 2009; Sinclair *et al.*, 2013).

The significant decline of harbour seals in some areas of Britain contrasts sharply with the stable populations in other regions and it is possible that changes in the available prey base as a consequence of overfishing, climate change or changes in foraging behaviour as a result of competition for prey with grey seals may present difficulties for survival. If prey were limiting to the population success of harbour seals in some regions, I would expect large differences in diet composition by region and I would also expect that any difference would be detectable over time and be identifiable when comparing the diet with previous studies in the same region. Any, changes large enough to cause such dramatic differences in population abundance were expected to involve declines in more calorific prey (*e.g.*, pelagic fish or sandeel) and increases in lower calorific prey (*e.g.*, large gadoids) in the diet.

When interested in the coexistence of possibly competing species it is not sufficient to consider only inter-specific interactions, it is important also to consider intra-specific competition. In theory, increasing intraspecific competition should expand a species niche, whereas increased inter-specific competition should reduce it (Connell, 1983). As such, I examined intra-specific variation in diet of male and female harbour seals in Chapter 4. I identified three sites in Scotland and one in England where sample sizes were adequate to assess sex-specific differences in diet. I used the same diet metrics (diet diversity, composition and quality) as in Chapter 3 to examine differences in the diet of male and female seals overall and at a seasonal level where possible. At an individual level, foraging success determines nutrient intake, and expenditure during fitness related activities (growth, reproduction and survival) determine life history patterns (Boggs, 1992). The annual life cycles of male and female harbour seals require different levels of energy expenditure at different times of the year. For example, females during summer lose up to 33% of body mass during lactation (Bowen *et al.*, 1992). Following weaning, adult females need to recover condition, particularly if mating has occurred because body condition has been linked to successful pregnancy and pup survival in pinnipeds (Trillmich and Limberger, 1985; Pitcher *et al.*, 1998). The need to replenish body condition may therefore influence nutrient requirements in female seals and if prey is limiting, prompt intra-specific competition for prey between the sexes. Should intra-specific competition for prey occur as a consequence of male/female annual life cycle I would expect difference in the diet to be evident at key times of the year. For females I would expect the months after the pupping/moult seasons to be very important when females may target higher calorific prey to rapidly improve their depleted body condition.

In Chapter 5, I compare the diet of harbour and grey seals estimated using hard prey remains from faeces collected around Britain, using the diet metrics of diversity, composition and quality, to explore the possibility of dietary niche overlap between these two sympatric higher predators. Despite differences in their body size, annual life cycles (Bonner, 1972) and at-sea movements (Thompson *et al.*, 1996a; McConnell *et al.*, 1999; Matthiopoulos *et al.*, 2004; Cunningham *et al.*, 2009; Sharples *et al.*, 2012; Jones *et al.*, 2013) there is overlap in the sizes of juvenile seals and in space use at-sea (Jones *et al.*, 2013) and on land (Figure 1.1). I use the 2010/11 data to describe the current diet of both species of seal and then compare these results to previous diet studies looking for changes in consumption that may have occurred as a consequence of competition for prey between the two seal species or as a result of changes in the available prey base.

The generalist nature of harbour seals as predators and their ability to change diet in response to changes in local abundance should in principle buffer them against changes in the prey base as a result of environmental or anthropogenic change (Fryxell and Lundberg, 1994; Furness, 1996). However, in the Moray Firth when harbour seals switched to alternative prey during seasons of low clupeid abundance, individuals had significantly poorer body condition (Thompson *et al.*, 1996b) and suffered physiological consequences such as macrocytic anaemia (Thompson *et al.*, 1997). It was not clear, however, whether these differences resulted from changes to prey-specific foraging strategies or from differences in the nutritional quality of prey.

From the outset I did not expect to find complete answers to questions regarding harbour seal declines in some regions around Scotland. However, by stratifying my scat collections over time and space, I hoped to highlight variation in both harbour and grey seal diet in relation to their: distribution, dynamic patterns in prey occurrence, seal at-sea movements and annual life cycles. The habitats and dominant prey species available to the east, west and north of Britain are distinct and so regional variation in diet was expected. For example, I anticipated that sandeels would constitute a greater proportion of the diet of seals in the North Sea than on the west coast. There are also well documented migration patterns and spawning patterns for some species *e.g.*, pelagic fish (Maravelias, 1997; Reid *et al.*, 1997; Baxter *et al.*, 2011; Marine Scotland, 2014a; b) and I expected the diet of seals to reflect some of these large scale patterns in prey distribution and abundance, *e.g.*, more herring/mackerel in the diet in spring and/or autumn.

Changes in the prey base available to seals will also have changed over time as a result of changes in fishing pressure and climate change, so inter-annual differences in diet were expected. The proportion of sandeels in the diet may have declined as a result of the heavy exploitation of this species in the North Sea (ICES, 2011b). Similarly the proportion of gadoids in the diet may also have changed as a consequence of the demersal trawl fishery (ICES, 2008b).

Comparing the diet of male and female harbour seals, I expected any differences to be driven by the annual life cycle of the seals, with females either eating a greater range of prey species or showing preference for prey of higher quality (*e.g.*, pelagic fish or sandeels), which would help them regain their body condition faster than consumption of lower energy prey.

I expected variation in diet as a result of intra- or inter-specific competition to be more difficult to identify considering time differences between studies (*e.g.*, Tollit and Thompson, 1996; Hammond and Harris, 2006), the different methods used to estimate diet (e.g., Pierce *et al.*, 1990a; Brown and Pierce, 1997) and the dynamic nature of the available prey resource (*e.g.*, Hatfield and Simmonds, 2002; ICES, 2008b).

The foraging ecology of predators and the interactions between predator and prey, is complex and for marine mammals difficult to observe directly because foraging usually occurs at depth and occurs over multiple spatial and temporal scales (Levin, 1992). Furthermore, present-day studies may not reveal evidence of competition as the mechanism for determining: distribution, abundance and diet *etc*., may have already been eliminated by past co-evolutionary divergence and current observations may only represent “the Ghost of Competition Past” (Connell, 1980). However, I have attempted to address specific questions relating to the foraging of harbour seals in relation to their distribution around Britain, the time of year, the annual life cycles of male and female seals, and the possibility of foraging overlap with grey seals using new diet data.

Chapter 2

IMPROVED ESTIMATES OF DIGESTION CORRECTION FACTORS AND PASSAGE RATES FOR HARBOUR SEAL PREY

2.1 Introduction

Due to the limited opportunities to directly observe what marine mammals eat, diet estimation relies primarily on indirect observation. Methods to estimate diet include: identification of prey remains recovered from faeces, stomachs and intestines, and comparison of fatty acid (FA) signatures or DNA from the tissues of predator and prey. Each method makes a number of assumptions, violation of which can lead to biased results (Pierce and Boyle, 1991; Budge *et al.*, 2006; Tollit *et al.*, 2006; Tollit *et al.*, 2010). Both captive feeding studies and computer simulations have been used to account for bias in these different methods (*e.g.*, Hammond and Rothery, 1996; Tollit *et al.*, 1997b; Iverson *et al.*, 2004; Deagle *et al.*, 2005; Thomas *et al.*, 2013)

2.1.1 Main diet estimation methods

The recovery of prey hard remains such as fish otoliths and cephalopod beaks from faeces is a widely used method to estimate phocid diet (Hammond *et al.*, 1994a; Hammond *et al.*, 1994c; Bowen and Harrison, 1996; Thompson *et al.*, 1996a; Tollit and Thompson, 1996; Hall *et al.*, 1998; Brown *et al.*, 2001; Hammond and Grellier, 2006; Hammond and Harris, 2006). Prey skeletal structures which are resistant to digestion can be collected from faeces, regurgitate, stomachs and intestines. Despite providing little information about the source animal, faecal samples are relatively easy and quick to collect in large numbers and disturbance is minimal or short term (Kucey and Trites, 2006).

Stomach and gastrointestinal tract contents can be analysed from dead animals alongside information on the source animal (Pierce and Boyle, 1991; Santos *et al.*, 2001). However stomachs and gastrointestinal tracts are often empty or contain little identifiable food remains. Stomach flushing (lavage) and rectal enemas of live animals can improve the sample size containing prey remains (*e.g.*, Rodhouse *et al.*, 1992; Boness *et al.*, 1994; Staniland *et al.*, 2003) but to carry out these procedures requires specialist methods where animals are captured, restrained and immobilised.

Molecular detection of single prey remains from scats or GI tracts using protein electrophoresis has been used with some success, however proteins degrade with digestion and mixtures of prey appear problematic (Pierce *et al.*, 1990b; Pierce *et al.*, 1993). However the identification of prey from DNA in faeces using polymerase chain reaction (PCR) amplification and species specific targets (Jarman *et al.*, 2002; Casper *et al.*, 2007a) has become popular and captive feeding studies have shown that prey DNA in faeces is representative of recent feeding (48 h) and not a composite of meals over many days (Deagle *et al.*, 2005). Furthermore, quantitative real-time PCR methods are being developed which have the potential to estimate relative quantities of species (Deagle and Tollit, 2007; Matejusova *et al.*, 2008).

Collection of predator adipose tissue (*e.g.*, blubber, milk and blood) can allow diet to be estimated using fatty acid (FA) signatures (Budge *et al.*, 2006; Iverson, 2009). The FA composition of the tissue collected can reflect the diet over hours (blood), or weeks to months (milk and blubber). Subcutaneous blubber can provide the best sample size for estimating diet as animal capture is not required and samples can be compared with those taken from carcasses. More recently quantitative FA signature analysis (QFASA, Iverson *et al.*, 2004) has been conducted using a statistical model and combinations of likely prey FA signatures to estimate predator diets (Iverson *et al.*, 2004; Iverson *et al.*, 2007).

2.1.2 Collection of faeces and identification of prey hard remains

Scat collection remains the most common method for obtaining information on the diet of seal populations in European waters. However, this method does have its limitations and collection of faeces is not useful for all species. Scat analysis is expected to be representative of recent feeding of individuals, within 12-48 h (Prime and Hammond, 1987; Markussen, 1993; Orr and Harvey, 2001; Grellier and Hammond, 2006; Phillips and Harvey, 2009). It is therefore a useful tool for estimating the diet of primarily coastal species for which the remains of prey consumed are likely to show up in scats collected on shore. The harbour seal (*Phoca vitulina*) is one such coastal species which makes short distance (11-100 km) and short duration (1-6 days) foraging trips (*e.g.*, Thompson *et al.*, 1996a; Cunningham *et al.*, 2009; Sharples *et al.*, 2012).

For species which do not typically forage near haul-out sites such as elephant seals (*Mirounga angustirostris*) scats rarely contain hard prey remains indicating that otoliths are completely digested or excreted before animals come ashore (Harvey and Antonelis, 1994). Similarly for some otariid species many of the hard prey remains are regurgitated and not present in faeces (Gales and Cheal, 1992). For such species scat analysis is not an appropriate method for estimating diet.

A wide array of hard prey material typically remains after all faecal matter has been washed away from scats, these can include: fish otoliths, vertebrae, hypobranchial, quadrates and dentary's and cephalopod beaks and eye lenses. Scat analysis assumes that all prey consumed have recoverable remains; in particular seals must eat the head of fish for the analysis of otoliths. Typically cephalopod beaks and fish otoliths are used solely for prey identification and size estimation (*e.g.*, Thompson *et al.*, 1996a; Tollit *et al.*, 1998; Brown *et al.*, 2001; Wilson *et al.*, 2002; Sharples *et al.*, 2009; Kavanagh *et al.*, 2010). Though detection rates of some species with fragile otoliths (*e.g.*, Salmonids) has been improved by the inclusion of other diagnostic features (Tollit *et al.*, 2003; Gosch *et al.*, 2014), it is not a requirement when detection is estimated (recovery rates) and accounted for in diet reconstruction.

Fish otoliths and cephalopod beaks are species-specific in their shape. For pristine specimens, this allows accurate identification to species of these structures and there are good allometric relationships between otolith or beak size and fish or cephalopod size, respectively, that allow the size of ingested prey to be estimated accurately (Clarke, 1986; Härkönen, 1986; Leopold *et al.*, 2001). However, when passing through the gastrointestinal tract of a seal, otoliths and beaks may be partially digested and thus reduced in size. In addition, some otoliths or beaks may be completely digested. Digestion correction factors (DCFs) need to be applied to remove these biases; that is, digestion coefficients and recovery rates to account for partial and complete digestion, respectively (Prime and Hammond, 1987; Harvey, 1989; Tollit *et al.*, 1997b; Bowen, 2000; Tollit *et al.*, 2004b; Grellier and Hammond, 2006). Failure to account for the digestion of hard prey remains will lead to estimates of diet composition and prey consumption that are subject to considerable bias.

Captive *in vivo* feeding trials have previously been conducted to quantify the extent of partial and complete digestion of otoliths and beaks consumed by harbour seals (Prime, 1979; da Silva and Neilson, 1985; Cottrell *et al.*, 1996; Tollit *et al.*, 1997b; Marcus *et al.*, 1998; Phillips and Harvey, 2009). However, available DCFs are limited for NE Atlantic prey species and methodology has varied. As a result, reconstruction of harbour seal diet in European waters has not been conducted consistently. Studies have used harbour seal DCFs for a limited number of prey species (*e.g.*, Brown *et al.*, 2001; Pierce and Santos, 2003), grey seal DCFs (Sharples *et al.*, 2009) or no DCFs (*e.g.*, Wilson *et al.*, 2002).

To obtain robust estimates of wild harbour seal diet composition robust estimates of DCFs are needed. This is particularly important if comparisons are to be made between the diet of conspecific harbour and grey seals around Britain (Chapter 5). To accurately estimate the diet of harbour seals in the wild *in vivo* feeding experiments were conducted to estimate DCFs and passage rates for harbour seal prey. Specifically, the aims of this study were (a) to obtain robust estimates of digestion coefficients and recovery rates to account for partial and complete digestion of otoliths and beaks of prey species commonly consumed by NE Atlantic harbour seals, and (b) to describe species-specific characteristics of the passage rate through the harbour seal gut of the remains of prey hard parts.

2.2 Methods

2.2.1 Feeding experiments

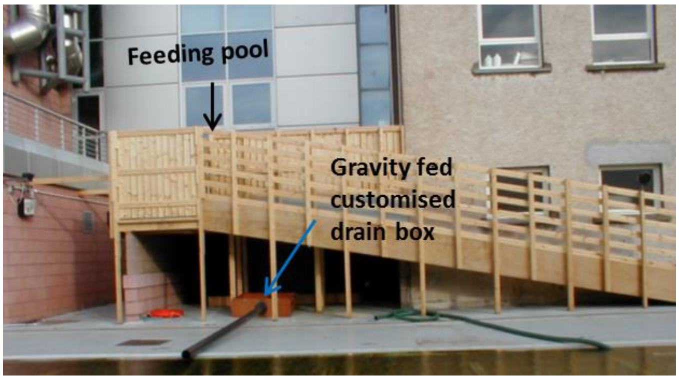
Feeding experiments were conducted with harbour seals during March-April 2009 (1 adult female) and August 2011 - December 2012 (1 juvenile male and 4 adult males) at the Sea Mammal Research Unit (SMRU), University of St Andrews (Scotland). Seals were captured either in the Eden estuary, St Andrews Bay or at Ardesier, Moray Firth and housed for up to 13 months before being released at the haul-out site from which they were caught. At SMRU, the seals were housed in ambient temperature seawater pools and fed a multi-species diet supplemented with vitamins and iron. This work was carried out under Home Office licences (60/4009 and 60/3303).

For the duration of the feeding experiment, seals were housed individually in an enclosure 6.20m x 4.85m, with access to water (a pool 3 m in diameter and 1.5 m deep, Figure 2.1) and a dry area. Overflow and outflow water passed through a 250µm filter (Figure 2.1). The recovery rate of the system was tested using a total of 730 plastic or glass beads which were scattered in the pool enclosure arbitrarily and counted on recovery.

In total, 17 fish and one cephalopod prey species were fed to and eaten by the seals; prey species and size ranges are given in Table 2.1. Prey were obtained commercially or through collaboration with Marine Scotland Science, Aberdeen, the Pittenweem Harbour Fishermen’s Mutual Association, Jack Wright (Fleetwood) Limited and Institute of Aquaculture University of Stirling. One hundred whole prey feeding trials were successfully conducted with six harbour seals and 18 prey species to derive estimates of digestion coefficients. A further seven feeding trials were attempted with the seals (n = 4 dragonet, *Callionnymus lyra* and n = 3 adult Atlantic salmon, *Salmo salar*) but these trials were excluded from any analysis because the seals refused to eat the meals offered (dragonet n = 4 and salmon n = 2) or no otoliths were recovered (salmon n = 1). The prey fed included those species most frequently observed in the diet of harbour seals in Britain (Pierce *et al.*, 1991a; Tollit and Thompson, 1996; Brown and Pierce, 1998; Hall *et al.*, 1998; Brown *et al.*, 2001; Pierce and Santos, 2003). Otoliths and beaks were fed *in situ* in whole or gutted prey (fish obtained commercially had been gutted prior to delivery) because feeding method has been shown to affect digestion in captive seals (Grellier and Hammond, 2005). Differences in prey availability meant that different combinations of prey were offered to each individual seal.

For a minimum of 5 days prior to the start of an experiment, each seal was fed decapitated fish to clear its digestive system of otoliths/beaks. During experiments, seals were offered single-species meals once a day in the late afternoon. Where prey availability allowed, seals were fed the same prey species multiple times. However, multiple meals of the same species were offered only if all otoliths previously fed of that species had been recovered or if there had been a 2 day period when no otoliths of that species were recovered. Meal size was kept constant for each individual seal but varied across individuals depending on their size. The total length of fish and mantle length of cephalopods fed were measured to the nearest 0.1cm. The size of otoliths and beaks of the prey fed to the seals was calculated using the relationships given in Table 2.2.

A)



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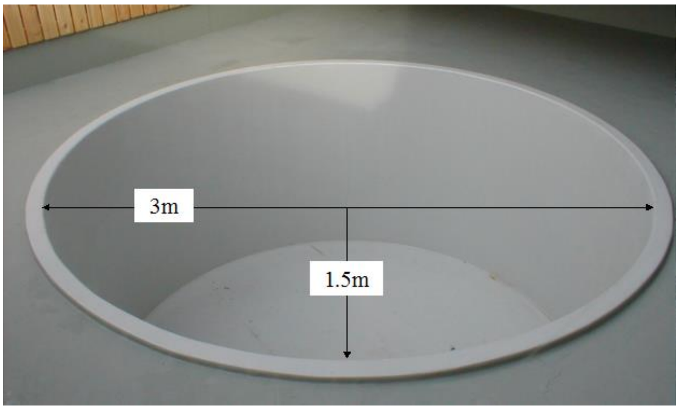

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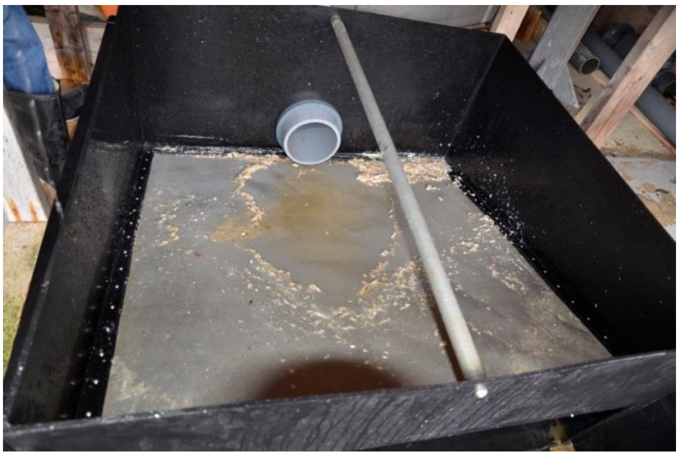


Figure 2.1: The custom designed feeding experiment set up housed individual seals in A) a raised enclosure 6.20m x 4.85m, with access to water B) a pool 3 m in diameter and 1.5 m deep**.** Overflow and outflow water passed through C) a 250µm filter.

The pool was drained and cleaned prior to the first experimental meal and then daily within 24h of an experimental meal being fed (average time between feeding and draining was 18:50h). All debris were collected during draining and cleaning, and were washed through a nest of sieves of mesh sizes 2mm, 1mm, 600µm, 335µm and 250µm.

All prey remains were sorted and all otoliths and beaks retained. Otoliths and beaks were identified to species and counted. Broken otoliths and beaks were only included if the widest or longest part of the otolith or the lower rostral length (LRL) of the beak was complete. Otolith length (OL) and width (OW) and cephalopod beak LRL were measured to the nearest 0.01 mm using digital callipers (Mitutoyo) under a binocular microscope (Kyowa optical 2D-2PL and Zeiss Stemi 2000-C). The callipers were zeroed between measurements and were frequently cleaned.

Uneaten prey remains (whole prey or fish heads) were recovered from the pool daily. Lengths of whole fish were measured directly. Otoliths were removed from the heads of damaged fish and lengths and widths measured. The length of the fish that they came from was estimated using the regression equations given in Table 2.3. Mean uneaten fish length was calculated from whole fish, or whole fish plus fish length estimated from either otolith length or otolith width.

For trials in which greater than 10% of prey was uneaten nonparametric bootstrap resampling to determine whether or not the size distribution of fish eaten was representative of the size distribution of prey fed. In each bootstrap resample, the mean length of a randomly selected sample, equal in size to the observed percentage of uneaten fish, was calculated. 95% confidence intervals were calculated from the distribution of 1000 mean lengths using the percentile method. If the observed mean length of uneaten fish, as calculated above, was outwith the 95% confidence interval, the trial was discarded.

Table 2.1: Details of the experimental prey consumed and recovered. Mean RR is the recovery rate; the proportion of otoliths/ beaks eaten that was recovered at the end of each feeding trial. A value of 1 means that all otoliths/beaks eaten were recovered. NCF is the number correction factor which was calculated as the inverse of the recovery rate (Bowen 2000).

		Length (cm)		No. of otoliths/ beaks		Mean			No. of	
Common name	**Scientific name**	**Min**	**Max**	**eaten**	**recovered**	**RR**	**SE**	**NCF**	**seals**	**trials**
Dab	*Limanda limanda*	10.2	33	585	415	0.755	0.036	1.379	3	5
Lemon sole	*Microstomus kitt*	15.6	32.1	210	83	0.474	0.060	2.440	2	3
Long rough dab	*Hippoglossoides platessoides*	8.6	23.7	438	386	0.887	0.020	1.133	2	2
Plaice	*Pleuronectes platessa*	13.9	36.4	492	403	0.854	0.035	1.219	6	9
Witch	*Glyptocephalus cynoglossus*	24.6	43.8	68	66	0.976	0.016	1.025	2	2
All flatfish		8.6	43.8	1793	1353	0.789	0.033	1.439	6	21
Atlantic cod	*Gadus morhua*	13.0	60.9	232	211	0.881	0.085	1.204	3	11
Haddock	*Melanogrammus aeglefinus*	11.5	40.6	486	485	1.005	0.005	0.995	3	9
Hake	*Merluccius merluccius*	45.1	54.1	26	23	0.893	0.055	1.136	1	2
Pollock	*Pollachius pollachius*	43.6	55.2	8	8	1.000	0.000	1.000	1	1
Whiting	*Merlangius merlangus*	11.5	36.7	1229	1180	0.940	0.028	1.071	6	14
All large gadoids		11.5	60.9	1981	1907	0.944	0.034	1.081	6	37
Greater sandeel	*Hyperoplus lanceolatus*	18.3	33.4	544	266	0.600	0.021	2.421	2	2
Sandeel	*Ammodytes tobianus*	7.5	22.1	13235	5692	0.389	0.013	3.704	5	10
All sandeels		7.5	33.4	13779	5958	0.494	0.017	3.062	5	12
Norway pout	*Trysopterus esmarkii*	9.3	19.9	3440	3477	1.026	0.003	0.980	6	8
Poor cod	*Trysopterus minutus*	7.8	23.7	1171	1186	1.008	0.002	0.993	5	7

Trisopterus spp		7.8	23.7	4611	4663	1.017	0.002	0.986	6	15
Herring	*Clupea harengus*	18.8	29.8	377	140	0.428	0.071	2.697	4	8
Red gurnard	*Chelidonichthys cuculus*	21.6	35.2	82	47	0.580	0.077	1.741	1	2
Salmon smolt	*Salmo salar*	13.8	18.9	448	137	0.306	0.031	3.310	2	2
Squid	*Loligo forbesii*	60.0	272.0	117	98	0.837	0.102	1.233	3	3

Table 2.2: Regressions used to infer the size of otoliths and beaks of the prey items fed to seals.

Species	**OL regression**	r^2	***N***	**OW regression**	r^2	***N***	**Source**
Atlantic cod	OL = 0.266 FL + 2.306	0.93	518	OW = 0.122 FL + 0.811	0.96	547	1
Haddock	OL = 0.383 FL + 1.560	0.97	450	OW = 0.137 FL + 0.703	0.96	469	1
Whiting	OL = 0.564 FL - 0.198	0.98	559	OW = 0.142 FL + 0.55	0.96	637	1
Hake	OL = 0.365 FL + 1.991	0.98	60	OW = 0.131 FL + 1.046	0.96	62	1
Pollack	OL = 0.243 FL + 2.551	0.97	294	OW = 0.097 FL + 1.066	0.96	304	1
Norway pout	OL = 0.436 FL + 0.028	0.98	257	OW = 0.186 FL + 0.002	0.98	257	1
Poor cod	OL = 0.362 FL + 1.718	0.95	267	OW = 0.178 FL + 0.731	0.93	275	1
Sandeel	OL = 0.185 FL - 0.056	0.93	332	OW = 0.085 FL + 0.079	0.91	337	1
Greater sandeel	OL = 0.141 FL + 0.510	0.96	399	OW = 0.057 FL + 0.409	0.95	410	1
Atlantic herring	OL = 0.154 FL + 0.386	0.96	514	OW = 0.061 FL + 0.472	0.93	541	1
European plaice	OL = 0.203 FL + 0.486	0.99	752	OW = 0.119 FL + 0.641	0.97	787	1
Common dab	OL = 0.179 FL + 0.734	0.97	508	OW = 0.107 FL + 0.699	0.95	513	1
Lemon sole	OL = 0.091 FL + 0.624	0.87	240	OW = 0.059 FL + 0.356	0.89	240	1

Long rough dab	OL = 0.213 FL + 0.477	0.95	322	OW = 0.137 FL + 0.730	0.91	338	1
Witch	OL = 0.114 FL + 1.602	0.89	81	----	----	----	2
Atlantic salmon	OL = 0.024 FL + 1.715	0.03	49	OW = 0.013 FL + 1.047	0.01	49	3
Gurnard*	OL = 0.111 FL + 0.726	0.94	735	OW = 0.079 FL + 0.697	0.90	741	1
Squid (lower rostral length)	LRL = 0.0099 ML + 0.807	0.85	518	----	----	----	4

Note: Otolith length (OL), otolith width (OW) and lower rostral length (LRL) were measured in mm; fish length (FL) and squid mantle length (ML) was measured in cm. * The gurnard regression was developed across measurements from both red and grey gurnard species. Source data provided by: 1) M. Leopold (Wageningen-IMARES, P.O. Box 167, Landsdiep 4, NRL-1797 SZ Den Hoorn, Texel, The Netherlands), 2) T. Härkönen (Swedish Museum of Natural History, Box 50007, 104 05 Stockholm, Sweden), 3) C. Sievers & L.J. Wilson (Sea Mammal Research Unit, Scottish Oceans Institute, University of St. Andrews, East Sands, KY16 8LB, UK) and 4) M.B. Santos (Instituto Español de Oceanografía, Centro Oceanográfico de Vigo, Spain) & G.J. Pierce (University of Aberdeen, Oceanlab, Newburgh, Aberdeenshire, AB41 6AA, UK). Sources 1 and 2 are summarised in Leopold *et al.*, (2001) and Härkönen (1986), respectively. Sources 3 and 4 are unpublished data.

Table 2.3: Regressions used to infer prey size from otoliths and beaks that were not eaten.

Species	OL regression	r^2	n	OW regression	r^2	n
Atlantic cod	FL = 3.49 OL - 6.64	0.88	268	FL = 7.84 OW - 5.51	0.86	275
Haddock	FL = 2.53 OL -3.27	0.90	236	FL = 6.99 OW - 4.00	0.90	240
Whiting	FL = 1.73 OL + 0.81	0.79	303	FL = 6.74 OW - 2.97	0.86	315
Poor cod	FL = 2.61 OL -3.84	0.96	144	FL = 5.22 OW - 2.98	0.94	144
Sandeel	FL = 5.00 OL + 1.16	0.86	170	FL = 10.92 OW	-	172
Dab	FL = 5.43 OL - 3.49	0.88	261	FL = 8.88 OW - 5.40	0.9	261
Plaice	FL = 4.85 OL - 2.07	0.76	405	FL = 8.15 OW - 4.70	0.79	405

Note: Otolith length (OL), otolith width (OW) were measured in mm; fish length (FL) was measured in cm.

2.2.2 Recovery Rates

Recovery rate was calculated as the proportion of otoliths eaten that was recovered at the end of each feeding trial. If all otoliths eaten were recovered, recovery rate = 1, if no otoliths were recovered, recovery rate = 0. The theoretical variance of recovery rate was calculated as $p(1 - p)/n$, where p is the recovery rate and n is the number of otoliths that were eaten. Recovery rates were averaged across trials to give mean values for each seal for each prey species, giving each trial equal weight. These values were then averaged across seals to give mean values for each prey species, giving equal weight to each seal.

2.2.3 Passage rates

Cumulative daily recovery rates were calculated for each prey species in each trial and combined as described above to give mean rates for each seal and each prey species. Prey species with similar taxonomy were grouped for presentation purposes. Cumulative daily recovery rates were also calculated for groupings for species: large gadoids (Atlantic cod *Gadus morhua*, haddock *Melanogrammus aeglefinus*, hake *Merluccius merluccius*, pollock *Pollachius pollachius*, whiting *Merlangius merlangus*), *Trisopterus* spp. (Norway pout *Trisopterus esmarkii* and poor cod *Trisopterus minutus*), flatfish, and all sandeels (sandeel *Ammodytes tobianus and greater sandeel Hyperoplus lanceolatus*).

2.2.4 Species-specific digestion coefficients

Digestion coefficients (mean otolith or beak size offered divided by mean otolith or beak size recovered) were calculated for fish OL and OW, and squid LRL. The delta method was used to calculate the variance of each digestion coefficient (Seber, 1982; Grellier and Hammond, 2005; Grellier and Hammond, 2006). All trials from which <10 otoliths were recovered were excluded from further analyses, except for large gadoid trials because of the constraints of feeding large fish and maintaining constant meal size. The digestion coefficients from each trial were averaged as described above for recovery rates (2.2.2) to give mean values for each seal, each prey species and each prey grouping.

2.2.5 Grade-specific digestion coefficients

All recovered otoliths were examined and the amount by which they had been digested was classified based on external morphological features (Leopold *et al.*, 2001). Pristine otoliths were classified as grade 1, moderately digested otoliths as grade 2, and considerably digested as grade 3. Because of the high number of grade 3 otoliths recovered, and the high level of digestion observed in this and other studies (Tollit *et al.*, 1997b; Grellier and Hammond, 2006), a further classification (grade 4, severely digested) was introduced. External morphological features used to classify grade 4 otoliths were: no visible sulcus or lobation or very worn surfaces (see Appendix 2.1). No attempt was made to classify beak digestion.

Where ≥10 otoliths by grade were recovered from a trial, grade-specific digestion coefficients and variances were calculated and combined in the same way as for species-specific digestion coefficients. For some species the recovery rate of specific grades of otoliths was very low and measurements from grade 2 and grade 3 otoliths were pooled.

2.2.6 Application of grade- or species- specific digestion coefficients

Possible bias in harbour seal diet estimates was explored by generating prey composition estimates from scats collected from the wild in autumn 2010 from the West coast – north region. Using the methods described in Chapter 3, prey composition was estimated using both species- and grade-specific digestion coefficients and the estimates compared.

2.2.7 Grading standardisation between multiple personnel

After establishing the grading method, I trained two technicians, who would each be working on the harbour seal wild otolith scats, to grade otoliths according to the protocol. Training included random follow up checks on the grading of different species over the first 2 weeks of work. These staff in turn used the same methods to train three other technicians who were recruited to the project. Variability in the grading method was examined across four of the six personnel responsible for grading and measuring otoliths collected during experiments and from scats collected in the field. Each person re-graded a subsample (n = 100) of whiting, sandeel, plaice and Norway pout otoliths from scats collected in the wild. To determine any differences a least squares linear regression analysis was conducted at a significance level of $p < 0.05$, using the open source software R (R Core Team, 2013).

2.3 Results

In total, 23,313 otoliths and beaks of 18 prey species were fed to and eaten by harbour seals during 100 whole prey feeding trials. 61.4% (14,306) of otoliths and beaks were recovered from scats. 98.1% (716/730) of beads were recovered and loss from the system was observed to be though human error. Some beads tossed into the air subsequently bounced out of the enclosure; scattering beads at a low level onto the haul-out area and into the water would have avoided this. Prey hard remains could not be lost in this way and loss of prey remains from the system is considered to be insignificant and can be ignored.

2.3.1 Recovery rates

Variation in prey recovery rates among seals (inter-individual variation) and within seals for prey fed to the same seal multiple times (intra-individual variability) is shown in Figure 2.2 and Appendix 2.2. Recovery rates for *Trisopterus* spp. were very high, all trials > 0.95 and mean = 1.017. For large gadoid species, recovery rate was high 0.5 - 1.063 (mean = 0.944, Table 2.1). Recovery rate was >0.9 in 78% of large gadoid trials, including 18 trials where recovery rate was ≥1. Flatfish recovery rates were lower, mean = 0.789, and more variable ranging from 0.235 to 1 (38% >0.9). Herring (*Clupea harengus*) otolith recovery was low, range 0.210 - 0.643; mean = 0.428, as it was for sandeel (range 0.121 - 0.679, mean = 0.389, n = 10 trials), greater sandeel (range 0.265 - 0.934, mean = 0.600, n = 2 trials), red gurnard (*Chelidonichthys cuculus*, range

0.639 - 0.522, mean = 0.580, n = 2 trials) and Atlantic salmon smolt (range 0.272 - 0.339, mean = 0.306, n = 2 trials). Squid (*Loligo forbesi*) lower beak recovery was high (mean = 0.816, range 0.649 - 1).

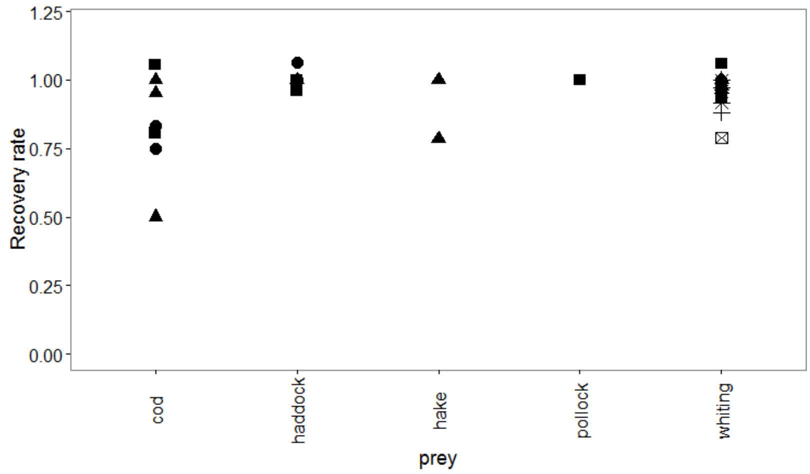
Recovery rates >1 were calculated for a few individual trials of cod (n = 2), whiting (n = 2), haddock (n = 1), Norway pout (n = 1) and poor cod (n = 2). Mean recovery rates >1 were calculated for haddock, Norway pout and poor cod. Recovery rates greater than one should be impossible; potential reasons for these anomalous results are discussed below.

The relationship between recovery rate and mean undigested otolith size for all trials of all fish prey species was positive up to OL = ~5mm and OW = ~3mm but then varied close to 1 for larger otoliths, with some lower values for the largest otoliths (Figure 2.3).

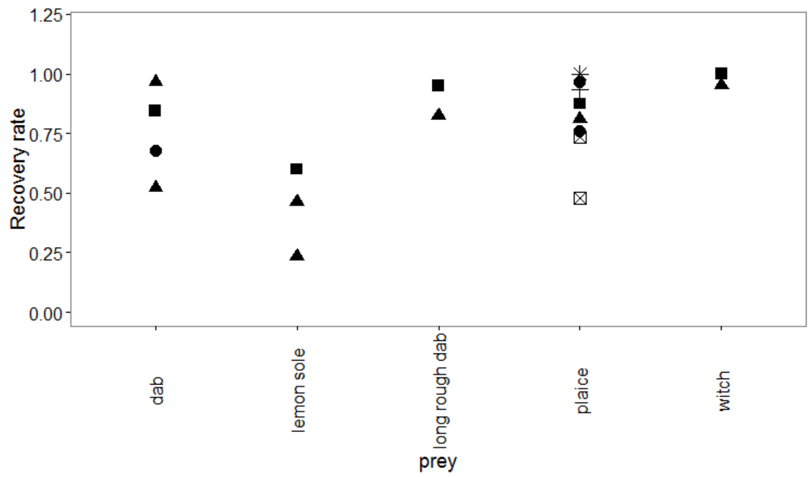
Although crustaceans were not fed in any experiment, crustacean remains were recovered from two seals during 51 whole fish feeding trials (half of the meals fed).

2.3.2 Species-specific digestion coefficients

Digestion coefficients varied among individual prey species (Table 2.5). OL digestion coefficients were greatest for hake, whiting and greater sandeel (1.93, 1.69 and 1.61, respectively), OW digestion coefficients were also greatest for hake and greater sandeel (1.80 and 1.75, respectively). Prey group digestion coefficients were greatest for all sandeels, then all large gadoids, all flatfish and *Trisopterus* spp. (Table 2.5).



a)



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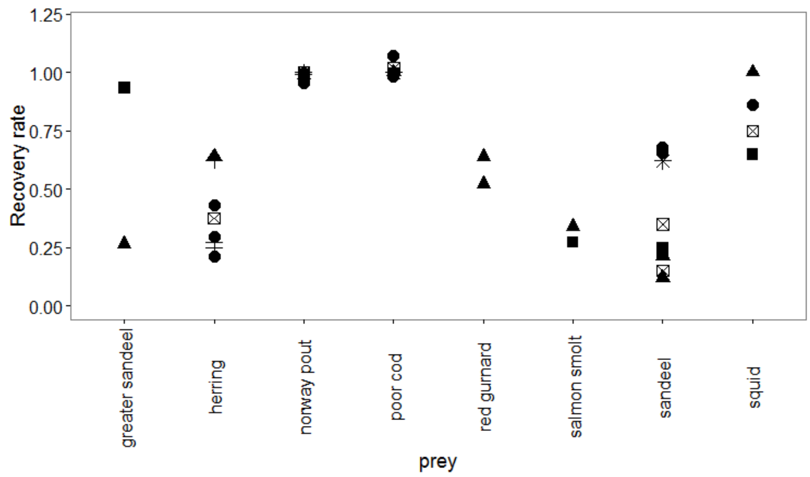


c)

Figure 2.2: Feeding trial recovery rates showing intra- and inter-individual variability. Each symbol represents a different seal. a) large gadoids, b) flatfish, c) other species.

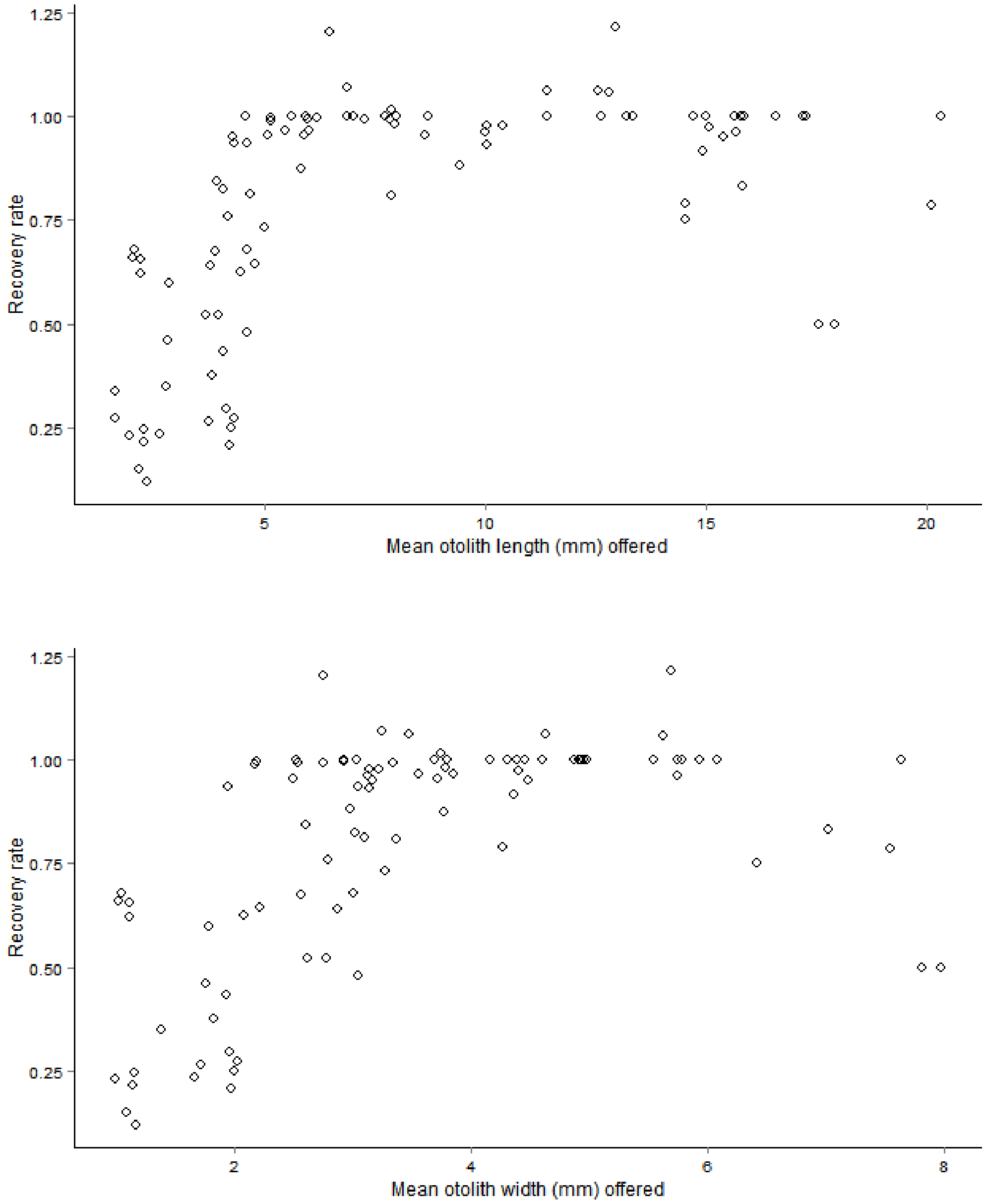
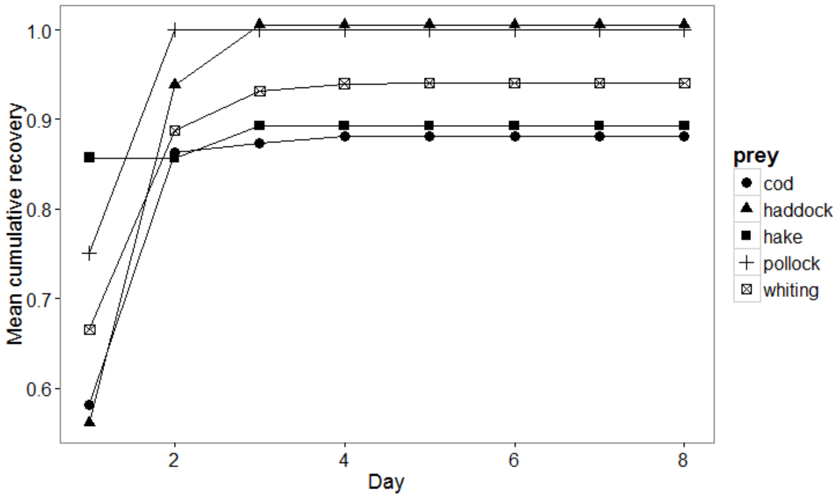


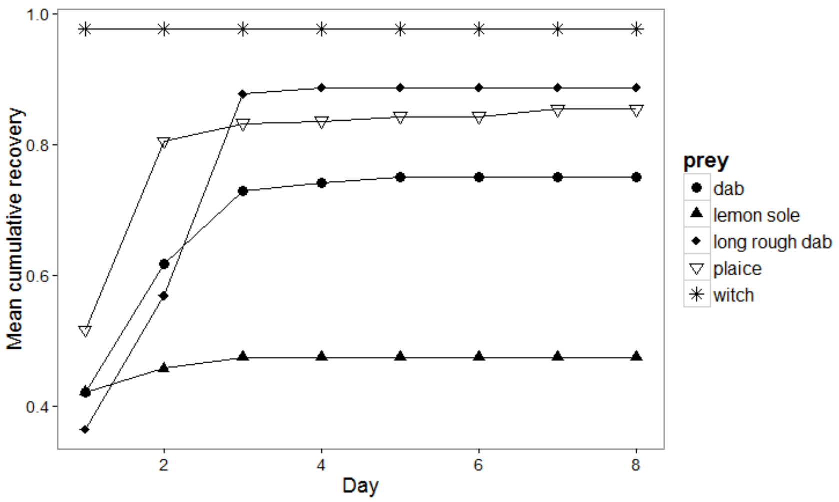
Figure 2.3: Recovery rate plotted against mean undigested otolith length (top) and width (bottom) for all trials.

Table 2.4: Percentage of the total number of otoliths and beaks recovered, calculated per day. The approximate number of hours after feeding is 16 h for day one then + 24 h for each subsequent day.

	Day													
Prey	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**
Flatfish	67.56	87.00	98.56	99.18	99.51	99.51	99.81	99.81	99.87	100	100	100	100	100
Large gadoids	73.19	96.21	99.68	99.98	100	100	100	100	100	100	100	100	100	100
Sandeels	46.16	91.65	99.55	99.70	99.80	99.85	99.94	99.96	99.99	100	100	100	100	100
Trisopterus spp	47.45	92.16	99.51	99.96	99.99	100	100	100	100	100	100	100	100	100
All fish	56.12	92.14	98.81	99.73	99.86	99.87	99.95	99.95	99.97	100	100	100	100	100
Squid	56.71	79.51	81.60	81.60	81.60	82.29	82.29	82.29	98.96	98.96	98.96	98.96	98.96	100



a)



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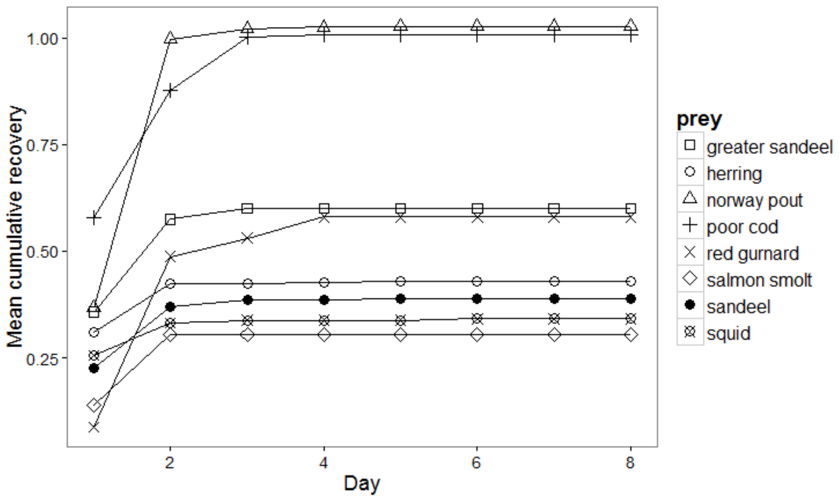


c)

Figure 2.4: Species-specific passage rates for a) large gadoids, b) flatfish, c) all other prey species.

Table 2.5: Species-specific digestion coefficients (DC) calculated for harbour seals.

				Number of		
Prey species	**DC**	**SE**	**CV**	**seals**	**trials**	**otoliths recovered**
Otolith length						
Dab	1.28	0.035	0.028	3	5	383
Lemon sole	1.22	0.112	0.092	2	3	57
Long rough dab	1.18	0.023	0.020	2	2	367
Plaice	1.17	0.048	0.041	6	9	358
Witch	1.09	0.033	0.030	2	2	61
All flatfish	1.19	0.050	0.042	6	21	1226
Atlantic cod	1.24	0.066	0.053	3	11	150
Haddock	1.17	0.038	0.032	3	9	376
Hake	1.93	0.172	0.089	1	2	14
Pollock	0.98	0.028	0.028	1	1	5
Whiting	1.69	0.090	0.053	5	12	537
All large gadoids	1.40	0.079	0.056	6	35	1082
Greater sandeel	1.61	0.048	0.030	2	2	213
Sandeel	1.28	0.020	0.016	5	10	5097
All sandeels	1.45	0.034	0.024	5	12	5310
Norway pout	1.18	0.013	0.011	6	8	3364
Poor cod	1.17	0.018	0.016	5	7	1138
Trisopterus spp	1.17	0.016	0.013	6	15	4502
Herring	1.16	0.051	0.044	4	8	87
Red gurnard	0.99	0.034	0.034	1	2	30
Salmon smolt	1.27	0.037	0.029	2	2	112
Squid (lower rostral length)	1.12	0.053	0.041	3	3	98
Otolith width						
Dab	1.35	0.035	0.026	3	5	414
Lemon sole	1.32	0.081	0.062	2	3	80
Long rough dab	1.22	0.024	0.019	2	2	385
Plaice	1.18	0.041	0.035	6	9	395

All flatfish	1.27	0.045	0.036	6	21	1340
Atlantic cod	1.23	0.063	0.051	3	11	210
Haddock	1.23	0.024	0.020	3	9	485
Hake	1.80	0.144	0.080	1	2	23
Pollock	1.10	0.071	0.065	1	1	8
Whiting	1.25	0.033	0.027	6	14	1180
All large gadoids	1.32	0.067	0.051	6	37	1906
Greater sandeel	1.75	0.049	0.028	2	2	266
Sandeel	1.40	0.022	0.015	5	10	5687
All sandeels	1.57	0.035	0.023	5	12	5953
Norway pout	1.13	0.012	0.011	6	8	3476
Poor cod	1.14	0.018	0.016	5	7	1186
Trisopterus spp	1.14	0.015	0.013	6	15	4662
Herring	1.30	0.058	0.044	4	8	139
Red gurnard	1.04	0.037	0.036	1	2	42
Salmon smolt	1.24	0.033	0.026	2	2	136

Inter- and intra-seal variability in digestion coefficients is shown in Figure 2.5 and Appendix 2.3. Overall, inter- and intra-seal variability in DCs was low, but the range was wider for some prey species than others. Relatively high variability was observed in OL digestion coefficients for whiting, plaice (*Pleuronectes platessa*) and lemon sole (*Microstomus kitt*) and in OW digestion coefficients for lemon sole.

Due to limited prey availability it was not possible to feed multiple size classes of prey. However, there was a slight significant positive relationship between digestion coefficient and mean estimated OL fed to seals (Figure 2.6, Adj R^2= 0.0523, inverse-variance weighted regression: intercept = 1.117; slope= 0.009; p = 0.015). The fragility of whiting otolith tips invalidates their use for estimating diet using OL measurements and so whiting were removed from the analysis and this reduced the estimated slope and removed the slight significance of the relationship (Adj R^2= -0.00065, inverse-variance weighted regression: intercept = 1.1396; slope= 0.0035; p = 0.333). The relationship between digestion coefficient and mean estimated OW fed to seals was not significant (Figure 2.6, Adj R^2= 0.0154, inverse-variance weighted regression: intercept = 1.134; slope= 0.0152; p = 0.125).

2.3.3 Grade specific digestion coefficients

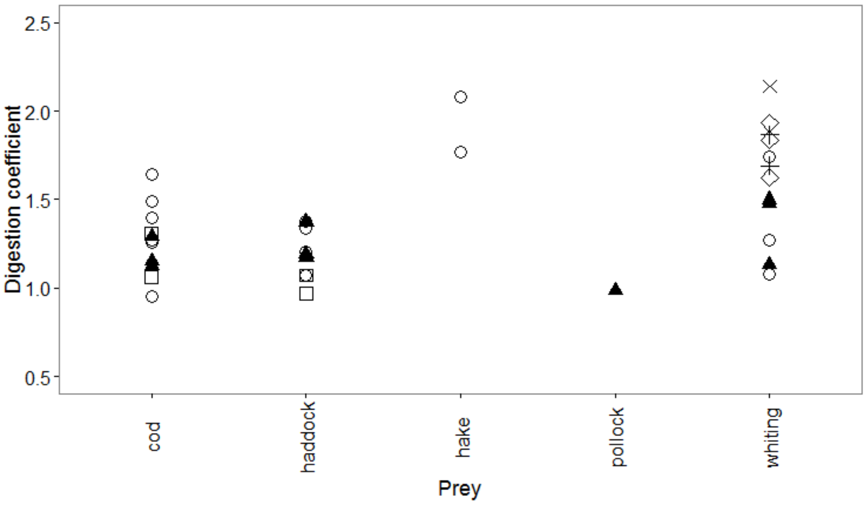
Of all otoliths recovered, 1.4% were classified as grade 1 (pristine), 5.0% as grade 2 (moderately digested), 27.8% as grade 3 (considerably digested) and 65.9% as grade 4 (severely digested). Recovery of grade 1 otoliths was thus very low. Because pristine otoliths have, by definition, not been affected by digestion the grade-specific digestion coefficient was fixed at 1.00 for grade 1 otoliths. For Atlantic cod, haddock and all large gadoids, measurements from grade 2 and 3 were pooled (Table 2.6). The majority of the species-specific digestion coefficients are for grades 3 and 4.

As for the species-specific digestion coefficients, there were differences between the grade-specific digestion coefficients based on OL and OW (Table 2.6). Standard errors were relatively small for almost all species. There was no overlap of 95% confidence intervals for grade 3 and 4 digestion coefficients for the same species; however, confidence intervals for grades 2 and 3 typically overlapped.

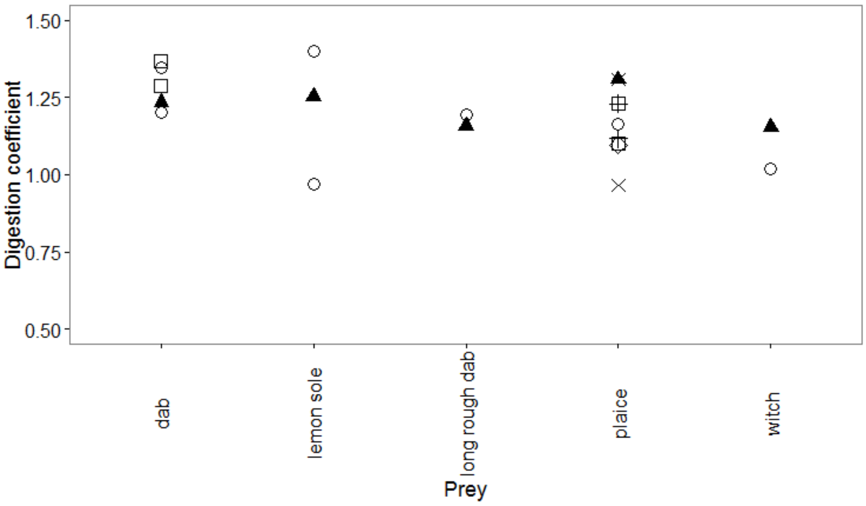
For a number of prey species, the grade- and species-specific digestion coefficient was <1 (Table 2.5 and Table 2.6) implying that mean otolith size increased post-digestion. This should be impossible and this point is discussed below.

2.3.4 Application of digestion coefficients to otoliths recovered from scats collected in the wild

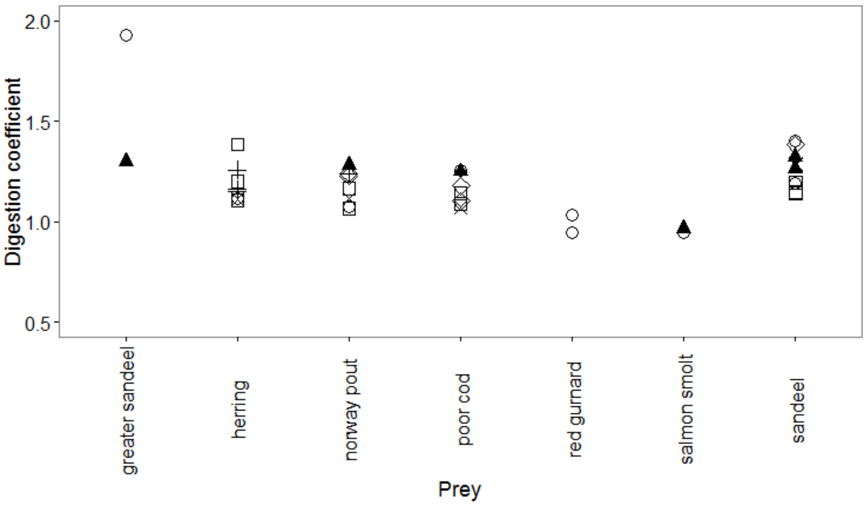
For species-specific digestion coefficients, in almost all cases the coefficient of variation (CV, Table 2.5) is smaller for OW than for OL. This is also the case for grade-specific digestion coefficients; however, Atlantic cod has notably smaller CV for OL than for OW (Table 2.5 and Table 2.6). Taking all the results into account, otolith width is generally the most appropriate measurement to use for correcting the size of otoliths recovered from scats collected in the wild. However, for cod and witch (*Glyptocephalus cynoglossus*) otolith length will be used; for cod this is the better measurement for that species (Hammond and Grellier, 2006) and for witch because no suitable regression is available for otolith width.


2.5
2.0
1.5
1.0
0.5
Digestion coefficient
cod
haddock
hake
pollock
whiting
Prey

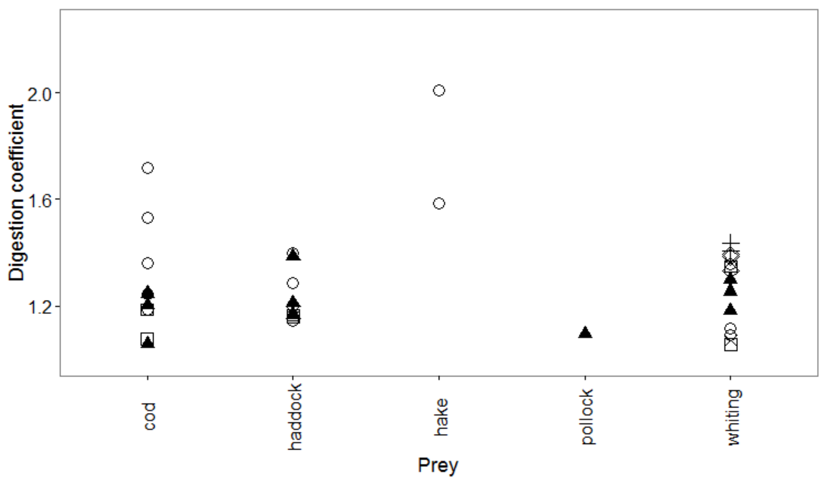
a)


1.50
1.25
1.00
0.75
0.50
Digestion coefficient
dab
lemon sole
long rough dab
plaice
witch
Prey

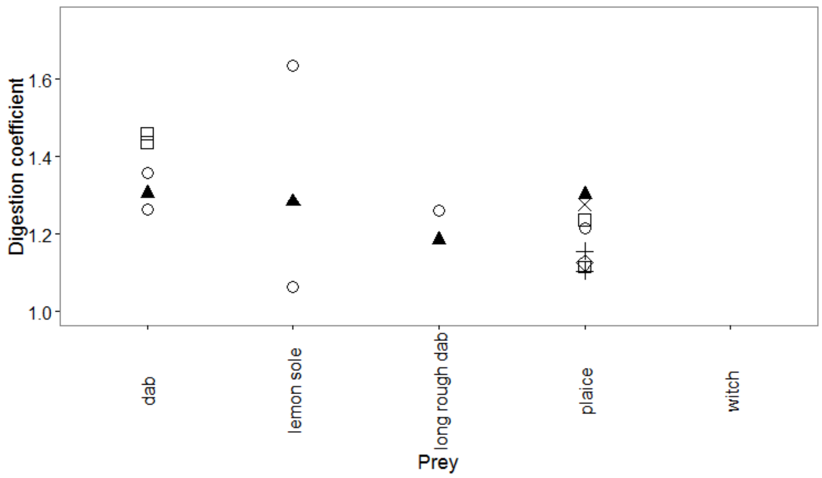
b)


2.0
1.5
1.0
0.5
Digestion coefficient
greater sandeel
herring
norway pout
poor cod
red gurnard
salmon smolt
sandeel
Prey

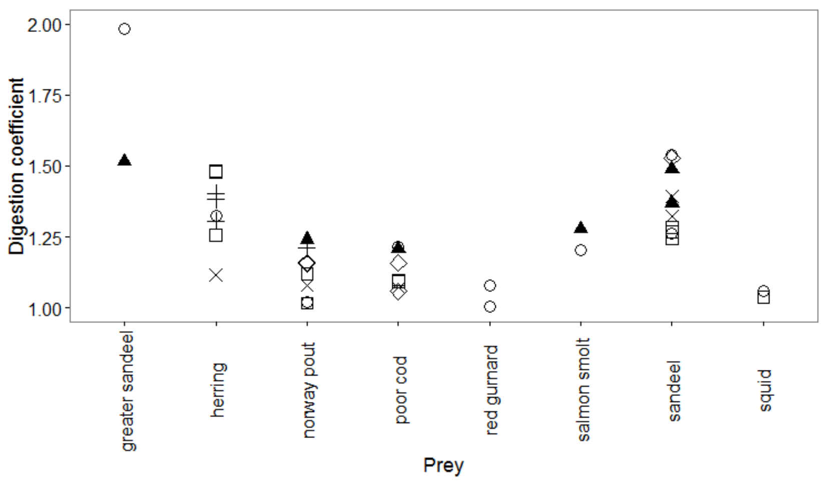
c)



d)

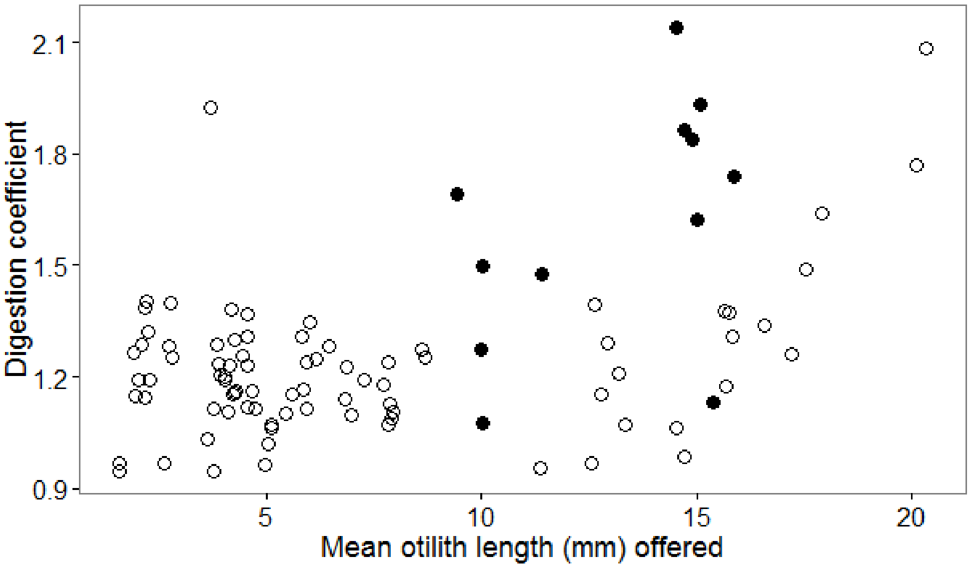


e)

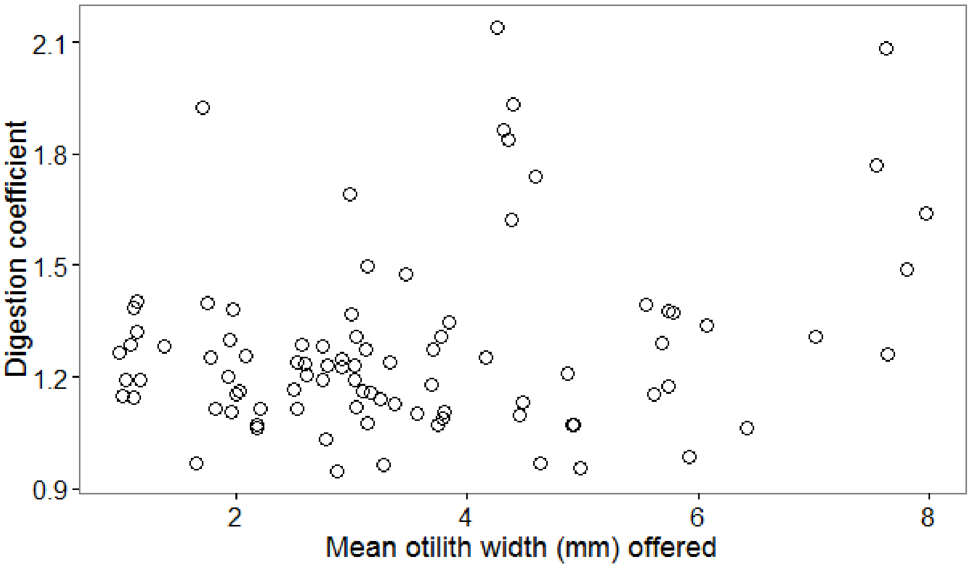


f)

Figure 2.5: Inter and intra-individual variation in digestion coefficients for each trial. Each symbol represents a different seal. Species-specific digestion coefficients by individual feeding trial are displayed for a) large gadoid otolith length b) large gadoid otolith width, c) flatfish otolith length, d) flatfish otolith width, e) other species otolith length f) other species otolith width



a)



b)

Figure 2.6: Inverse-variance weighted linear regression of digestion coefficient (DC) on mean estimated otolith length (a) and width (b). Otolith measurements are from all fish fed for all trials of all size ranges of prey. In a) whiting otolith measurements are shaded black. The relationship was slightly significant for OL however, the fragility of whiting otolith tips invalidates their use for estimating diet using OL measurements and so whiting were removed from the analysis and the relationship became non-significant. The relationship between digestion coefficient and mean estimated OW fed to seals was not significant.

Table 2.6: Grade-specific digestion coefficients (DC) calculated for harbour seals (*Phoca vitulina*).

Prey species	Grade	DC	SE	CV	Number of seals	Number of trials	No. of otoliths recovered
Otolith length							
Dab	2	1.09	0.052	0.048	1	2	28
	3	1.18	0.033	0.028	3	5	143
	4	1.45	0.075	0.052	3	4	205
Lemon sole	3	1.12	0.076	0.068	1	1	16
	4	1.45	0.137	0.095	2	3	37
Long rough dab	3	1.07	0.019	0.018	2	2	246
	4	1.48	0.047	0.032	2	2	119
Plaice	2	1.03	0.019	0.019	1	1	27
	3	1.02	0.052	0.051	2	3	85
	4	1.32	0.070	0.053	3	3	94
Witch	3	1.00	0.032	0.032	1	1	13
	4	1.10	0.036	0.032	2	2	46
All flatfish	2	1.06	0.036	0.034	2	3	55
	3	1.08	0.042	0.039	3	12	503
	4	1.36	0.073	0.054	3	14	501
Atlantic cod	2+3	1.15	0.053	0.046	3	7	30
	4	1.31	0.046	0.035	3	9	115
Haddock	2+3	1.05	0.033	0.031	3	6	25
	4	1.21	0.023	0.019	3	8	351
Hake	4	1.93	0.134	0.070	1	2	14
Whiting	2	1.07	0.034	0.031	2	2	15
	3	1.12	0.018	0.016	2	3	39
	4	1.39	0.033	0.023	2	6	403
All large gadoids	2+3	1.10	0.043	0.039	3	13	55
	4	1.46	0.059	0.040	3	25	883
Greater sandeel	4	1.68	0.043	0.026	2	2	199
Sandeel	2	0.93	0.020	0.022	2	4	344
	3	1.02	0.032	0.031	4	7	1275

	4	1.40	0.026	0.018	4	8	2526
All sandeels	2	0.93	0.020	0.022	2	4	344
	3	1.02	0.032	0.031	4	7	1275
	4	1.54	0.034	0.022	4	10	2725
Norway pout	2	0.91	0.018	0.020	2	3	60
	3	1.01	0.018	0.018	3	4	915
	4	1.22	0.011	0.009	3	4	1609
Poor cod	2	0.99	0.045	0.045	1	1	11
	3	1.11	0.024	0.022	2	3	135
	4	1.23	0.021	0.018	3	4	748
Trisopterus spp	2	0.95	0.031	0.033	2	4	71
	3	1.06	0.021	0.020	3	7	1050
	4	1.22	0.016	0.013	3	8	2357
Red gurnard	3	1.01	0.034	0.034	1	2	23
Salmon smolt	3	1.12	0.022	0.020	2	2	35
	4	1.37	0.050	0.036	2	2	73
Otolith width							
Dab	2	1.14	0.045	0.040	1	2	30
	3	1.23	0.031	0.026	3	5	148
	4	1.53	0.060	0.039	3	4	229
Lemon sole	3	1.13	0.070	0.062	1	1	16
	4	1.49	0.116	0.077	2	3	55
Long rough dab	3	1.10	0.020	0.018	2	2	251
	4	1.54	0.047	0.031	2	2	132
Plaice	2	1.03	0.014	0.014	1	1	27
	3	1.08	0.046	0.043	2	3	94
	4	1.29	0.074	0.057	3	3	100
All flatfish	2	1.09	0.030	0.027	2	3	57
	3	1.14	0.042	0.037	3	12	523
	4	1.46	0.074	0.051	3	14	566
Atlantic cod	2+3	1.16	0.059	0.051	3	7	34
	4	1.32	0.068	0.052	3	10	169
Haddock	2+3	1.07	0.035	0.033	3	6	40
	4	1.25	0.023	0.018	3	9	445

Hake	4	1.80	0.144	0.080	1	2	23
Whiting	2	1.02	0.017	0.016	3	4	29
	3	1.03	0.011	0.011	3	4	89
	4	1.22	0.021	0.017	3	8	791
All large gadoids	2+3	1.12	0.047	0.042	3	13	74
	4	1.39	0.061	0.044	3	30	1431
Greater sandeel	4	1.82	0.047	0.026	2	2	252
Sandeel	2	0.95	0.021	0.022	2	4	359
	3	1.07	0.035	0.033	4	7	1375
	4	1.54	0.028	0.018	4	8	2914
All sandeels	2	0.95	0.021	0.022	2	4	359
	3	1.11	0.060	0.054	4	9	1387
	4	1.68	0.038	0.022	4	10	3166
Norway pout	2	0.90	0.019	0.022	2	3	61
	3	0.98	0.014	0.014	3	4	944
	4	1.16	0.010	0.009	3	4	1636
Poor cod	2	0.97	0.043	0.045	1	1	11
	3	1.09	0.023	0.021	2	3	141
	4	1.19	0.021	0.018	3	4	773
Trisopterus spp	2	0.93	0.031	0.034	2	4	72
	3	1.03	0.018	0.018	3	7	1085
	4	1.18	0.016	0.013	3	8	2409
Herring	3	1.28	0.038	0.030	1	1	18
Red gurnard	3	1.02	0.029	0.028	1	2	25
	4	1.22	0.064	0.052	1	1	10
Salmon smolt	3	1.10	0.025	0.023	2	2	37
	4	1.34	0.046	0.034	2	2	95

2.3.5 Application of grade- or species- specific digestion coefficients

Using species-specific digestion coefficients over grade-specific DCs the proportion of saithe, ling and herring decreased by 4.2%, 2.9% and 1.9% respectively and the amount of haddock, mackerel, saithe/ pollack and cod increased by 2.3%, 2.3%, 1.9% and 1.2% respectively.

2.3.6 Grading standardisation between multiple personnel

There were significant differences among personnel in the grading of Norway pout, sandeel and whiting otoliths but not in the grading of plaice (Table 2.7A). In this analysis person 1 is embedded in the intercept and is the standard against which the others are compared. In three species (Norway pout, sandeel and whiting) all the coefficient values are positive indicating that person 1 tended to assign lower grades (more grade twos assigned than any other person). Grading of whiting and Norway pout was most different between the individuals and person 1 ($P \leq 0.05$ Table 2.7B).

Table 2.7: Summary of the linear model results for examining variation in the grading of otoliths across laboratory personnel. Table 7A shows the analysis of variance. Table 7B shows the coefficient estimates and their significance.

A)

Species	**Df**	**Sum sq**	**Mean Sq**	**F value**	**P**	
Norway pout	3	5.01	1.67	5.49	<0.05	*
Sandeel	3	2.9	0.97	3.75	<0.05	*
Plaice	3	0.49	0.16	1.45	0.22	
Whiting	3	3.06	1.02	3.89	<0.05	*

B)

	Estimate	SE	t value	P	
Norway Pout					
Intercept	3.49	0.06	63.29		
Person 2	0.31	0.78	3.98	<0.05	*
Person 3	0.17	0.78	2.18	<0.05	*
Person 4	0.21	0.78	2.69	<0.05	*
Sandeel					
Intercept	3.53	0.05	69.52		
Person 2	0.23	0.07	3.2	<0.05	*
Person 3	0.16	0.07	2.23	<0.05	*
Person 4	0.09	0.07	1.25	0.21	
Plaice					
Intercept	3.89	0.03	116.7		
Person 2	-0.04	0.05	-0.84	0.40	
Person 3	-0.06	0.05	-1.27	0.20	
Person 4	0.03	0.05	0.64	0.53	
Whiting					
Intercept	3.61	0.05	70.48		
Person 2	0.21	0.07	2.9	<0.05	*
Person 3	0.18	0.07	2.49	<0.05	*
Person 4	0.21	0.07	2.9	<0.05	*

2.4 Discussion

In this study I quantified the passage, recovery and digestion of otoliths and beaks of typical prey of north eastern European harbour seal diet. The six seals used in this study were wild caught and kept in captivity for the duration of the experiments before being released at their capture location. The seals were generally willing to eat a varied diet; however, some individuals were more selective in their feeding than others. This suggests that some specialisation in prey selection may occur within what is usually considered to be a generalist predator species.

Several studies report that harbour seals target locally abundant prey species (Pierce *et al.*, 1991c; Thompson *et al.*, 1997; Brown *et al.*, 2001). However, variation in harbour seal foraging behaviour has been shown at a regional level around Britain (Sharples *et al.*, 2012) and there is some evidence for individual variation in foraging strategy. Thompson and Miller (1990) showed that two individuals returned regularly to bathymetrically distinct areas in the Moray Firth and individual harbour seals tagged in the Eden estuary, St Andrews Bay regularly returned to particular foraging sites (SMRU, unpublished telemetry data). Furthermore, Tollit *et al.*, (1998) found that local geographical variations in the diet of harbour seals in the Moray Firth were related to local differences in foraging habitats. Specialisation in foraging behaviour has also been observed in grey seals (*Halichoerus grypus*) tracked using Argos satellite relay dataloggers, with individuals showing predictability in foraging trips to localised off-shore areas with characteristic sediment types (McConnell *et al.*, 1999). The individual foraging behaviours exhibited by seals around Britain have not been linked to individual preferences in diet and the choice to feed or not exhibited by captive seals must be interpreted with caution.

The method by which seals consumed prey in the experiments varied depending on the size of prey fed to the seals. Small prey were typically ingested underwater while larger prey were brought to the surface and some very large prey were left untouched by the seals. I observed larger prey (Atlantic salmon, Atlantic cod and flatfish) being ripped into small pieces before ingestion and saw seals struggle without success to consume whole the heads of large prey (Atlantic salmon and cod). Some heads were torn into pieces during consumption and otoliths possibly crushed and in the wild this could also lead to otoliths being lost. The non-consumption of very large prey and the breaking up of large or wide prey during feeding is likely a morphological limitation linked to mouth-gape size or, as in odontocetes, the size of the pharynx limiting the largest size of prey that can be consumed whole (MacLeod *et al.*, 2007).

Whether harbour seals in the wild attempt to consume very large prey is unknown. The estimated sizes of harbour seal prey in the Wash were <30 cm (Hall *et al.*, 1998). The distribution of fish size estimated from prey remains from the 2010-12 scat collections provide further information on this (Chapter 3). However, if some large prey are eaten in the wild but the heads are not consumed or are broken up; otoliths will be lost, resulting in some bias in estimates of diet composition and prey consumption. Assessment of the magnitude of any potential bias would likely require additional approaches.

For example, in a study of the diet of Steller sea lions (*Eumetopias jubatus*) Tollit *et al.*, (2009) compared DNA analysis of prey soft parts with morphological analyses of prey hard parts and found that 35% of prey were undetected by hard parts. These were mainly large species (*Salmonidae*), cartilaginous fishes (*Elasmobranchii*), soft bodied prey (*Cephalopoda*) and flounders (*Pleuronectidae*). Similarly, in a study of lactating Antarctic fur seals (*Arctocephalus gazella*) Casper *et al.*, (2007a) found that estimates of the number of animals consuming mackerel icefish (*Champsocephalus gunnari*) would have been underestimated by around 26% using either DNA-based or prey hard remains methods alone. However, in the study by Tollit *et al.*, (2009) diet composition from both techniques combined did not differ significantly from hard-part identification alone. This suggests that major dietary components are not missed by hard-part analysis, however differences may exist in relative diet contributions. Alternative diet methods were not used as part of this study. The potential of combining techniques to improve insight into trophic interactions for otariids is clear (Casper *et al.*, 2007a; Deagle *et al.*, 2007; Tollit *et al.*, 2009), however in the study of phocid diet a robust approach to improving diet estimates using matched techniques has not been presented and the recovery of prey hard parts to estimate diet remains the most common and widely used approach

Single-species meals of the major prey of British harbour seals were fed to estimate recovery rates, passage rates and digestion coefficients. Within-species differences in these parameters related to the size of prey consumed have been shown for both harbour and grey seals (Tollit *et al.*, 1997b; Grellier and Hammond, 2006); however, in this study there was no significant difference in DC as a function of otolith size. Furthermore, it is not clear how size specific DCs might be applied to otoliths recovered from scats collected in the wild. We conducted experiments with a range of prey sizes representative of the diet of wild harbour seals and have minimised potential bias by combining values from trials by individual, then by prey species and finally by prey grouping.

2.4.1 Recovery rates

In this study, recovery rates ranged from 1.02 (Norway pout) to 0.27 (sandeel). Recovery rates greater than 1 should be impossible. However, to reflect the ingestion of prey in the wild the majority of the fish fed to the seals was not gutted and so the otoliths of some small fish recovered in the scats are actually from the stomachs of the larger fish that were fed; so-called secondary prey/ingestion.

Norway pout, poor cod and haddock had recovery rates slightly greater than 1, reflecting the presence of otoliths in the diet through secondary ingestion. Simple calculations based on the otoliths found in grey seal scats and stomach contents of large gadoids (Atlantic cod, haddock, whiting and saithe *Pollachius virens*) showed that the contribution of secondary prey to the estimates of diet composition is much less than 1% (Hammond and Grellier, 2006). *Crustacea* are often found in wild scats but there is no evidence that harbour seals target them as prey and we assume that they are secondary prey. This is supported by the result that crustacean remains were present in 50% of pool drains although they were never specifically fed.

Previous studies have shown that large otoliths are less likely to be completely digested (Tollit *et al.*, 1997b; Tollit *et al.*, 2003; Grellier and Hammond, 2005; Grellier and Hammond, 2006) and, as expected, recovery rates for harbour seals were greater for prey species with large, robust otoliths. Species-specific differences in recovery rates are important and if not incorporated into diet composition estimates the estimated contribution of prey species to the diet may be significantly biased and the numerical importance of small fish is likely to be underestimated (Bowen, 2000).

The recovery rate for squid beaks was higher in this study (0.837 SE=0.102) than the 0.437, SD=0.488 and 0.704 recovery rates reported for harbour seals by Harvey (1989) and Tollit *et al.*, (1997b), respectively. Recovery rate of beaks from squid (*Loligo opalescens*) fed to Pacific harbour seals *P. vitulina richardii* of 0.895, SD=0.155 (Phillips and Harvey, 2009) and *Loligo forbesii* fed to grey seals of 0.942, SE=0.021 (Grellier and Hammond, 2006) were higher than reported in this study.

Low recovery rate of prey remains was recorded in *Arctocephalus* spp. that were fed mixed species meals and where faecal matter ‘at sea’ in the enclosure pools was not collected (Casper *et al.*, 2006). Our study does not take into consideration possible differences in defecation rates on land and in the water - all faeces and prey remains were collected daily.

Recovery of otoliths from multiple prey species in harbour seal scats collected in the wild is common. In this study only single species meals were fed to seals and the effect of meal composition warrants further investigation.

2.4.2 Passage rates

For harbour seals, the majority of otoliths and beaks were passed within 2-3 days and, despite some species-specific differences, these results are comparable with those from studies of grey seals (Grellier and Hammond, 2006) and Pacific harbour seals (Phillips and Harvey, 2009). Harbour seal diet composition estimated using scat analysis is thus likely to be representative of the true diet of this species which has average foraging trip durations between 1 day in the Thames, England and 4.5 days in the Moray Firth, Scotland (Sharples *et al.*, 2012).

It is likely that passage rate is affected by food intake rate, meal composition and the activity state of a seal and these are unlikely to be similar in wild and captive seals (Pierce *et al.*, 1991a). Furthermore, grey seals can delay the onset of food processing (digestion) by up to 11 hours, as observed by a delayed increase in metabolic rate (Sparling *et al.*, 2007). Harbour seals face similar competing physiological processes for maximising diving/foraging efficiency and for food processing, further work on harbour seals that takes into account some of these complexities would be interesting.

2.4.3 Species-specific digestion coefficients

In agreement with other studies, I have shown that the amount by which an otolith is digested is related to the species of the fish fed (Murie and Lavigne, 1986; Tollit *et al.*, 1997b; Grellier and Hammond, 2006). Digestion coefficients were calculated based on otolith length and width for all fish species except for witch for which no suitable OW regression is available. Digestion coefficients for particular size ranges of prey have not been calculated. However, by feeding prey of a size range representative of what seals eat in the wild, I have incorporated prey size variability into the final species-specific digestion coefficients. After the removal of whiting, which are poorly described by otolith length there was no significant relationship between digestion coefficients and otolith size. Furthermore, no significant relationship existed for otolith width.

2.4.4 Grade-specific digestion coefficients

The use of grade specific digestion coefficients can help to reduce intra-specific variation and potential bias in correction for partial digestion. Sources of variation include the size, frequency, and species composition of meals and activity level of the seals (Tollit *et al.*, 1997b; Marcus *et al.*, 1998). I used standard methods to produce these grade-specific digestion coefficients by using external morphological features to classify the degree of digestion (Tollit *et al.*, 1997b; Grellier and Hammond, 2006). However, I extended the standard range of three grade/wear classes to four in an attempt to reduce variability and bias because average digestion rates may be artificially high in captive seals (Thompson *et al.*, 1991b; Tollit *et al.*, 1997b; Grellier and Hammond, 2006).

Grade-specific digestion coefficients less than 1 were calculated for grade 2 sandeel, Norway pout and poor cod OL and OW and for grade 3 Norway pout OW. These species are shown to be major components of the diet of wild harbour seals (Chapter 3). Because it is not possible for otoliths to increase in size post digestion, this raises a number of questions in relation to the experiments and analysis.

First, were all otoliths and beaks correctly measured? Some measurement error could have occurred but there is no evidence that this could have led to a tendency for digestion coefficients to be biased in this way.

Second, were the regression equations used to estimate uneaten otolith size appropriate for the prey size-range fed? The data used to calculate regressions for fish prey were from fish of a size range similar to those fed in all trials. Nevertheless, these regressions are from the published literature and not from our studies (excepting the regression for salmon smolts), and so could potentially have led to bias in some cases.

Third, are smaller otoliths eroded and completely digested at greater rates than larger otoliths? Intuitively, smaller otoliths would be more likely to digest completely than larger otoliths. Harvey (1989) suggested that otoliths which are small, thin or encased in a thinner cranium or optic capsule may be more susceptible to complete digestion. If smaller otoliths do have a higher probability of being completely digested, the mean undigested size of those remaining will be larger than the mean size fed and could lead to a bias in digestion coefficient estimation. However, preliminary exploratory analysis has not revealed any evidence that this has led to bias; otoliths which are larger do not have significantly larger digestion coefficients than smaller otoliths (Figure 2.6).

2.4.5 Application of grade- or species- specific digestion coefficients

Although the application of grade-specific digestion coefficients should generally reduce bias in estimates of prey size, in an exploration of possible bias in harbour seal diet, using overall species-specific rather than grade-specific digestion coefficients resulted in only a very small bias in diet in the autumn of 2010 in the West coast – north region. A small bias was also found comparing diet estimates using overall species-specific rather than grade-specific digestion coefficients for grey seals in the first quarter of 2002 in Orkney. The amount of sandeels in the diet increased by around 4% and the amount of cod decreased by around 5% (Grellier and Hammond, 2006). The application of grade-specific digestion coefficients and the use of external morphological features to grade the degree of digestion of otoliths improves the estimates of prey biomass consumed (Tollit *et al.*, 1997b; Tollit *et al.*, 2004b; Grellier and Hammond, 2006) and will be used in all analyses of wild harbour seal diet composition in this thesis (Chapters 3, 4 and 5).

2.4.6 Comparison with other studies

This study followed the methods of Grellier and Hammond (2006) and therefore direct comparison with grey seal recovery rate, digestion coefficient and passage rate estimates are possible. I also compared our results to those for harbour seals from Tollit *et al.*, (1997b) although the experimental feeding method was different and the method of otolith delivery has been shown to affect digestion (Grellier and Hammond, 2005) and, where appropriate, to results for Pacific harbour seals (Phillips and Harvey, 2009).

Species composition of meals is thought to influence passage rates of prey remains through a seal's gut (Prime and Hammond, 1987; Bowen, 2000; Tollit *et al.*, 2004b; Casper *et al.*, 2006; Phillips and Harvey, 2009). However, the majority of otoliths and beaks were passed within 2-3 days regardless of prey species composition of the individual single species meals. This is similar to findings for grey seals (Grellier and Hammond, 2006) and Pacific harbour seals (Phillips and Harvey, 2009).

Recovery rates are comparable with grey seal estimates (Grellier and Hammond, 2006) although a lower proportion of lemon sole otoliths were recovered in this study. Our recovery rates are similar to those for harbour seals for cod but were higher than those previously reported for herring, whiting, lemon sole, plaice, sandeel and squid (Tollit *et al.*, 1997b). Although the feeding method differed between the two harbour seal studies the results are comparable as Grellier and Hammond (2005) showed that recovery rates are not affected by feeding method.

Digestion coefficients have previously been reported for seven harbour seal prey species (Tollit *et al.*, 1997b). Our mean species-specific digestion coefficients were similar to these results for plaice and lemon sole but smaller for cod and whiting (OW) and larger for herring and sandeel (*A. marinus*, Tollit *et al.*, 1997b). Smaller digestion coefficients were expected in this study compared to Tollit *et al.*, (1997b) due to differences in the experimental protocol. Otoliths in this study were fed in situ in whole prey, while Tollit *et al.*, (1997b) used herring as a carrier species to present the heads of fish and buccal masses of cephalopods. Feeding otoliths in situ better imitates feeding in the wild and Grellier and Hammond (2006) concluded that the application of digestion coefficients derived from carrier experiments resulted in an overestimation of fish size.

The harbour seal digestion coefficients estimated in our study are generally smaller than those published for grey seals (Grellier and Hammond, 2006). However, those for poor cod, whiting (OW), herring, dab and lemon sole are similar for both species. Digestion coefficient estimates for hake are larger for harbour seals but the sample size is very small compared to the grey seal study.

The grading systems used to classify grade-specific digestion coefficients across harbour and grey seal studies were not identical but they are similar enough to allow comparison of results. Grade-specific digestion coefficients in this study are smaller than those previously reported for both harbour and grey seals. Differences in feeding method may explain the higher levels of otolith digestion reported by Tollit *et al.*, (1997b).

Smaller digestion coefficients than those estimated for grey seals might be expected if the otoliths pass more quickly through the gut of harbour seals; however, I have shown the passage rates of both species to be similar. Grey seals are larger than harbour seals and have been shown to be able to delay food processing in situations where it is physiologically advantageous, such as during active foraging (Sparling *et al.*, 2007). Differences in physiology and food processing strategies between these species may account for differences in rates of otolith erosion.

The digestion correction factors estimated in this Chapter allow robust estimation of the number and size of prey consumed by harbour seals based on the recovery of otoliths and beaks from scats collected in the wild. They will be used to describe regional and temporal variation in the diet of Scottish harbour seals (Chapter 3) and investigate overlap in diet composition between harbour and grey seals (Chapter 5) as a possible contributing factor to the decline of harbour seals in Scottish waters over the last decade (Lonergan *et al.*, 2007).

2.4.7 Grading comparison between multiple personnel

As expected there were some differences in the grading of otoliths among individuals working in the laboratory. This is despite consistent levels of training, access to the same reference materials and a collaborative work atmosphere where we engaged with others when unsure about a species and grading.

These differences in grading are largest for otoliths which have more morphological patterning, *e.g,.* whiting, for which it can be difficult to discern the levels of erosion and smallest for otoliths with simple morphology, such as plaice and sandeel. The strongest differences were seen between person 1, the longest running member of the team, and person 2, who joined the group in the last 6 months of work and was the least experienced grader. Examination of the data revealed that person 2 was less likely to use grade 2. The least difference was seen between person 1 and person 3, both of whom had worked on the project for the longest time and so were already experienced graders at the time the comparison tests were conducted. The two individuals who did not participate in the standardisation checks had left their university positions after working within the group for more than 1 year and it was not possible to check their work in this way.

Though a visual and annotated guide was available to all members of the laboratory team at all times the grading of otoliths is partially subjective and some differences are to be expected. In this study, all personnel worked on batches of otoliths chosen randomly from across the experiments (this Chapter) and the scats collected from haul-out sites (Chapters 3, 4 and 5). Consequently, no individual worked on material from a single region and/or season and so any bias that may have been introduced by grader differences applies equally to all region/ season combinations and so comparisons among regions and seasons should not be affected.

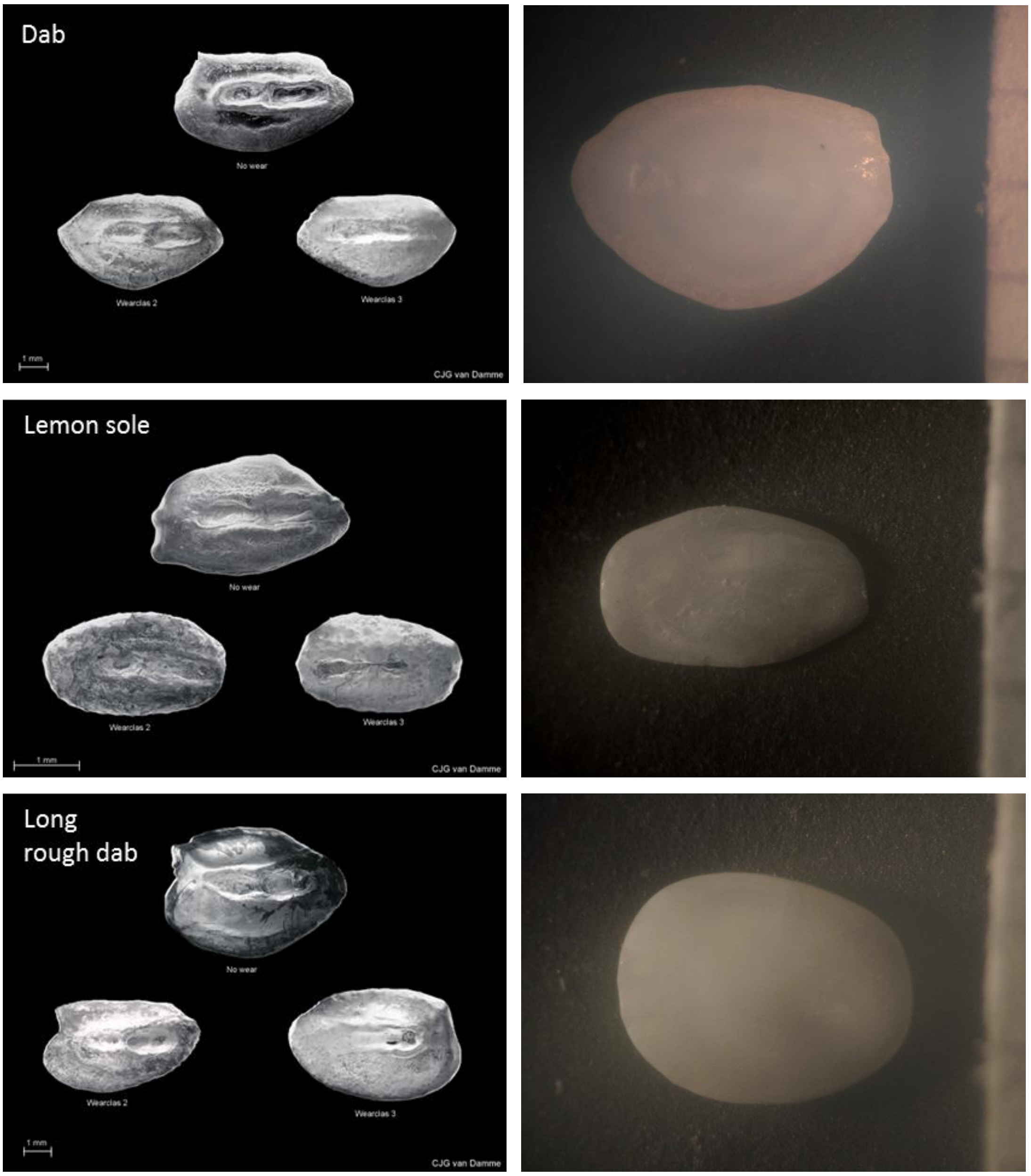
The magnitude of the bias introduced by the differences in grading has not been explored. However, when ignoring grades completely and using only species-specific digestion coefficients the changes observed in estimates of prey composition were minor (2.3.5 and 2.4.5). Differences in estimated prey composition as a result of variation in grading are therefore expected to be smaller than those presented in 2.3.5 and introduced bias is likely to be small.

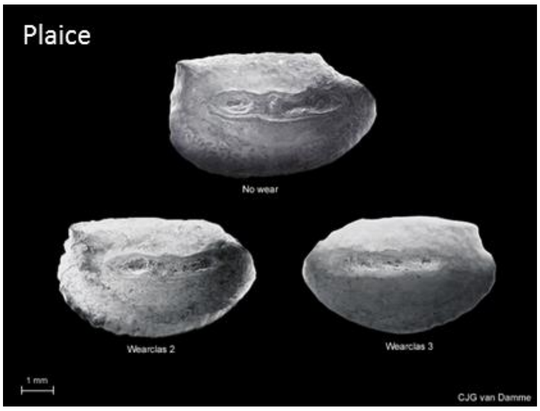
In the future, to account for any bias introduced by variation among multiple graders, grader-specific correction factors could be developed. This may be particularly relevant when comparing long term or geographically distinct projects.

2.4.8 Final Remarks

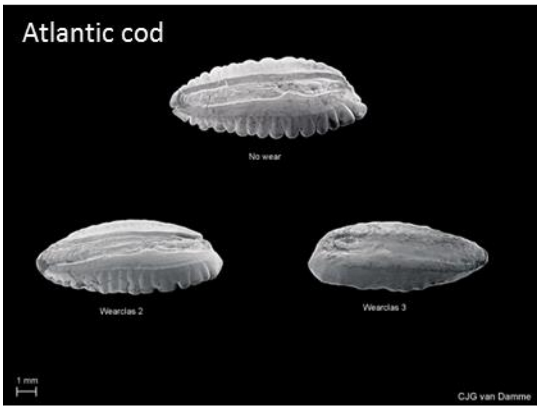
Diet composition estimates for pinnipeds are widely conducted using prey hard remains recovered from faeces. To estimate the size and number of prey consumed accurately, digestion correction factors must be applied to measurements and counts of fish otoliths and cephalopod beaks. 100 whole prey feeding trials were conducted with six harbour seals (*Phoca vitulina*) and 18 prey species to derive estimates of digestion coefficients (DC; accounting for partial digestion using otolith width (OW) or length (OL) and recovery rates (RR) accounting for complete digestion. Differences found in partial and complete digestion rates among prey species and between harbour and grey seals highlight the importance of applying predator- and prey-specific digestion correction factors when reconstructing diet.

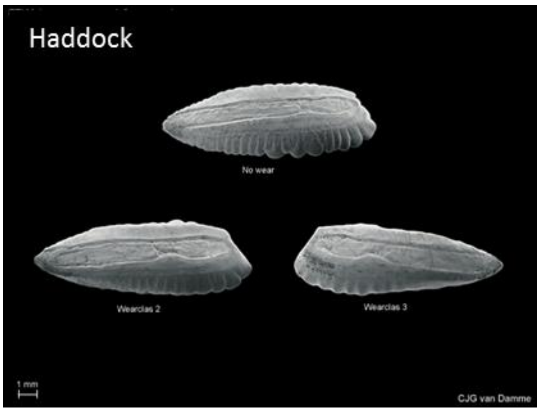
Appendix 2.1: Images in the left column of pristine (grade 1, upper image), moderately digested (grade 2, lower left image) and considerably digested (grade 3, lower right image) otoliths and in the right column severely digested (grade 4) otoliths. These images were used as a guide to classify otoliths by the level of digestion. No wear classes were listed for witch, hake, greater sandeel or Atlantic salmon and for these species we used wear classes for species with similar otoliths (long rough dab, whiting, sandeel and brown trout, respectively). Images of grade 1, 2 and 3 otoliths taken from Leopold *et al.*, (2001).

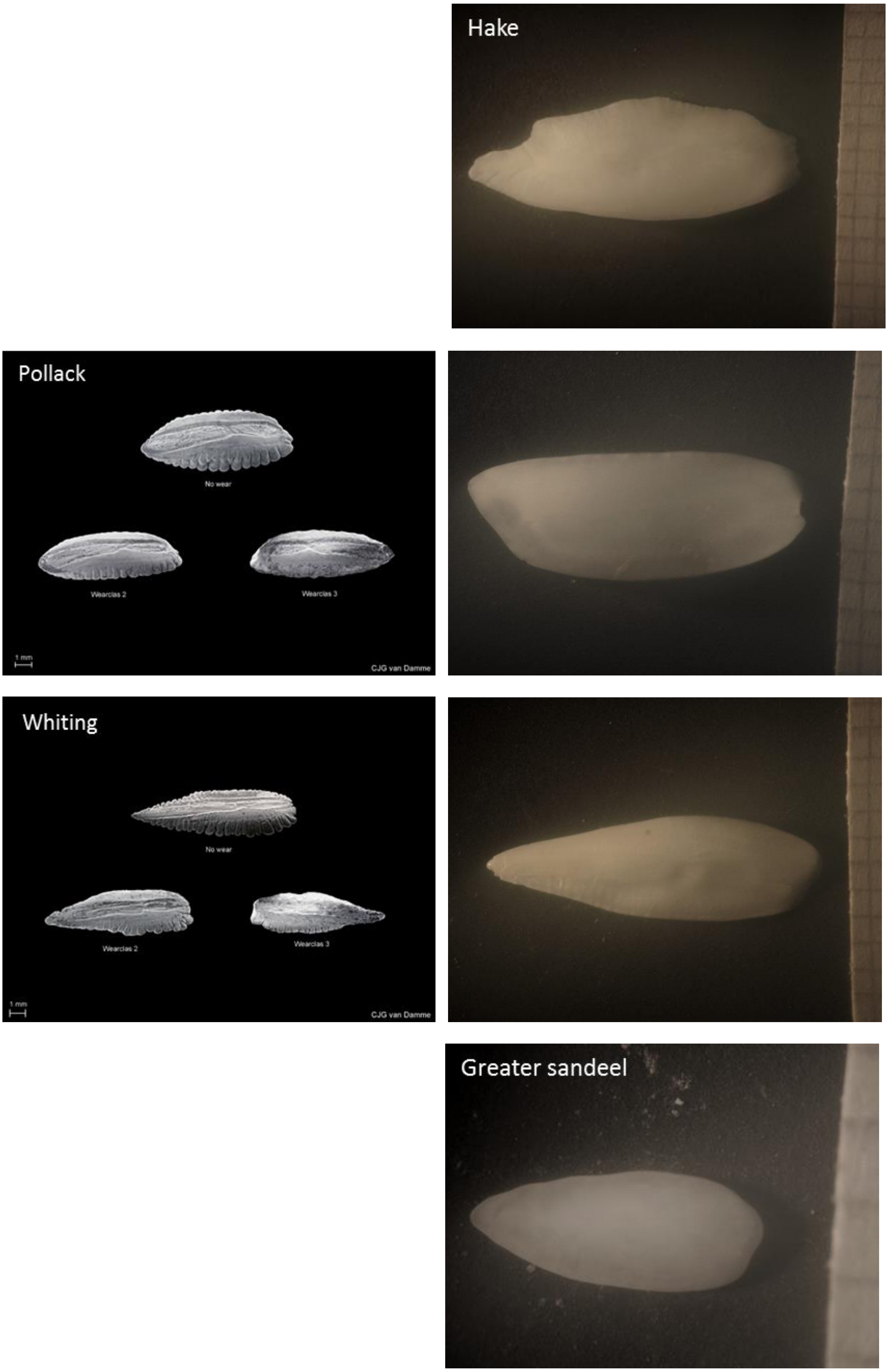


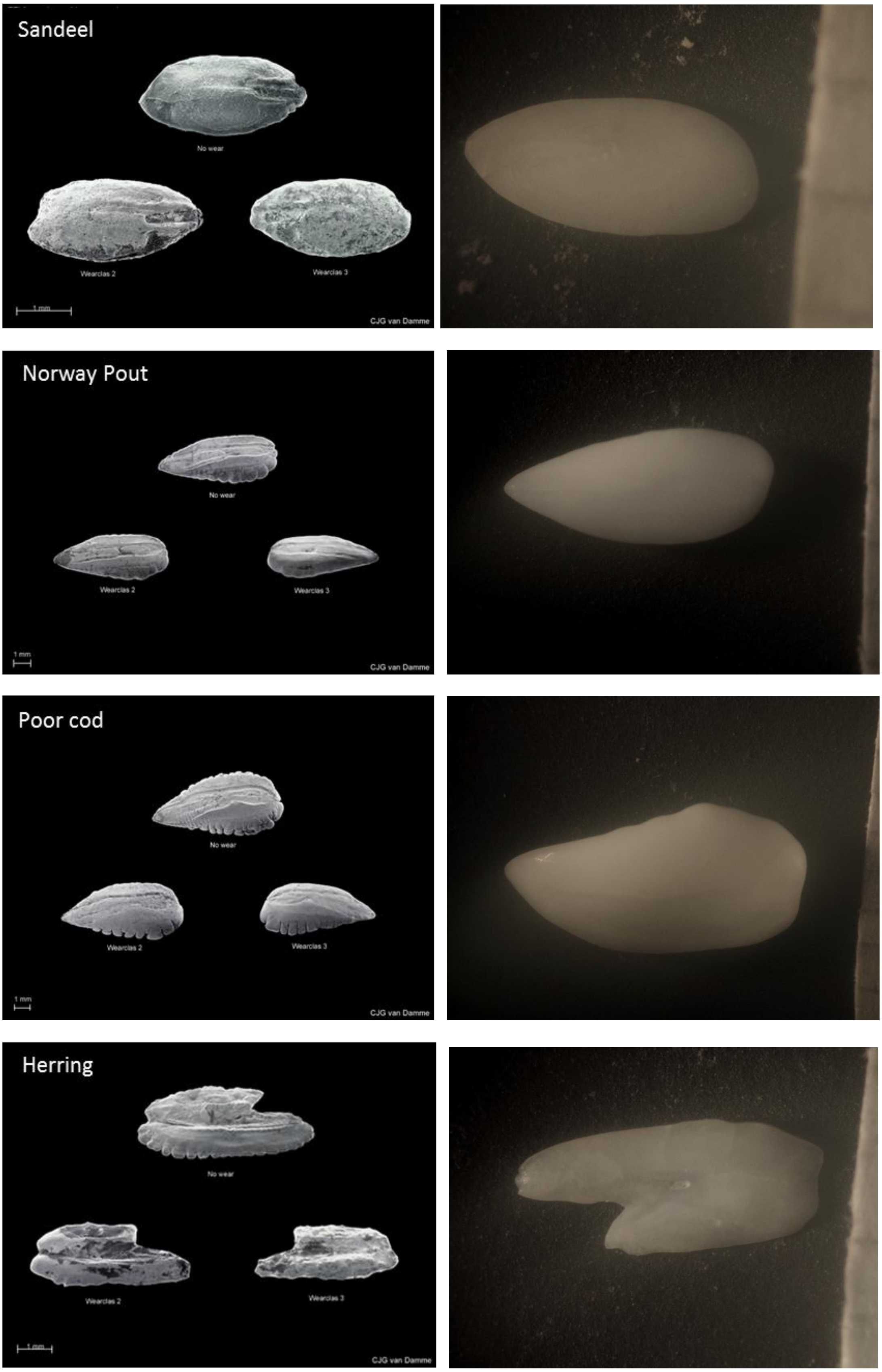

Plaice
No wear
Wearclas 2
Wearclas 3
1 mm
CJG van Damme

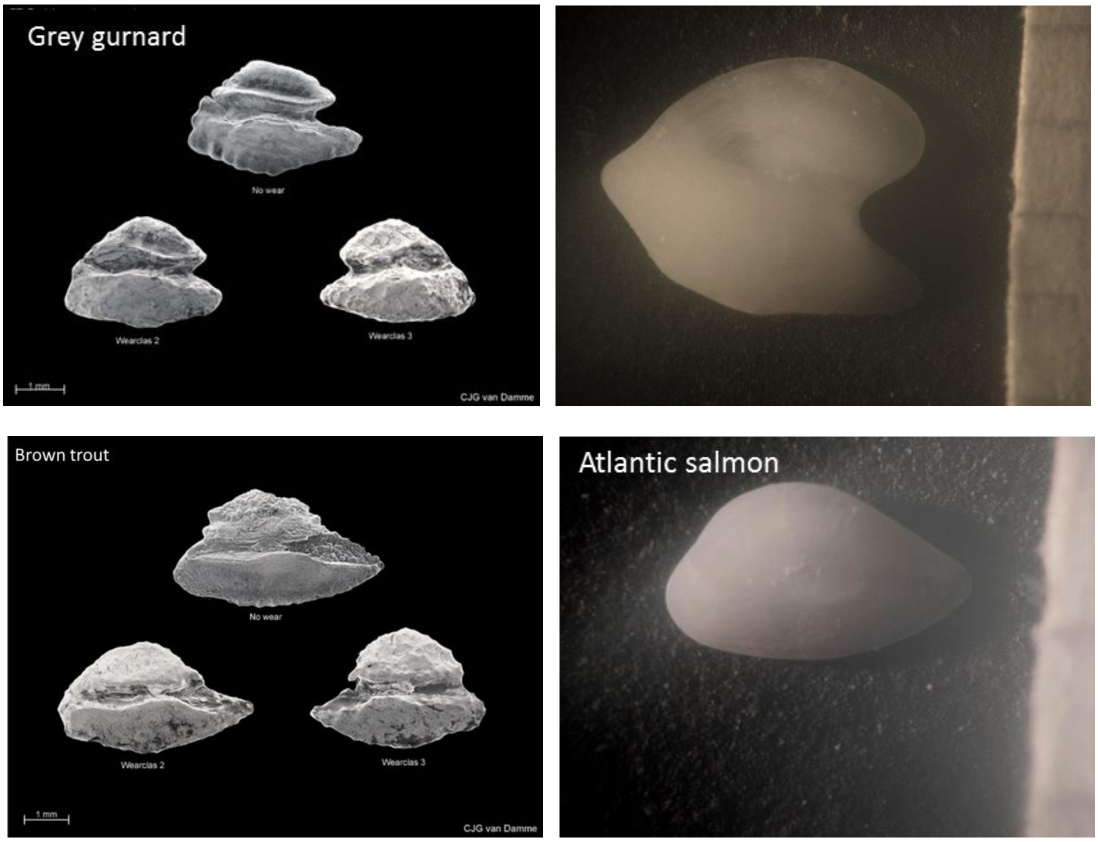

Witch


Atlantic cod
No wear
Wearclas 2
Wearclas 3
1 mm
CJG van Damme


Haddock
No wear
Wearclas 2
Wearclas 3
1 mm
CJG van Damme


Hake
Pollack
No wear
Wearclas 2
Wearclas 3
1 mm
CJG van Damme
Whiting
No wear
Wearclas 2
Wearclas 3
1 mm
CJG van Damme
Greater sandeel


Sandeel
No wear
Wearclas 2
Wearclas 3
1 mm
CJG van Damme
Norway Pout
No wear
Wearclas 2
Wearclas 3
1 mm
CJG van Damme
Poor cod
No wear
Wearclas 2
Wearclas 3
1 mm
CJG van Damme
Herring
No wear
Wearclas 2
Wearclas 3
1 mm
CJG van Damme


Grey gurnard
No wear
Wearclas 2
Wearclas 3
1 mm
CJG van Damme
Brown trout
No wear
Wearclas 2
Wearclas 3
1 mm
CJG van Damme
Atlantic salmon

Appendix 2.2: Prey-specific recovery rates (RR) with standard errors (SE) and number correction factors (NCF) from each trial were averaged to give mean values for each seal, averaged across seals to give mean values for each prey species and averaged across prey species to give mean values for each prey group (fl = flatfish, lg = large gadoid, oth = other spp., se = sandeels, tc = *Trisopterus* spp.).

Trial							Seal					Prey & Group			
seal	**prey**	**Gp**	**trial**	**RR**	**SE**	**NCF**	**seal**	**prey**	**RR**	**SE**	**NCF**	**prey**	**RR**	**SE**	**NCF**
D	Dab	fl	48	0.68	0.04	1.48	D	cod	0.79	0.15	1.27	dab	0.76	0.04	1.38
D	Dab	fl	59	0.68	0.05	1.47	D	plaice	0.86	0.03	1.18	lemon sole	0.47	0.06	2.44
D	plaice	fl	41	0.76	0.04	1.32	D	dab	0.68	0.05	1.48	LR dab	0.89	0.02	1.13
D	plaice	fl	54	0.97	0.02	1.04	D	haddock	1.03	0.00	0.97	plaice	0.85	0.03	1.22
D	Cod	lg	50	0.83	0.15	1.20	D	whiting	0.99	0.01	1.01	witch	0.98	0.02	1.03
D	Cod	lg	55	0.75	0.15	1.33	D	herring	0.31	0.06	3.49	cod	0.88	0.09	1.20
D	haddock	lg	43	1.06	NA	0.94	D	squid	0.86	0.05	1.16	haddock	1.01	0.00	1.00
D	haddock	lg	60	1.00	0.00	1.00	D	sandeel	0.66	0.01	1.50	hake	0.89	0.05	1.14
D	whiting	lg	47	1.00	0.00	1.00	D	norway pout	0.97	0.01	1.03	pollock	1.00	0.00	1.00
D	whiting	lg	53	0.98	0.02	1.02	D	poor cod	1.03	0.01	0.98	whiting	0.94	0.03	1.07
D	herring	oth	46	0.21	0.05	4.77						herring	0.43	0.07	2.70
D	herring	oth	52	0.43	0.06	2.31						red gurnard	0.58	0.08	1.74
D	herring	oth	57	0.30	0.06	3.39						salmon smolt	0.31	0.03	3.31
D	squid	oth	44	0.86	0.05	1.16						squid	0.84	0.04	1.23
D	sandeel	se	42	0.66	0.01	1.52						G. sandeel	0.60	0.02	2.42
D	sandeel	se	49	0.66	0.01	1.52						sandeel	0.39	0.01	3.70

D	sandeel	se	56	0.68	0.01	1.47
D	norway pout	tc	40	0.95	0.01	1.05
D	norway pout	tc	58	1.00	0.00	1.00
D	poor cod	tc	45	0.98	0.01	1.02
D	poor cod	tc	51	1.07	NA	0.93
E	dab	fl	61	0.97	0.03	1.03
E	dab	fl	88	0.52	0.04	1.92
E	lemon sole	fl	80	0.46	0.07	2.17
E	lemon sole	fl	124	0.23	0.04	4.26
E	LR dab	fl	83	0.82	0.02	1.21
E	plaice	fl	91	0.81	0.04	1.23
E	witch	fl	76	0.95	0.03	1.05
E	cod	lg	69	0.50	0.25	2.00
E	cod	lg	74	0.50	0.25	2.00
E	cod	lg	77	1.00	0.00	1.00
E	cod	lg	89	1.00	0.00	1.00
E	cod	lg	120	0.95	0.03	1.05
E	cod	lg	125	1.00	0.00	1.00
E	haddock	lg	71	1.00	0.00	1.00
E	haddock	lg	81	1.00	0.00	1.00
E	haddock	lg	90	1.00	0.00	1.00

E	cod	0.83	0.09	1.34
E	lemon sole	0.35	0.06	3.21
E	LR dab	0.82	0.02	1.21
E	plaice	0.81	0.04	1.23
E	witch	0.95	0.03	1.05
E	dab	0.74	0.04	1.48
E	haddock	1.00	0.00	1.00
E	hake	0.89	0.05	1.14
E	whiting	0.98	0.01	1.02
E	herring	0.64	0.07	1.56
E	red gurnard	0.58	0.08	1.74
E	salmon smolt	0.34	0.03	2.95
E	squid	1.00	0.00	1.00
E	G. sandeel	0.27	0.02	3.77
E	sandeel	0.17	0.01	6.47
E	norway pout	0.99	0.00	1.01

norway pout	1.03	0.00	0.98
poor cod	1.01	0.00	0.99

Group	**RR**	**SE**	**NCF**
Flatfish	0.79	0.03	1.44
Lg. gadoids	0.94	0.03	1.08
Other	0.53	0.07	2.25
Sandeels	0.49	0.02	3.06
Trisopterus	1.02	0.00	0.99

E	haddock	lg	126	1.00	0.00	1.00	E	poor cod	1.00	0.00	1.00
E	hake	lg	84	1.00	0.00	1.00					
E	hake	lg	123	0.79	0.11	1.27					
E	whiting	lg	66	0.98	0.01	1.03					
E	whiting	lg	75	0.96	0.01	1.04					
E	whiting	lg	86	1.00	0.00	1.00					
E	herring	oth	78	0.64	0.07	1.56					
E	red gurnard	oth	79	0.64	0.08	1.57					
E	red gurnard	oth	85	0.52	0.07	1.92					
E	salmon smolt	oth	122	0.34	0.03	2.95					
E	squid	oth	36	1.00	0.00	1.00					
E	G. sandeel	se	121	0.27	0.02	3.77					
E	sandeel	se	65	0.12	0.01	8.29					
E	sandeel	se	73	0.21	0.01	4.65					
E	norway pout	tc	64	0.99	0.00	1.01					
E	poor cod	tc	72	1.00	0.00	1.00					
F	dab	fl	111	0.84	0.03	1.18	F	cod	1.03	0.01	1.00
F	lemon sole	fl	92	0.60	0.06	1.67	F	lemon sole	0.60	0.06	1.67
F	LR dab	fl	107	0.95	0.02	1.05	F	LR dab	0.95	0.02	1.05
F	plaice	fl	116	0.88	0.04	1.14	F	plaice	0.88	0.04	1.14
F	witch	fl	97	1.00	0.00	1.00	F	witch	1.00	0.00	1.00
F	cod	lg	93	1.21	NA	0.82	F	dab	0.84	0.03	1.18

F	cod	lg	104	1.06	NA	0.95
F	cod	lg	110	0.81	0.04	1.24
F	haddock	lg	98	0.96	0.04	1.04
F	haddock	lg	108	1.00	0.00	1.00
F	haddock	lg	117	0.99	0.01	1.01
F	pollock	lg	119	1.00	0.00	1.00
F	whiting	lg	100	0.93	0.02	1.07
F	whiting	lg	105	1.06	NA	0.94
F	whiting	lg	114	0.95	0.03	1.05
F	salmon smolt	oth	118	0.27	0.03	3.67
F	squid	oth	37	0.65	0.08	1.54
F	G. sandeel	se	113	0.93	0.02	1.07
F	sandeel	se	99	0.25	0.01	4.07
F	sandeel	se	106	0.23	0.01	4.30
F	norway pout	tc	95	1.20	NA	0.83
F	poor cod	tc	103	0.99	0.00	1.01
Q	plaice	fl	33	1.00	0.00	1.00
Q	plaice	fl	37	0.94	0.03	1.07
Q	whiting	lg	32	1.00	0.00	1.00
Q	whiting	lg	38	0.88	0.02	1.13
Q	herring	oth	31	0.63	0.09	1.60

F	haddock	0.98	0.01	1.02
F	pollock	1.00	0.00	1.00
F	whiting	0.98	0.01	1.02
F	salmon smolt	0.27	0.03	3.67
F	squid	0.65	0.08	1.54
F	G. sandeel	0.93	0.02	1.07
F	sandeel	0.24	0.01	4.19
F	norway pout	1.20	0.00	0.83
F	poor cod	0.99	0.00	1.01
Q	plaice	0.97	0.01	1.03
Q	whiting	0.94	0.01	1.07
Q	herring	0.38	0.07	3.08
Q	norway pout	0.99	0.01	1.01

Q	herring	oth	34	0.28	0.07	3.64					
Q	herring	oth	39	0.25	0.07	4.00					
Q	norway pout	tc	35	0.99	0.01	1.01					
V	plaice	fl	11	0.73	0.08	1.36	V	plaice	0.61	0.08	1.73
V	plaice	fl	17	0.48	0.07	2.09	V	whiting	0.79	0.09	1.27
V	whiting	lg	18	0.79	0.09	1.27	V	herring	0.38	0.08	2.67
V	herring	oth	14	0.38	0.08	2.67	V	sandeel	0.25	0.02	4.74
V	sandeel	se	10	0.15	0.01	6.64	V	norway pout	1.00	0.00	1.00
V	sandeel	se	16	0.35	0.02	2.85	V	poor cod	1.02	0.00	0.98
V	norway pout	tc	9	1.00	0.00	1.00					
V	poor cod	tc	13	1.02	NA	0.98					
X	plaice	fl	25	1.00	0.00	1.00	X	plaice	1.00	0.00	1.00
X	whiting	lg	1	0.92	0.06	1.09	X	whiting	0.96	0.03	1.04
X	whiting	lg	8	1.00	0.00	1.00	X	sandeel	0.62	0.01	1.61
X	whiting	lg	24	0.97	0.03	1.03	X	norway pout	1.00	0.00	1.00
X	sandeel	se	27	0.62	0.01	1.61	X	poor cod	1.00	0.00	1.00
X	norway pout	tc	7	1.00	0.00	1.00					
X	norway pout	tc	26	0.99	0.00	1.01					
X	poor cod	tc	4	1.00	0.00	1.00					
X	poor cod	tc	21	1.00	0.00	1.00					

Appendix 2.3: Prey-specific digestion coefficients (DC) and standard errors (SE) from each trial were averaged to give mean values for each seal, averaged across seals to give mean values for each prey species and averaged across prey species to give mean values for each prey group (fl = flatfish, lg = large gadoid, oth = other spp., se = sandeels, tc = *Trisopterus* spp.) for otolith length, width and lower rostral length.

Trial						**Seal**			**Prey & Group**		
seal	**prey**	**Gp**	**trial**	**DC**	**SE**	**Prey**	**DC**	**SE**	**prey**	**DC**	**SE**
Otolith length or lower rostral length											
D	dab	fl	48	1.29	0.03	Dab	1.33	0.05	dab	1.28	0.04
D	dab	fl	59	1.37	0.06	Plaice	1.17	0.06	lemon sole	1.22	0.11
D	plaice	fl	41	1.23	0.07	Cod	1.18	0.08	LR dab	1.18	0.02
D	plaice	fl	54	1.10	0.04	Haddock	1.02	0.05	plaice	1.17	0.05
D	cod	lg	50	1.31	0.03	Whiting	NA	NA	witch	1.09	0.03
D	cod	lg	55	1.06	0.14	Herring	1.23	0.10	cod	1.24	0.07
D	haddock	lg	43	0.97	0.08	Sandeel	1.16	0.01	haddock	1.17	0.04
D	haddock	lg	60	1.07	0.03	norway pout	1.11	0.01	hake	1.93	0.17
D	whiting	lg	47	NA	NA	poor cod	1.12	0.02	pollock	0.98	0.03
D	whiting	lg	53	NA	NA				whiting	1.69	0.09
D	herring	oth	46	1.38	0.11				herring	1.16	0.05
D	herring	oth	52	1.20	0.06				red gurnard	0.99	0.03
D	herring	oth	57	1.11	0.12				salmon smolt	1.27	0.04

D	squid	oth	44	1.04	0.04
D	sandeel	se	42	1.14	0.01
D	sandeel	se	49	1.15	0.01
D	sandeel	se	56	1.19	0.01
D	norway pout	tc	40	1.17	0.02
D	norway pout	tc	58	1.06	0.01
D	poor cod	tc	45	1.09	0.01
D	poor cod	tc	51	1.14	0.02
E	dab	fl	61	1.35	0.04
E	dab	fl	88	1.20	0.02
E	lemon sole	fl	80	1.40	0.17
E	lemon sole	fl	124	0.97	0.11
E	LR dab	fl	83	1.19	0.03
E	plaice	fl	91	1.16	0.05
E	witch	fl	76	1.02	0.02
E	cod	lg	69	1.64	0.04
E	cod	lg	74	1.49	0.03
E	cod	lg	77	0.95	0.09
E	cod	lg	89	1.26	0.03
E	cod	lg	120	1.27	0.07
E	cod	lg	125	1.40	0.04

Dab	1.27	0.03
lemon sole	1.18	0.14
LR dab	1.19	0.03
Plaice	1.16	0.05
Witch	1.02	0.02
Cod	1.33	0.05
Haddock	1.25	0.03
Hake	1.93	0.17
Whiting	1.36	0.06
Herring	1.11	0.02
red gurnard	0.99	0.03
salmon smolt	1.25	0.03
G. sandeel	1.92	0.08

squid	0.88	0.05
G. sandeel	1.61	0.05
sandeel	1.28	0.02
norway pout	1.18	0.01
poor cod	1.17	0.02

Group	**DC**	**SE**
Flatfish	1.19	0.05
Lg. gadoids	1.40	0.08
Other	1.04	0.04
Sandeels	1.45	0.03
Trisopterus	1.17	0.02

E	haddock	lg	71	1.34	0.06	Sandeel	1.30	0.03
E	haddock	lg	81	1.07	0.02	norway pout	1.07	0.01
E	haddock	lg	90	1.21	0.03	poor cod	1.25	0.02
E	haddock	lg	126	1.38	0.03			
E	hake	lg	84	2.08	0.18			
E	hake	lg	123	1.77	0.16			
E	whiting	lg	66	1.08	0.03			
E	whiting	lg	75	1.27	0.02			
E	whiting	lg	86	1.74	0.14			
E	herring	oth	78	1.11	0.02			
E	red gurnard	oth	79	0.95	0.04			
E	red gurnard	oth	85	1.03	0.03			
E	salmon smolt	oth	122	1.25	0.03			
E	squid	oth	63	1.06	0.04			
E	G. sandeel	se	121	1.92	0.08			
E	sandeel	se	65	1.19	0.03			
E	sandeel	se	73	1.40	0.04			
E	norway pout	tc	64	1.07	0.01			
E	poor cod	tc	72	1.25	0.02			
F	Dab	fl	111	1.23	0.02	Dab	1.23	0.02
F	lemon sole	fl	92	1.25	0.09	lemon sole	1.25	0.09

F	LR dab	fl	107	1.16	0.02	LR dab	1.16	0.02
F	plaice	fl	116	1.31	0.05	Plaice	1.31	0.05
F	witch	fl	97	1.15	0.04	Witch	1.15	0.04
F	cod	lg	93	1.29	0.08	Cod	1.19	0.06
F	cod	lg	104	1.15	0.05	Haddock	1.25	0.03
F	cod	lg	110	1.13	0.07	Pollock	0.98	0.03
F	haddock	lg	98	1.17	0.03	Whiting	1.37	0.07
F	haddock	lg	108	1.37	0.04	salmon smolt	1.28	0.04
F	haddock	lg	117	1.19	0.01	G. sandeel	1.30	0.02
F	pollock	lg	119	0.98	0.03	Sandeel	1.29	0.02
F	whiting	lg	100	1.50	0.02	norway pout	1.28	0.01
F	whiting	lg	105	1.48	0.03	poor cod	1.25	0.02
F	whiting	lg	114	1.13	0.15			
F	salmon smolt	oth	118	1.28	0.04			
F	squid	Oth	94	0.98	0.09			
F	G. sandeel	Se	113	1.30	0.02			
F	sandeel	Se	99	1.32	0.02			
F	sandeel	Se	106	1.26	0.02			
F	norway pout	Tc	95	1.28	0.01			
F	poor cod	Tc	103	1.25	0.02			

Q	plaice	Fl	33	1.23	0.07	Plaice	1.17	0.04
Q	plaice	Fl	37	1.12	0.02	Whiting	1.78	0.08
Q	whiting	Lg	32	1.86	0.10	Herring	1.19	0.04
Q	whiting	Lg	38	1.69	0.06	norway pout	1.24	0.01
Q	herring	oth	31	1.26	0.04			
Q	herring	oth	34	1.16	0.03			
Q	herring	oth	39	1.15	0.05			
Q	norway pout	tc	35	1.24	0.01			
V	plaice	fl	11	0.97	0.04	Plaice	1.14	0.04
V	plaice	fl	17	1.31	0.04	Whiting	2.14	NA
V	whiting	lg	18	2.14	NA	Herring	1.11	0.04
V	herring	oth	14	1.11	0.04	Sandeel	1.28	0.03
V	squid	oth	15	0.45	0.02	norway pout	1.12	0.02
V	sandeel	se	10	1.29	0.03	poor cod	1.07	0.02
V	sandeel	se	16	1.28	0.03			
V	norway pout	tc	9	1.12	0.02			
V	poor cod	tc	13	1.07	0.02			
X	plaice	fl	25	1.10	0.05	Plaice	1.10	0.05
X	whiting	lg	1	1.84	0.34	Whiting	1.80	0.15
X	whiting	lg	8	1.62	0.02	Sandeel	1.38	0.01
X	whiting	lg	24	1.93	0.09	norway pout	1.23	0.02
X	sandeel	se	27	1.38	0.01	poor cod	1.14	0.02

X	norway pout	tc	7	1.23	0.02
X	norway pout	tc	26	1.24	0.02
X	poor cod	tc	4	1.10	0.02
X	poor cod	tc	21	1.18	0.01

Trial						**Seal**			**Prey & Group**		
Seal	**prey**	**Gp**	**trial**	**DC**	**SE**	**Prey**	**DC**	**SE**	**prey**	**DC**	**SE**
Otolith width											
D	dab	fl	48	1.44	0.04	Cod	1.13	0.06	dab	1.35	0.03
D	dab	fl	59	1.46	0.06	Dab	1.45	0.05	lemon sole	1.32	0.08
D	plaice	fl	41	1.24	0.06	Haddock	1.16	0.03	LR dab	1.22	0.02
D	plaice	fl	54	1.12	0.04	Herring	1.41	0.08	plaice	1.18	0.04
D	cod	lg	50	1.19	0.01	norway pout	1.07	0.01	cod	1.23	0.06
D	cod	lg	55	1.08	0.11	Plaice	1.18	0.05	haddock	1.23	0.02
D	haddock	lg	43	1.17	0.03	poor cod	1.10	0.02	hake	1.80	0.14
D	haddock	lg	60	1.16	0.02	Sandeel	1.26	0.01	pollock	1.09	0.07
D	whiting	lg	47	1.35	0.03	Whiting	1.20	0.02	whiting	1.25	0.03
D	whiting	lg	53	1.06	0.01				herring	1.30	0.06
D	herring	oth	46	1.48	0.11				red gurnard	1.04	0.04
									salmon		
D	herring	oth	52	1.26	0.05				smolt	1.24	0.03
D	herring	oth	57	1.48	0.10				G. sandeel	1.75	0.05

D	sandeel	se	42	1.28	0.01
D	sandeel	se	49	1.24	0.01
D	sandeel	se	56	1.27	0.01
D	norway pout	tc	40	1.12	0.02
D	norway pout	tc	58	1.02	0.01
D	poor cod	tc	45	1.09	0.01
D	poor cod	tc	51	1.10	0.02
E	dab	fl	61	1.36	0.03
E	dab	fl	88	1.26	0.03
E	lemon sole	fl	124	1.06	0.10
E	lemon sole	fl	80	1.63	0.07
E	LR dab	fl	83	1.26	0.03
E	plaice	fl	91	1.22	0.04
E	witch	fl	76	NA	NA
E	cod	lg	120	1.53	0.09
E	cod	lg	125	1.36	0.03
E	cod	lg	69	1.72	0.05
E	cod	lg	74	1.36	0.04
E	cod	lg	77	1.19	0.11
E	cod	lg	89	1.25	0.02
E	haddock	lg	126	1.40	0.03

Cod	1.40	0.06
Dab	1.31	0.03
G. sandeel	1.98	0.07
Haddock	1.26	0.02
Hake	1.80	0.14
Herring	1.32	0.04
lemon sole	1.35	0.08
LR dab	1.26	0.03
norway pout	1.02	0.01
Plaice	1.22	0.04
poor cod	1.22	0.02
red gurnard	1.04	0.04
salmon smolt	1.20	0.03
Sandeel	1.40	0.03

sandeel	1.40	0.02
norway pout	1.13	0.01
poor cod	1.14	0.02

Group	**DC**	**SE**
Flatfish	1.27	0.05
Lg. gadoids	1.32	0.07
Other	1.17	0.05
Sandeels	1.57	0.04
Trisopterus	1.13	0.02

E	haddock	lg	71	1.29	0.03	Whiting	1.19	0.02
E	haddock	lg	81	1.14	0.02	Witch	NA	NA
E	haddock	lg	90	1.20	0.02			
E	hake	lg	123	1.58	0.14			
E	hake	lg	84	2.01	0.15			
E	whiting	lg	66	1.09	0.01			
E	whiting	lg	75	1.12	0.01			
E	whiting	lg	86	1.36	0.04			
E	herring	oth	78	1.32	0.04			
E	red gurnard	oth	79	1.01	0.04			
E	red gurnard	oth	85	1.08	0.04			
E	salmon smolt	oth	122	1.20	0.03			
E	G. sandeel	se	121	1.98	0.07			
E	sandeel	se	65	1.26	0.03			
E	sandeel	se	73	1.54	0.04			
E	norway pout	tc	64	1.02	0.01			
E	poor cod	tc	72	1.22	0.02			
F	dab	fl	111	1.30	0.03	Cod	1.17	0.07
F	lemon sole	fl	92	1.28	0.08	Dab	1.30	0.03
F	LR dab	fl	107	1.18	0.02	G. sandeel	1.52	0.02
F	plaice	fl	116	1.30	0.04	Haddock	1.26	0.02

F	witch	fl	97	NA	NA	lemon sole	1.28	0.08
F	cod	lg	104	1.06	0.03	LR dab	1.18	0.02
F	cod	lg	110	1.20	0.08	norway pout	1.24	0.01
F	cod	lg	93	1.25	0.09	Plaice	1.30	0.04
F	haddock	lg	108	1.39	0.03	Pollock	1.09	0.07
F	haddock	lg	117	1.21	0.01	poor cod	1.21	0.02
F	haddock	lg	98	1.17	0.03	salmon smolt	1.28	0.04
F	pollock	lg	119	1.09	0.07	Sandeel	1.43	0.02
F	whiting	lg	100	1.30	0.02	Whiting	1.25	0.02
F	whiting	lg	105	1.26	0.02	Witch	NA	NA
F	whiting	lg	114	1.18	0.02			
F	salmon smolt	oth	118	1.28	0.04			
F	G. sandeel	se	113	1.52	0.02			
F	sandeel	se	106	1.37	0.02			
F	sandeel	se	99	1.49	0.02			
F	norway pout	tc	95	1.24	0.01			
F	poor cod	tc	103	1.21	0.02			
Q	plaice	fl	33	1.16	0.04	Herring	1.36	0.07
Q	plaice	fl	37	1.10	0.02	norway pout	1.21	0.01
Q	whiting	lg	32	1.41	0.05	Plaice	1.13	0.03

Q	whiting	lg	38	1.44	0.03	Whiting	1.42	0.04
Q	herring	oth	31	1.40	0.04			
Q	herring	oth	34	1.38	0.08			
Q	herring	oth	39	1.31	0.09			
Q	norway pout	tc	35	1.21	0.01			
V	plaice	fl	11	0.98	0.04	Herring	1.12	0.04
V	plaice	fl	17	1.28	0.05	norway pout	1.08	0.02
V	whiting	lg	18	1.07	0.06	Plaice	1.13	0.04
V	herring	oth	14	1.12	0.04	poor cod	1.07	0.02
V	sandeel	se	10	1.39	0.03	Sandeel	1.36	0.03
V	sandeel	se	16	1.32	0.03	Whiting	1.07	0.06
V	norway pout	tc	9	1.08	0.02			
V	poor cod	tc	13	1.07	0.02			
X	plaice	fl	25	1.13	0.04	norway pout	1.16	0.02
X	whiting	lg	1	1.33	0.06	Plaice	1.13	0.04
X	whiting	lg	24	1.39	0.03	poor cod	1.11	0.02
X	whiting	lg	8	1.39	0.03	Sandeel	1.53	0.01
X	sandeel	se	27	1.53	0.01	whiting	1.37	0.04
X	norway pout	tc	26	1.16	0.02			
X	norway pout	tc	7	1.16	0.02			
X	poor cod	tc	21	1.16	0.01			
X	poor cod	tc	4	1.06	0.02			

Chapter 3

REGIONAL AND SEASONAL VARIATION IN THE DIET OF HARBOUR SEALS AROUND BRITAIN

3.1. Introduction

Harbour seals in Britain were stable or increasing until around 2000 when declines were detected in Shetland and Orkney (Lonergan *et al.*, 2007; SCOS, 2011). In The Wash, England population declines have been associated with the 1988 and 2002 phocine distemper virus epidemics (PDV). The Wash population since 2009 has shown a dramatic population increase (SCOS, 2012) but across Scotland populations are experiencing differing population trajectories. Major declines have been reported since 2000 of 75 % in Orkney, 30 % in Shetland and 85 % in the Firth of Tay (Lonergan *et al.*, 2007; SCOS, 2013). However, the populations in the Moray Firth, Outer Hebrides and Inner Hebrides remain stable (Lonergan *et al.*, 2007; SCOS, 2013).

Reduced availability of suitable prey is a potential cause of the decline as reductions in the quantity or relative quality of prey available has been shown to compromise fecundity and survival in; birds (*e.g.*, Arcese and Smith, 1988; Thorup *et al.*, 2010) and mammals (*e.g.*, Trites and Donnelly, 2003; Ford *et al.*, 2010). A negative physiological and/or behavioural state which is triggered by sub-optimal quantity or quality of food is termed nutritional stress. Animals suffering from nutritional stress can be affected in a number of ways including: reduced body size, reduced birth rates, increased infant and juvenile mortality, changes in blood chemistry and body composition and behavioural modifications such as extended foraging trips and the impacts of nutritional stress on the individual are expected to affect the dynamics of the population as a whole (*e.g.*, Trites and Donnelly, 2003).

Studies of Steller sea lions (*Eumetopias jubatus*) have indicated that changes in available prey and very low diversity in diet have presented difficulties for survival in some regions. Wild and captive studies have indicated that animals in regions of population decline were nutritionally compromised because of the quality of prey available (chronic nutritional stress) rather than because of the quantity of prey available (acute nutritional stress, Trites and Donnelly, 2003). Poor body condition and macrocytic anaemia has been reported in harbour seals eating a winter diet of non-preferred prey (gadoid fish over clupeid fish) in the Moray Firth (Thompson *et al.*, 1997). However, an examination of harbour seal health and body condition during a similar period to the recent declines (1988-2006) revealed no evidence of nutritional stress using morphometric and clinical blood chemistry data (Hall *et al.*, 2007).

Despite the confounding differences which may exist in the different regional ecosystems and the very limited information available about historical ecosystem and dietary differences, nutritional stress as a result of decreased quality (*e.g.*, calorific content of prey) or quantity of prey is still considered a potential cause of harbour seal population declines (SCOS, 2013). Furthermore, comparison of diet and diversity in diet between regions of different population trajectories has been used as an alternative approach to evaluating food limitation in studies of Steller sea lion decline in Alaska (Merrick *et al.*, 1997; Trites *et al.*, 2007a).

Prior to the population declines harbour seal diet has been described across different spatial and temporal scales in Britain (Thompson *et al.*, 1996b; Tollit and Thompson, 1996; Brown *et al.*, 2001; Pierce and Santos, 2003). From the early studies of seal stomachs and digestive tracts to more recent studies of faecal samples differences in diet have been identified across regions, seasons and years. Prey most commonly identified include; sandeels (*Ammodytidae*), gadoids (whiting *Merlangius merlangus* and Atlantic cod *Gadus morhua*), flatfish (dab *Limanda limanda*, plaice *Pleuronectes platessa* and flounder *Platichthys flesus*) and in some regions salmonids (Atlantic salmon *Salmo salar* and sea trout *Salmo trutta*).

These studies have described seasonal and regional variation in diet composition in isolation as concurrent assessments across time and space have rarely been conducted. Pierce *et al.*, (1990a) described the diet of harbour seals across the Moray Firth and Orkney contemporaneously in the mid-1980s. Gadoids and flatfish were important in the diet in both regions however; whiting, flounder and plaice dominated in the Moray Firth whereas cod and lemon sole were more important in Orkney (Pierce *et al.*, 1990a). In April – June gadoids were more frequently eaten in Orkney and flatfish more frequently in the Moray Firth and in July – September clupeids (particularly herring) were important in the diet in Orkney (Pierce *et al.*, 1990a). Parallel studies of the diet of harbour seals across locations on the west coast of Scotland were subsequently conducted by Pierce and Santos (2003). They noted the relative unimportance of sandeel in the diet across the West coast and recorded variation in the importance of *Trisopterus* spp. and whiting both of greater importance in the diet around Mull than Skye (Pierce and Santos, 2003).

Overall harbour seals have a mainly coastal at sea distribution around Britain, though foraging offshore and movements between regions and countries does occur (Cunningham *et al.*, 2009; Sharples *et al.*, 2012). The coastal habitat around Britain is varied including the shallow and sandy North Sea to the east and the complex fjord, reef and island systems of the Inner Seas and Atlantic Ocean to the west of Scotland. Orkney and Shetland straddle the boundary between the North Sea and Atlantic Ocean to the north of mainland Britain. The diverse habitat and environment utilised by harbour seal populations around Britain is reflected in the dominant substrate, water depth, temperature, salinity and fish species present as well as impacted by the anthropogenic influence of commercial fishing (see Chapter 1).

The different population trajectories displayed by harbour seal populations around Britain continue to be investigated as regions of steep decline contrast sharply with more stable or increasing populations (SCOS, 2013). Information on the diet of harbour seals is considered to be important for understanding if reduced food availability is influencing population trends at a regional scale (SCOS, 2013). However there has been no comprehensive study of the diet of harbour seals in the UK.

3.1.1 The aims of this study

This study describes the diet and feeding ecology of harbour seals across the whole of Scotland and The Wash, England including regions of population increase, stability and decline. I examined: diversity in species richness and evenness between seal populations, evidence of seasonal and regional variation in diet composition and variation in the size and quality of prey in the diet.

I based my expectations for this study on the extensive work carried out on the Steller sea lion population decline. Despite some recent opposition to the research linking the Steller sea lion decline and nutritional stress (NOAA Fisheries, 2010; Bowen, 2012; Stewart, 2012; Stokes, 2012; NOAA Fisheries, 2014) changes in prey availability, prey diversity and prey quality (*e.g.*, calorific content, Trites and Donnelly, 2003; Trites *et al.*, 2007a; Rosen, 2009; Sinclair *et al.*, 2013) remains a leading hypothesis to explain the dramatic decline since the mid-1970s of the western stock of Steller sea lions (Loughlin *et al.*, 1992). The most striking difference between the diet of the western stock and eastern (increasing/stable) stock was the diversity of prey consumed; as diet diversity decreased, the population decreased (Merrick *et al.*, 1997; Sinclair and Zeppelin, 2002; Trites *et al.*, 2007a). Overall, prey species in the diet across both regions has been shown to be similar, though the relative abundances of each prey type differed considerably (Sinclair and Zeppelin, 2002; Trites *et al.*, 2007a; Trites *et al.*, 2007b). Noticeable shifts in composition in periods before and during the population decline have also been recorded; in the 1970s Pitcher (1981) found that capelin (*Mallotus villosus*) and walleye pollock (*Theragra chalcogramma*) were common in the summer diet, whereas in the mid-1980s capelin was no longer evident and walleye pollock dominated the diet (Merrick and Calkins, 1996).

Changes in the proportion of small, fatty schooling fish such as capelin to larger less calorific fish such as walleye pollock in the diet is expected to affect the food requirements of individuals. Based on the relative amounts of low-energy density prey versus high-energy density prey in the diet Winship and Trites (2003) estimated food requirements were highest in regions where Steller sea lions consumed higher proportions of low-energy density prey; the regions which had experienced the highest rates of population decline. Recent assessment of the size of the main prey however, revealed no difference in the average size of walleye pollock consumed in the eastern or western stock of Steller sea lions (Tollit *et al.*, 2004a; Zeppelin *et al.*, 2004). Though the main prey of the western stock have been shown to be larger than in previous studies (Pitcher, 1981; Zeppelin *et al.*, 2004).

It is the established view from theoretical and empirical research that as food becomes limiting dietary diversity in consumers increases (Schoener, 1971; Roughgarden, 1972; Krebs *et al.*, 1977; Thompson and Colgan, 1990). Therefore I used detailed measures of species richness and evenness in the diet to examine harbour seal diet diversity to determine if food could be considered limiting for harbour seals in any regions around Britain. Although differences in overall ecosystem diversity are expected due to inherent physical and environmental differences by using individual seals as the sampling unit, any diversity in diet will represent a combination of the prey which were available and what was eaten. I used biomass reconstruction to estimate the contribution of different prey species to the diet of harbour seals across seasons and regions expecting to find differences in composition between regions of population decline and stability/ increase. I also hoped to make comparisons with previous studies to see if any noticeable switch in diet composition had occurred. Furthermore, I expected any differences in the contribution of prey type to reveal changes the proportions of low and high energy density prey. For example in regions of decline I expected to see greater abundance of flatfish and gadoids and less consumption of high-energy density prey such as herring, mackerel and sandeel. Any differences in the size of prey consumed I anticipated would reflect fishing effort which shows that proportions of larger fish has decreased in catches during the 20th century (Rogers and Ellis, 2000).

3.2. Methods

3.2.1 Scat collection

Scat collections were carried out in Scotland (June 2010 – May 2011) and additionally in the Northern Isles in September 2011 from a small boat or on foot. Collections were also conducted in The Wash, England (June 2011 – May 2012). Scats were collected up to 2 hours before and 2 hours after low water (derived from POLTIPS, National Oceanographic Centre, NERC). Collection trips were planned to cover as many major haul-outs of harbour seal as possible (Appendix 3.1 documents the main haul-out sites where successful scat collections were conducted). Haul-out sites were chosen based on annually updated maps showing the number and distribution of harbour seals around the coast of Scotland (Figure 3.1) and The Wash, England (Figure 3.2). Scats were collected into separate plastic bags and stored at -20°C. All scats collected were expected to be < 2 weeks old, or the time since the last spring tide.

Scat collections were stratified on a spatial and temporal basis and as weather allowed. Collections were distributed spatially in Scotland to match the Scottish Government designated Seal Management Regions (Baxter *et al.*, 2011) and included the ten Special Areas of Conservation for harbour seals, which are listed under Annex II of the EU Habitats Directive (Figure 3.3). Through the Special Committee on Seals (SCOS), the Sea Mammal Research Unit (SMRU) gives annual advice on matters related to the management of seals in Britain; this advice includes data on the number of harbour seals counted in Management Regions in Scotland and the Greater Wash in England (*e.g.*, SCOS, 2013).

Samples were collected within a 3 month time-window and these quarters were chosen following Sharples *et al.*, (2009): summer (June–August, harbour seal pupping, breeding and early moult), autumn (September–November, harbour seal end of moult and start of the principal period of foraging), winter (December–February, period mainly defined by foraging) and spring (March–May, pre-pupping).

Before entering a haul-out site the number of harbour seals was counted and any grey seals were identified and counted. Haul-outs were designated as a single species site if the area contained ≥ 90 % of one species (Pierce *et al.*, 1991c; Tollit and Thompson, 1996; Matejusova *et al.*, 2008) or if the seals were spatially segregated at the haul-out. If the haul-out consisted of ≥ 80 % of a single species the site was designated as a “likely harbour” or “likely grey” seal haul-out. All other haul-out sites where animals were observed were classified as “mixed” species haul-outs. Scat collections also took place at sites where no animals were observed but their presence was expected based on local knowledge, prior experience or expert opinion; these haul-out sites were classified as “unknown (advised harbour seal)”.

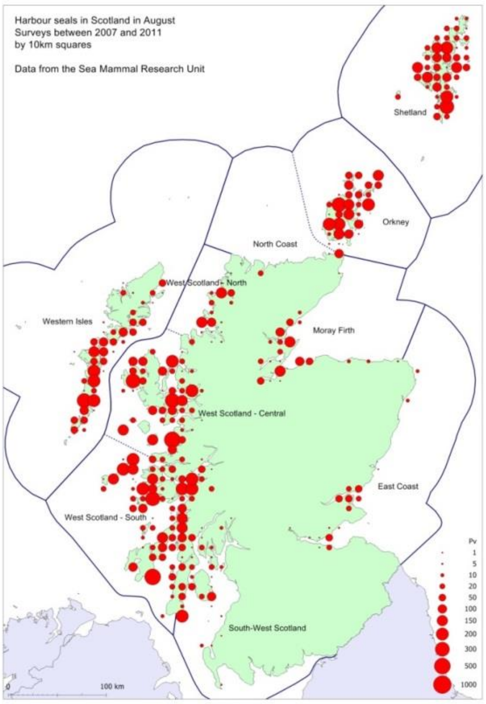


Figure 3.1: Number and distribution of harbour seals in Management Regions around the coast of Scotland, from surveys carried out in August between 2007 and 2011 (SCOS, 2013). All areas were surveyed using a thermal imaging camera.

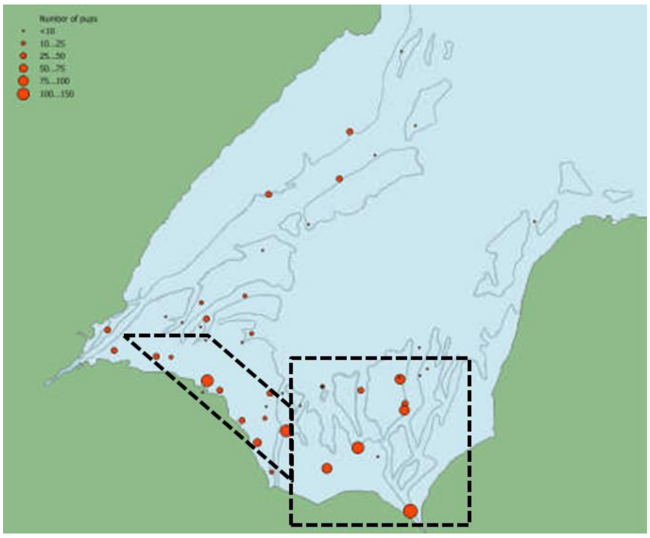


Figure 3.2: Distribution of pups in the Wash, England 2010 (SCOS, 2011). Numbers of pups are represented by the areas of the circles on each site. Locations given to the nearest 500 m. The dashed boxes indicate the haul-out sites visited for scat collections.

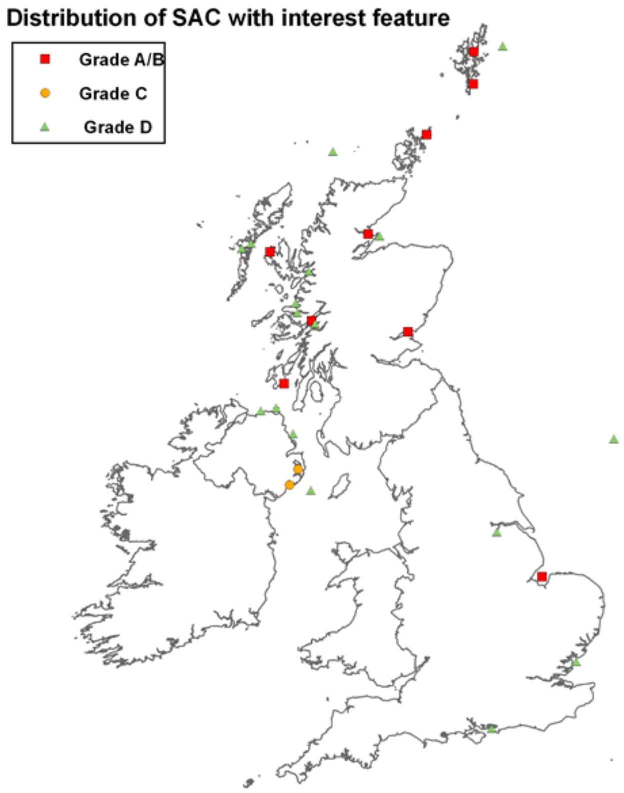


Figure 3.3: Distribution of Special Areas of Conservation (SACs) for harbour seals in the UK. At Grade A or B sites harbour seal are the species of primary interest, at Grade C sites, they are of qualifying interest, at Grade D sites, they are known to occur but are not a significant feature. Source: http://jncc.defra.gov.uk/protectedsites/sacselection/species.asp?FeatureIntCode=S1365.

3.2.2 Molecular analysis

Because scats cannot visually be assigned to species (Matejusova *et al.*, 2008; Masland *et al.*, 2010), species identification was conducted on a sample of scats from all haul-out types. Ideally such analysis would be conducted only on scats which contained otoliths and/ or beaks. However, due to the availability of time and collaborative resources throughout the project the DNA testing was mostly completed before I knew if an individual scat contained hard prey remains.

Scats were thawed and a subsample (0.6-1 g) of faeces was taken using a disposable spatula. To increase the chance of collecting DNA from the defaecator the subsample was scraped from the outside of each scat, an area expected to contain cells sloughed from the seals gut (Reed *et al.*, 1997). Care was taken not to remove any hard prey remains during subsampling. Subsamples were stored at -20 °C until processing.

Genomic DNA was extracted using QIAamp DNA Stool Mini kit protocol (Qiagen, Crawley, UK http://www.qiagen.com/). Control samples with no faecal material were included frequently to monitor for cross-sample contamination. Harbour and grey seal tissues were included as positive controls. Quantitative real-time Polymerase Chain Reaction (qPCR) was used to amplify the target DNA of interest (defaecating seal) and species-specific Taqman qPCR assays for harbour and grey seals were used (Matejusová *et al.*, 2013).

Molecular analysis was focused on haul-out sites classified as "harbour seal" then "mixed", "likely grey seal", "likely harbour seal", "grey seal" and "unknown" (Table 3.1). In total 2,600 scats were tested for species identification (51.1 % of all scats collected). Both harbour (n = 1,957) and grey seal (n = 240) species were identified and inconclusive results were reported for 402 scats (most likely a result of low quantity and/ or quality of DNA). The proportion of harbour seal scats identified was calculated ± the standard error (SE) at each haul-out type, where SE is the theoretical SE calculated as: $SE\ (proportion) = \frac{\sqrt{\mathrm{p \times 1 - p}}}{\mathrm{n}}$. Where p is the proportion of harbour seal scats identified and n is the number of scats confirmed as either harbour or grey seal.

At haul-out sites where ≥ 80 % of the animals counted were harbour seals (classified harbour seal and likely harbour seal haul-out sites) the probability of any scat collected having been produced by a harbour seal was very high; ≥ 0.97 (Table 3.2). Based on these results, any scats collected at sites where ≥ 80 % of the animals counted were harbour seals were considered to be from harbour seals and were included in analysis. Including all additional faecal samples positively identified as harbour seal scats, the total number of scats containing hard prey remains included in analysis to estimate harbour seal diet ranged from 1 to 142 across all regions and seasons in Scotland and 23 to 122 in England (Table 3.3 A).

Table 3.1: The total number of scats collected at each haul-out type, the number of species-specific qPCRs conducted, and the number of positively identified harbour seal scats.

Haul-out classification	No. of scats	qPCR analysis confirmed Harbour seal	Grey seal	Inconclusive	Total
Harbour seal	2504	1197	38	351	1586
Likely harbour seal	130	52	0	10	62
Mixed	1320	607	127	35	769
Likely grey seal	228	62	48	5	115
Grey seal	818	21	15	1	37
Unknown	85	18	12	1	31
TOTAL	5085	1957	240	403	2600

Table 3.2: The proportion of harbour seal scats identified ± SE at each haul-out type is given alongside the total number of scats collected and the number of qPCR analyses which gave positive identification of either harbour of grey seal.

Haul-out classification	No. of scats	Confirmed harbour or grey seal qPCR result	Proportion harbour seals	SE
Likely harbour seal	130	52	1	<0.001
Harbour seal	2504	1235	0.97	<0.001
Mixed	1320	734	0.83	<0.001
Unknown	85	30	0.6	0.01
Grey seal	818	36	0.58	0.01
Likely grey seal	228	110	0.56	<0.001
TOTAL	5085	2197		

The proportion of harbour seal scats identified at mixed haul-out sites was also high - 0.83 (Table 3.2). In an effort to increase the sample size in the regions and quarters where the number of scats containing hard prey remains was small (<50) I investigated whether inclusion of scats collected from mixed haul-out sites would markedly increase these sample sizes. The inclusion of mixed haul-out scats did not improve the sample size for the regions and quarters with low numbers of scats collected (Table 3.3 B). Consequently, analysis was limited to scats positively identified as being produced by a harbour seal plus all scats collected at haul-out sites where ≥ 80% of the animals counted were harbour seals (Table 3.3 A), henceforth called “harbour seal scats”.

3.2.3 Extraction, identification and measurement of prey remains

A target of 100 scats containing hard prey remains was set to estimate the diet in each region and season. Where possible scats were used which had been collected at a number of different haul-out sites within the region/ season, for example; hard prey remains were used from Moray Firth scats collected in summer from: Ardesier, Beauly Firth, Findhorn, Cromarty Firth and Dornoch Firth haul-out sites.

Individual scats were defrosted, placed in nested mesh bags (inner 350 µm, outer 240 µm) and soaked in warm water with 25 g detergent (Dreft) for 2 – 24 h. Scats were subsequently machine washed (Orr *et al.*, 2004) following the protocol developed by S. Brasseur (pers.comm.); on a 2 h 40°C pre-wash with 50 g detergent and 0.5 h wool wash at 40°C with 50 g detergent, the spin cycle was deactivated for all wash cycles. If pebbles had been picked up as part of the individual scat collection then otoliths and beaks were extracted using running water through a nest of sieves to avoid damage to prey hard remains; mesh sizes 1 mm, 600 µm, 335 µm and 250 µm. The presence of other possible prey remains (*e.g.*, feathers and crustacean carapaces) was noted.

Otoliths were stored dry and identified to the lowest possible taxonomic group based on morphological criteria using a reference collection and two identification guides (Härkönen, 1986; Leopold *et al.*, 2001). Beaks were stored in 70% IMS and identified to species where possible using a reference collection and identification guide (Clarke, 1986). Where prey remains could not be identified to species, they were recorded at a higher level (*e.g.,* sandeel, unidentified gadoid) or as unknown species.

Table 3.3: The number of harbour seal scats containing hard prey remains. A) All scats identified using molecular techniques or collected from haul-out sites containing ≥80% harbour seals. B) As A, but also includes all scats collected at mixed haul-out sites.

A)

Management Region	Summer 2010	Autumn 2010	Winter 2010	Spring 2011
SE Scotland	13	13	4	9
Moray Firth	89	21	52	103
Orkney	117	113*	4	23
Shetland	47	111*		28
Outer Hebrides	99	7	6	
W coast north	93	12	1	43
W coast central	82	142	68	80
W coast south	83	134	34	57
SW Scotland				3
	2011	**2011**	**2011**	**2012**
England	122	81	62	23

*Samples collected in a subsequent year due to low sample size

B)

Management Region	Summer 2010	Autumn 2010	Winter 2010	Spring 2011
SE Scotland	13	20	4	9
Moray Firth	101	23	53	129
Orkney	199	207*	4	23
Shetland	47	163*		29
Outer Hebrides	99	7	9	
W coast north	93	13	1	43
W coast central	82	160	68	80
W coast south	83	146	35	57
SW Scotland				6
	2011	**2011**	**2011**	**2012**
England	128	81	62	23

*Samples collected in a subsequent year due to low sample size

Otolith lengths and widths and cephalopod lower rostral or lower hood lengths were measured to the nearest 0.01 mm using digital callipers (Mitutoyo) under binocular microscopes. Although upper beaks are useful for identification robust relationships do not exist for upper hood length/upper rostral length and cephalopod mantle length and so upper beaks were not used in this study. Broken otoliths and beaks were counted and only measured if an appropriate dimension (otolith length, otolith width or lower rostral length) was complete. Fragments of otoliths or beaks which were not large enough to be measured were not counted or measured to avoid miss-identification of species and double counting.

Where the total per species ≤ 30 all otoliths or beaks were measured. For prey species represented by 30 - 120 otoliths or beaks in a single scat, 30 were randomly chosen and measured. For scats containing more than 120 otoliths or beaks of the same species, 25% were measured.

The degree by which each measured otolith was digested was recorded after examination of individual morphological features (after Leopold *et al.*, 2001 and Chapter 2). Four grades of digestion were allocated; grade 1 was pristine, grade 2 moderately digested, grade 3 considerably digested and grade 4 severely digested. Digestion of beaks was not classified.

3.2.4 Diversity of prey

Diet diversity was estimated for each region within a season using estimates of species richness and the relative abundance of species (species evenness). Species Richness (S) was calculated as the total number of species identified in the sample and evenness was measured using Pielou's evenness index (PIE), the most widely used evenness metric in ecology (*e.g.*, Pielou, 1966; Dahlberg and Odum, 1970; Cook and Graham, 1996; Dangles and Malmqvist, 2004). PIE provides a measure of how different the abundances of the species in a community were from each other (Smith and Wilson, 1996) as such evenness is highest when species abundance is evenly spread and a sample is not dominated by one or a few species with high abundance.

Studies involving comparisons of species richness among different regions, sites or communities need to use rarefaction techniques to standardise richness data (Simberloff, 1978; Gotelli and Colwell, 2001; Gotelli and Colwell, 2011) as the number of species recorded in a sample is very sensitive to the number of samples collected and is furthermore affected by the effective area sampled and by the spatial arrangement of the replicates. It is not suitable therefore to 'standardise' the species richness of samples of two or more assemblages by dividing observed richness by a measure of effort *e.g.*, area sampled, number of individuals or number of samples (in this case number of scats collected). Calculation of the ratio of species richness to number of samples will grossly overestimate species density when the index is extrapolated to larger areas (Gotelli and Colwell, 2011). Rarefaction to a common sampling effort adjusts for differences in sampling intensity, and allows for meaningful standardisation and comparison of datasets.

To generate the rarefied species richness, the expected number of *n* species was generated through the repeated re-sampling of the pool of *N* individuals sampled at random within each re-sampling. The data were individually rarefied to the minimum number of scats in this chapter; across all regions within a season; as such species richness cannot be compared across seasons. This process does incur loss of information from equalising the sample size to the smallest sample in the data series however, this is necessary to allow valid comparison of species richness.

PIE was calculated as $J = \frac{H'}{log(S)}$ where H' is Shannon Weiner diversity and S is the rarefied total number of species in a sample. The value of *J* ranges from 0 to 1, with larger values representing more even distributions in abundance among species.

Prior to rarefaction and analysis the total number of otoliths/beaks in each scat was converted to the estimate of total number of each fish/cephalopod prey species in each scat. To account for species-specific differences in complete digestion, the number of otoliths was adjusted using experimentally derived number correction factors (Chapter 2). Numbers were also corrected to account for fish having two identifiable prey structures (otoliths) per individual as opposed to one (beak) in cephalopods. As the analysis takes into account individual prey species, I re-allocated prey identified to the family level *e.g.*, species identified as unidentified gadoid or poor cod/Norway pout. The numbers of prey identified to the family level were split into individual prey species from the same family proportionally based on the prey species occurring in the individual scat.

If family specific prey species had not been identified in that individual scat, family level otoliths were allocated species codes based on the proportion of that prey family in all scats from the same region and season or if none were found in that season, the proportion of that prey family in any scats from that region. Very rarely otoliths were allocated a species code based on the proportion of otoliths from the same family in an adjoining region; <15 occurrences of unidentified *Cottidae* otoliths on the west coast of Scotland.

3.2.5 Estimation of diet composition

Estimation of harbour seal diet composition generally followed the methods used in previous assessments of seal diet by SMRU; otolith/beaks recovered from scats were corrected for digestion and used to estimate the weight of prey ingested, values were summed over species and expressed as percentages in the diet by weight (Prime and Hammond, 1987; 1990; Hammond *et al.*, 1994a; Hammond *et al.*, 1994b; Hammond and Rothery, 1996; Hall *et al.*, 1998; Hammond and Grellier, 2006; Hammond and Harris, 2006).

Measurements of partially digested otolith/beak size were converted to estimates of undigested otolith/beak size using experimentally derived grade-specific digestion coefficients (Chapter 2). For each prey species (or higher taxon) the preferred measurement (otolith length or width, or lower rostral or lower hood length) was determined based on the availability of experimental data, the precision of the estimated digestion coefficients (see Chapter 2), the measurement available from recovered hard parts and the availability of regression equations to estimate prey size. Where species specific correction factors were not available group-specific values were used (*e.g.,* gadoids, flatfish) or values from prey species with otoliths of similar size and robustness (Härkönen, 1986) were applied. The use of values from other species only occurred for prey species that were minor components of the diet.

For some prey species there was no suitable substitution and general "round fish" otolith length and width digestion coefficients were calculated by averaging the grade-specific digestion coefficients of the following species: cod, whiting, haddock (*Melanogrammus aeglefinus*), hake (*Merluccius merluccius*), Norway pout (*Trisopterus esmarkii*), poor cod (*Trisopterus minutus*), salmon, sandeel, herring (*Clupea harengus*), red gurnard (*Chelidonichthys cuculus*) and pollock (*Pollachius pollachius*, otolith width only). The standard error of each grade specific round fish digestion coefficient was estimated as $\frac{\sqrt{var(p)}}{n}$, where *p* is the average round fish digestion coefficient and *n* is the number of grade-specific digestion coefficients.

For dragonet (*Callionnymus lyra*) and the *Cottidae* species (hooknose *Agonus cataphractus*, bullrout *Myoxocephalus scorpius*, sea scorpion *Taurulus bubalis* and unidentified *Cottidae*) harbour seal specific digestion coefficients were not available (Chapter 2). However, digestion coefficients (DCs) were available for grey seals (Grellier and Hammond, 2006). Species-by-species comparison showed that on average 74 % of all harbour seal digestion coefficients (Chapter 2) were smaller than grey seal DCs by 0.083. Grey seal DCs for dragonet and short-spined sea scorpion were therefore multiplied by 0.917 (the proportional average) to create digestion coefficient estimates for harbour seals.

In studies of grey seal diet, a high proportion of grade 3 otoliths were recovered (Grellier and Hammond, 2006); these authors suggested that future studies should introduce an additional grade to better reflect high levels of digestion. In this study I developed a grade 4 to account for these high levels of digestion (Chapter 2). For these species for which grey seal DCs were used, to account for differences in grading and the high levels of digestion in both grey and harbour seal otoliths, I used the grey seal grade 3 DC as harbour seal grade 4 and the grey seal species-specific DC for harbour seal grade 3.

To test the sensitivity of harbour seal diet estimates to changes in dragonet and *Cottidae* DCs, I generated diet predictions using three sets of digestion coefficients: (i) grade-specific DCs for harbour seals estimated by multiplying grey seal DCs by 0.917

(creating an average proportional reduction in DCs), (ii) grade-specific DCs for harbour seals estimated as in (i) but using grade 3 estimates for both grades 3 and 4 and (iii) grade-specific grey seal DCs (Grellier and Hammond, 2006). I estimated percentage diet by weight for summer and autumn, using the three sets of DCs on otolith and beak measurement data from The Wash, England (a region which contained a high proportion of dragonet and bullrout otoliths, Table 3.4).

The majority of differences in diet estimation were small (<1% in both quarters). From this point on, the dragonet and scorpion fishes DCs used will be DC type (i), grey seal DC * 0.917. By using these smaller estimated harbour seal DCs for dragonet and *Cottidae* species, the possibility of overestimating their contribution to the overall diet should be lessened.

Estimates of fish/cephalopod weight were derived from the estimates of undigested otolith/beak size using published allometric equations (Clarke, 1986; Härkönen, 1986; Leopold *et al.*, 2001). Where no equations were available for prey species, equations for the closest matching species were used.

For scats containing more than 30 but fewer than 120 otoliths or beaks of the same species and for prey species with greater than 120 otoliths recovered per scat (*e.g.,* sandeel) for which a 25% sub-sample of otoliths had been graded and measured the mass of the fish represented by each unmeasured otolith was assumed to equal the mean mass of all measured otoliths. In cases where there were no measured otoliths of a particular species in the scat, the mean fish mass over all scats was used.

To account for species-specific differences in complete digestion, the mass estimated for each prey species was adjusted using experimentally derived number correction factors (Chapter 2). Where no experimental data were available, values for group-specific (*e.g.,* gadoids, flatfish) or closest matching species were used.

Table 3.4: Variation in estimated harbour seal diet composition (expressed as the percentage of each species in the diet by weight) using 3 different sets of digestion coefficients for dragonet and *Cottidae* species and the percentage differences in weight between type (i) and (ii) and (ii). Prey species listed are those contributing > 2% using any DC type.

A) Summer

	Digestion coefficient type			**Difference in % weight**	
Species	**(i)**	**(ii)**	**(iii)**	**(i) - (ii)**	**(i) - (iii)**
Dragonet	38.8	44.3	39.7	-5.5	-0.9
Sandeel	22.2	20.2	21.9	2.0	0.3
Plaice	9.0	8.1	8.8	0.8	0.1
Dover sole	6.0	5.4	5.9	0.5	0.1
Dab	5.0	4.5	4.9	0.5	0.1
Goby	4.2	3.8	4.2	0.4	0.1
Flounder (Butt)	3.7	3.4	3.7	0.3	0.1
Cod	2.4	2.2	2.4	0.2	0.0
Unidentified flatfish	2.3	2.1	2.3	0.2	0.0

B) Autumn

	Digestion coefficient type			**Difference in % weight**	
Species	**(i)**	**(ii)**	**(iii)**	**(i) - (ii)**	**(i) - (iii)**
Whiting	30.3	28.7	30.0	1.5	0.2
Dragonet	19.1	22.7	19.3	-3.6	-0.2
Plaice	10.3	9.7	10.2	0.5	0.1
Dover sole	9.6	9.1	9.5	0.5	0.1
Sandeel	6.6	6.3	6.6	0.3	0.0
Lemon sole	5.9	5.6	5.8	0.3	0.0
Unidentified flatfish	5.2	4.9	5.2	0.3	0.0
Dab	4.0	3.8	4.0	0.2	0.0
Bullrout	2.0	2.3	2.4	-0.3	-0.4

3.2.6 Estimation of variability

Variances of estimates of diet composition were estimated using the method described by Hammond & Rothery (1996) and implemented in Hammond & Grellier (2006) and Hammond & Harris (2006).

Sampling error was estimated using non-parametric bootstrap resampling with scat as the sampling unit. Measurement error was estimated using parametric resampling of the coefficients describing the relationships used to obtain estimates of diet composition from otolith/beak measurements. Measurement error included variability associated with (a) estimating undigested otolith/beak size from partially digested measurements via species- or grade-specific digestion coefficients; (b) estimating fish/cephalopod weight from estimated undigested otolith/beak size via species-specific allometric relationships; and (c) accounting for complete digestion of otoliths/beaks using estimated recovery rates.

Estimates of the variability associated with experimentally derived estimates of digestion coefficients and recovery rates were taken from Chapter 2. Estimates of variability associated with otolith size - fish weight relationships were taken from Leopold *et al.* (Leopold *et al.*, 2001) and from GJ Pierce & MB Santos (Pers. Comm.) for cephalopod beak size - cephalopod weight. We assumed that seal population estimates and the estimate of grey seal daily energy requirement had coefficients of variation of 10%.

For estimates of diet composition within each region/season, 95% confidence limits were estimated as the 2.5%-ile and 97.5%-ile of the bootstrapped distributions from a thousand replications.

3.2.7 Diet Quality

To estimate diet quality, the average energy density predicted to be represented in the sample of scats was compared regionally and seasonally. Following Spitz *et al.*, (2012), for each individual scat, estimated mass for each prey species w_j (g), were converted to their energy value, using published energy densities E_j (cal g-1) (Murray and Burt, 1977; Clarke *et al.*, 1985): where n_j is the number of otoliths of species j, w_{ij} is the weight of otoliths i of species j.

$$Total\ calories_j = \left(\sum_{i=1}^{n_j} w_{ij}\right) x\ E_j$$

The energy values of all prey species were then summed within each scat to give the total energy value represented by each scat. Mean energy density (diet quality) in each scat was calculated as the total calories divided by the total weight represented by the prey remains recovered from each scat.

$$Mean\ calorific\ density\ of\ diet = \frac{Total\ calories_j}{\sum w_{ij}}$$

Differences in diet quality were investigated using generalised linear models (GLM) with a factorial analysis of variance (ANOVA) design for categorical variables, a Gaussian error distribution and identity link function. Shetland a region which has experienced a rapid decline in harbour seal numbers in recent years was chosen as the Intercept region. Three models were tested: a region model, a season model and a region + season model. The best model was selected using Akaike's Information Criterion (AIC, Akaike, 1973). Forward stepwise selection was performed using the open source software R (R Core Team, 2013).

3.2.8 Prey size

Distributions of fish length were generated for those species making major contributions to the diet. Fish lengths were estimated using equations relating otolith width/ length to fish length from Leopold *et al.*, (2001) and from otolith measurements corrected for digestion.

GLMs using a factorial ANOVA design for categorical variables with a Gaussian error distribution and identity link function were used to investigate whether there were differences in the length of fish eaten between seasons and regions. Both region and season were tested as separate explanatory variable before a third model was run testing the relationship between the two variables beyond their independent affect. The best model using each individual and combined covariates was determined using Akaike's Information Criterion (AIC, Akaike, 1973). Forward stepwise manual model selection was performed using the open source software R (R Core Team, 2013).

3.3. Results

Harbour seal diet was sampled seasonally at major haul-out sites in Scotland and The Wash, England. Between March 2010 and December 2013 1,617 harbour seal haul-out surveys were conducted and 901 haul-out sites were searched for scats. On 549 (61.0%) occasions the haul-out site was classified as a harbour seal site and on 69 (7.7%) occasions the haul-out site was classified as a grey seal site.

3.3.1 Diet sampling

The number of scats collected across the harbour seal Management Regions in different seasons varied substantially (Table 3.5). The reasons for not collecting many scats included: weather conditions unsuitable for accessing haul-out sites, the behaviour of the seals tending to haul-out at the water's edge, or on rocks covered with weed or very few animals hauled out. The greatest numbers of scats containing prey remains were collected in the summer and/or autumn (see Appendix 3.2 for details on the numbers of scats and prey remains recovered and measured).

In some regions/ seasons no scats were collected and in others the number of scats containing hard prey remains was very small (Table 3.5). In Scotland the majority of scats were collected from June 2010 – May 2011 and in England from June 2011 – May 2012. In an effort to improve sample size some further scat collections were conducted in Shetland and Orkney September 2011. It was not however, possible to conduct extra scat collections in all regions/ seasons with very small sample size and so some were excluded from analysis (Table 3.6).

Table 3.5: Number of harbour seal scat samples containing hard prey remains (fish otoliths and cephalopod beaks), the number of hard prey remains recovered and the number and proportion measured for each season and region in Scotland and The Wash, England. WC = west coast of Scotland.

Region	Season	Scats containing otoliths/ beaks	Otoliths/ beaks recovered	Otoliths/ beaks measured	Proportion of otoliths/ beaks measured
The Wash	Summer	122	3534	2473	0.70
The Wash	Autumn	81	1371	1178	0.86
The Wash	Winter	62	1419	741	0.52
The Wash	Spring	23	614	317	0.52
SE Scotland	Summer	13	1821	610	0.33
SE Scotland	Autumn	13	1108	590	0.53
SE Scotland	Winter	4	3100	829	0.27
SE Scotland	Spring	9	197	106	0.54
Moray Firth	Summer	89	10509	3752	0.36
Moray Firth	Autumn	21	2078	764	0.37
Moray Firth	Winter	52	1406	742	0.53
Moray Firth	Spring	103	6528	2700	0.41
Orkney	Summer	117	4142	2391	0.58
Orkney	Autumn	113	1377	914	0.66
Orkney	Winter	4	152	72	0.47
Orkney	Spring	23	790	422	0.53
Shetland	Summer	47	1654	860	0.52
Shetland	Autumn	111	2622	1642	0.63
Shetland	Spring	28	491	373	0.76
Outer Hebrides	Autumn	7	81	81	1.00
Outer Hebrides	Winter	6	718	304	0.42
Outer Hebrides	Summer	99	1584	1180	0.74
WC – north	Summer	93	3095	2530	0.82
WC – north	Autumn	12	115	106	0.92
WC – north	Winter	1	35	35	1.00

WC – north	Spring	43	468	420	0.90
WC – central	Summer	82	1963	1563	0.80
WC – central	Autumn	139	2693	1790	0.66
WC – central	Winter	71	2399	1520	0.63
WC – central	Spring	80	656	603	0.92
WC – south	Summer	83	3421	2783	0.81
WC – south	Autumn	134	1971	1565	0.79
WC – south	Winter	34	398	368	0.92
WC – south	Spring	57	1024	905	0.88

Table 3.6: Summary of the region/season combinations of data that were analysed to estimate the diet of harbour seals in Scotland and The Wash, England. Regions/quarters shaded in grey were not analysed.

Management Regions	**Summer**	**Autumn**	**Winter**	**Spring**
The Wash, England	Y	Y	Y	Y
SE Scotland	Y			
Moray Firth	Y	Y	Y	Y
Shetland	Y	Y*		Y
Orkney	Y	Y*		Y
Outer Hebrides	Y			
W coast north	Y			Y
W coast central	Y	Y	Y	Y
W coast south	Y	Y	Y	Y
SW Scotland				

*Samples collected in a subsequent year due to low sample size

3.3.2 Diversity of prey in harbour seal diet

The number of otoliths/beaks of the main prey recovered from scats is detailed in Appendix 3.2. Greater than 1,000 otoliths were recovered for 12 species/higher taxa across all regions and seasons. Sandeel otoliths were the most common prey remains recovered (29,092 otoliths) followed by gobies *Gobiidae* (5,479), Norway pout (4,862), poor cod (4,421), whiting (4,421), plaice (2,765), dragonet (1,591), unidentified gadid

(1,504), blue whiting *Micromesistius poutassou* (1,220), unidentified flatfish (1,170), cod (1,118) and saithe *Pollachius virens* (1,072).

Regional variation in the species richness and evenness of prey in the diets of harbour seals around Britain was examined on a seasonal basis (Table 3.7). The standardised (rarefied) species richness was smaller than the observed number of species as expected (Table 3.7); standardised species richness is hereafter referred to simply as species richness.

In most regions, species richness (S) in the summer ranged from 18 to 21 species with the greatest number of species recovered in the West coast – south region (S =27). However, the species evenness was more variable (Table 3.7). The Outer Hebrides, West coast – north, central and south regions and The Wash, England all had a relatively even distribution of abundance amongst the species eaten (PIE >0.7). Harbour seals from the Northern Isles showed less evenness in the summer diet (PIE <0.4) and Moray Firth seals had a diet of very uneven abundance of prey throughout the seasons (PIE <0.2).

The greatest number of species recovered in the autumn was in the West coast central and south regions (S >18) however similar levels of species richness (S = 13-14) were seen in all other regions: The Wash, Moray Firth, Orkney and Shetland. The autumn diet followed a similar pattern of evenness as in summer with seals eating a more even diet (PIE >0.7) in the West coast central and south regions and in The Wash, while in Orkney and Shetland the diet of harbour seals was more uneven (PIE <0.5).

In winter the greatest number of species was recovered in the West coast – central region (S = 26) with lesser numbers eaten in The Wash and West coast – south regions (S = 18) and Moray Firth (S = 13). Greater evenness in the diet was found in both West coast sites (PIE >7.8), a moderately even distribution of abundance amongst species in the diet was observed for the Wash (PIE = 0.61) and the least even diet was recorded for the Moray Firth (PIE = 0.19). The number of scats collected from regions of population decline in winter was not great enough to include in the diet analyses.

Harbour seals in The Wash and the Moray Firth both had low species richness in the diet in spring (S = 9-10). Orkney, Shetland and the West coast – north regions had moderate species richness (S = 12-16) and the greatest number of species eaten was detected in the West coast - central and south regions (S = 20-21). The greatest evenness in the diet was also detected in the West coast - central and south regions (PIE = 0.84-0.87). Despite similar species richness in Orkney, Shetland and the West coast – north, Shetland and West coast – north diets showed much greater evenness in diet (PIE ≥0.69) than in Orkney where the diet was very uneven (PIE = 0.19). Similarly the proportion of each species was very different in the Moray Firth and Wash diets. The Moray Firth diet was highly specialised on a few species (PIE = 0.05) while The Wash diet was more even (PIE = 0.45).

3.3.3 Diet composition

The diet of harbour seals expressed as percentage by weight of each species is given in Table 3.8 and summarised by prey type (gadoids, flatfish etc.) in Appendix 3.3 and Figure 3.4. The 95% confidence limits are presented by prey type and species in Appendices 3.4 and 3.5 respectively.

3.3.3.1 The Wash, England

Seasonal differences in diet composition were evident in The Wash (Table 3.8 A and Figure 3.4 A). In the summer, sandy benthic species (43.3%), flatfish (28.4%) and sandeel (22.2%) dominated the diet. Dragonet was the main prey item and the main flatfish were plaice, Dover sole (*Solea solea*) and dab. Large gadoids contributed <4% in summer.

Autumn diet in The Wash was dominated by flatfish (37.1%) with major contributions of plaice, Dover sole, lemon sole (*Microstomus kitt*) and unidentified flatfish. The large gadoid contribution to the diet was dominated by whiting (30.3%) and dragonet was the second most prolific prey species by weight (19.1%).

In winter, after large gadoids (mainly whiting 22.4%) the major prey groups in the diet were; scorpion fish (bullrout and sea scorpion) and sandy benthic prey (dragonet and goby). Pelagic species showed a seasonal peak (14.1%; made up of sprat *Sprattus sprattus* and herring) and flatfish a seasonal low (<14%). Cephalopod contribution to the diet peaked in winter.

In spring, the highest contribution was from flatfish, dominated by Dover sole. Other major spring prey were; dragonet, goby and bullrout. Sandeel, large gadoids and pelagic species made very small contributions to the spring diet

3.3.3.2 South east Scotland

The diet of harbour seals in southeast Scotland (pooled across all seasons) was dominated by flatfish (45.1%) with major contributions of sandeel (18.4%) and large gadoids (14.1%, Table 3.8 B, Figure 3.4 B). Lesser prey were pelagic species (8.3%). Species contributions to the diet revealed plaice as the dominant prey species overall (28.1%), with dab (7.3%) and flounder (5.4%) as other important flatfish contributors. Whiting (8.3%) and cod (3.4%) were the main gadoid prey recovered and sprat (4.6%) and mackerel (*Scomber scombrus* 3.6%) the main pelagic prey. *Loligo* species made a greater contribution to the diet than any cephalopod in any other region/season.

3.3.3.3 Moray Firth

Sandeel dominated the diet in all seasons in the Moray Firth contributing a minimum 58.3% in summer and maximum 85.5% in spring (Figure 3.4 C, Table 3.8 C). Flatfish peaked in the diet in summer (31.5%) and the main prey were dab (15.3%) and plaice (11.0%). Bullrout contributed 3.4%. The summer contribution of other prey groups was very small; scorpion fish <4%, gadoids and cephalopod species <3%, *Trisopterus* species, sandy benthic and salmonid prey < 1%.

In autumn bullrout (6.5%) and unidentified salmonid species (5.8%), flatfish (4.7%) and gadoids (4.2%) sustained the diet of harbour seals around the dominant prey sandeel (75.2%). In winter, pelagic and large gadoid prey in the diet peaked, constituting mainly sprat (8.9%) and saithe (5.6%), respectively. Flatfish contribution to the diet was dominated by flounder (5.9%). In spring, after sandeels (85.5%) flounder was the most important prey species (6.3%). Saithe and sprat made small contributions <3%.

Table 3.7: Variation in the number of scats collected with hard prey remains, observed and rarefied species richness and species evenness across each region and season. WC = west coast of Scotland.

Region	No. scats	Observed No. prey species	Species richness (S)	Species Evenness (PIE)
Summer				
The Wash	122	23	18	0.77
Moray Firth	89	25	18	0.16
Orkney	117	30	20	0.33
Shetland	47	21	17	0.37
Outer Hebrides	99	23	18	0.71
WC - north	93	26	21	0.75
WC - central	82	27	21	0.81
WC - south	83	36	27	0.81
Autumn				
The Wash	81	25	14	0.8
Moray Firth	21	16	14	0.06
Orkney	113	23	13	0.49
Shetland	111	27	14	0.48
WC - central	139	32	18	0.73
WC - south	134	43	21	0.81
Winter				
The Wash	62	24	18	0.61
Moray Firth	52	17	13	0.19
WC - central	71	37	26	0.82
WC - south	34	21	18	0.79
Spring				
The Wash	23	11	10	0.45
Moray Firth	103	19	9	0.05
Orkney	23	17	14	0.19
Shetland	28	14	12	0.69
WC - north	43	23	16	0.74
WC - central	80	31	20	0.87
WC - south	57	29	21	0.84

3.3.3.4 Orkney

In Orkney a high percentage of the diet was made up of sandeels in summer and spring but their contribution to the diet was small in autumn when pelagic prey peaked in the diet (Figure 3.4 D and Table 3.8 D). Large gadoid prey were consistently important across summer, autumn and spring. Due to small sample size the winter diet is not described.

Main prey of harbour seals in summer was sandeels (49.6%) and large gadoids (30.0%, mainly cod 22.5%). Lesser contributors to the summer diet were flatfish (7.4%) and pelagic prey (7.0%).

The autumn diet of harbour seals in Orkney was dominated by pelagic prey (herring 32.8% and mackerel 7.4%) and large gadoid fish (mainly cod 26.0%). Sandeel was the next most important prey type making up 13.3% of the diet.

In spring sandeels peaked in the diet (61.8%) and large gadoids (31.6%) were also important (mainly saithe 24.1%). Pelagic prey (3.2%), *Trisopterus* species (1.5%) and cephalopods (1.0%) were lesser contributors to the diet.

3.3.3.5 Shetland

The diet of harbour seals in Shetland was most similar in summer and autumn when diet composition was split across pelagic prey, sandeel and large gadoid fish (Table 3.8 E, Figure 3.4 E). In spring pelagic prey and large gadoid fish remained important in the diet however, sandy benthic prey peaked while the contribution of sandeel was seasonally low.

In summer pelagic prey (36.1%, mostly herring) and sandeel (33.4%) dominated with major contributions of large gadoid prey (18.2%, mainly ling *Molva molva*). Sandeel (29.7%), large gadoids (26.0%, mainly saithe) and pelagic prey (24.6%) were also the main prey types consumed by harbour seals in Shetland in autumn.

In spring herring was an important constituent of the diet (39.4%) as was dragonet (20.5%). Large gadoids made up 25.6% of the spring diet and comprised mostly saithe and rockling. Sandeel made a small contribution to the diet in spring (5.9%).

3.3.3.6 *Outer Hebrides*

The summer diet of the Outer Hebrides comprised *Trisopterus* species (23.9%) and pelagic fish (22.3%) as major prey (Table 3.8 F, Figure 3.4 F). Large gadoids (16.7%), scorpion fish (unidentified *Cottidae* species 15.8%) and sandeel (12.7%) were also important and Octopus made up 3.7% of the diet. At a species level Norway pout dominated the diet (19.3%) and mackerel (12.3%) and herring (7.3%) dominated the pelagic prey group. Individual contributions of large gadoid species were small: rockling (3.8%), cod (3.6%), ling (2.6%) and whiting (2.2%).

3.3.3.7 *West coast - north*

In the West coast – north region; large gadoid, pelagic fish and *Trisopterus* spp. were major components of harbour seal diet (Table 3.8 G, Figure 3.4 G). In summer the large gadoid proportion of the diet (49.8%) was made up of mostly cod (12.9%), saithe (8.8%) whiting (8.6%) and blue whiting (7.0%). Similar proportions of Norway pout (9.9%) and poor cod (8.5%) were eaten in summer while herring dominated the pelagic contribution (15.1% herring and 5.6 % mackerel). Squid made very little contribution in summer (<1%)

In spring the largest contributor to the diet was large gadoids (ling 16.1%, saithe 7.6% and rockling (5.5%). Norway pout dominated the *Trisopterus* species contribution (16.0%) and contributions of pelagic species: mackerel and herring were similar (11.8% and 9.4% respectively). *Loligo* species constituted 5.6% of the diet.

3.3.3.8 *West coast – central*

Large gadoid fish dominated the diet of West coast – central harbour seals in all seasons except autumn when pelagic prey dominated (Figure 3.4 H, Table 3.8 H).

In the summer blue whiting (17.2%) and whiting (14.9%) were the dominant large gadoid prey items. Summer showed high importance of unidentified *Cottidae* species (18.6%) and *Trisopterus* species (19.0%). Pelagic fish (9.6%) and sandeel (5.9%) was a lesser contributors to the summer diet.

Large gadoid prey in the diet of harbour seals in winter was mostly blue whiting (16.7%), whiting (9%) and ling (7%). *Trisopterus* species (18.1%) and sandy benthic fish (15.5%, mainly dragonet) were also important. The smallest contributions of pelagic fish (6.3%) and sandeel (2.9%) were eaten in this season.

Pelagic fish contributions were greatest in autumn (28.1% mackerel and 13.1% herring). Sandy benthic prey (20.1%) and large gadoid prey (13.2%) were also important in the autumn diet. Dragonet was the only sandy benthic prey species present and cod was the most important large gadoid prey item (4.0%). Sandeel (7.0%) and flatfish (6.7%) peaked in the diet in autumn and *Trisopterus* species made only a small contribution (5.1%).

In spring, blue whiting (18.6%), haddock (9.7%), cod (7.7%) and saithe (7.1%) were the main large gadoid prey eaten. Pelagic fish (31.1%) were also a major component of the diet with more mackerel eaten than herring. *Trisopterus* species (5.1%), flatfish (5.4%) and sandeel (3.7%) were lesser contributors to the diet in spring and cephalopod presence peaked (*Eledone* species 2.2% and *Loligo* species 2.0%)

3.3.3.9 West coast - south

Sandeel contributed very little to the diet of West coast – south harbour seals (<2%) in most seasons and large gadoid contribution was high (>42%, Figure 3.4 I and Table 3.8 I). The summer diet was dominated by whiting (23.6%), haddock (16.3%) and unidentified large gadoid species (7.3%). Contributions of pelagic fish were also important; mackerel showed a seasonal peak (10.8%) as did the sandy benthic prey dragonet (12.7%). The *Trisopterus* species contribution (8.5%) was split between Norway pout and poor cod.

In autumn herring was the dominant prey species overall (26.2%) and haddock (21.2%) the dominant gadoid species with whiting (6.8%) and cod (6.4%) as lesser contributors. Dragonet (9.6%) and mackerel (5.3%) were also important in the diet. In winter predation on gadoids was high: cod (19.7%), whiting (19.1%), saithe (13.5%), haddock (13.4%) and ling (6.9%). Poor cod contribution was greatest for the region (7.2%) and pelagic contribution to the diet in winter was least (<6.0%). Dragonet contribution was also relatively small (6.1%) and no flatfish were recorded in the winter diet.

In spring large gadoids dominated the diet including; haddock (26.5%), cod (21.7%) and whiting (13.6%) with lesser contributions of unidentified large gadoid species (5.3%) and poor cod (5.1%). Dragonet contribution was least (1.6%) in spring and flatfish contribution was greatest (witch 2.1%). Pelagic contributions were also low (herring 4.6% and mackerel 3.9%).

Table 3.8: Seasonal variation in harbour seal diet (expressed as the percentage of each species in the diet by weight). Prey species listed are those contributing >2% in any season. Species which contributed >10% are in bold.

A) The Wash

Species	Summer	Autumn	Winter	Spring
Cod	2.4	0.2	4.1	0.0
Whiting	1.5	**30.3**	**22.4**	2.2
Sandeel	**22.2**	6.6	5.9	3.4
Plaice	9.0	**10.3**	2.0	0.6
Lemon sole	1.9	5.9	6.5	0.0
Unidentified flatfish	2.3	5.2	0.7	0.2
Dover sole	6.0	9.6	1.9	**34.7**
Flounder (Butt)	3.7	1.1	0.0	0.0
Dab	5.0	4.0	0.7	0.7
Dragonet	**38.8**	**19.1**	8.8	**29.7**
Goby	4.2	0.6	6.2	**16.3**
Bullrout	0.0	2.0	**14.1**	**10.2**
Sea Scorpion	0.1	0.3	5.5	0.0
Herring	0.0	0.1	5.9	0.0
Sprat	0.0	0.0	7.5	1.8
Loligo	0.0	1.4	3.8	0.0

B) SE Scotland

Species	**All**
Cod	3.8
Whiting	8.3
Sandeel	**18.4**
Plaice	**28.1**
Unidentified flatfish	3.8
Flounder (Butt)	5.4
Dab	7.3
Goby	2.2
Mackerel	3.6
Sprat	4.6
Loligo	8.4

C) Moray Firth

Species	**Summer**	**Autumn**	**Winter**	**Spring**
Saithe	0.2	1.5	5.6	1.1
Sandeel	58.3	75.1	69.0	85.4
Plaice	11.0	1.8	0.9	0.6
Unidentified flatfish	3.4	0.6	1.4	1.8
Flounder (Butt)	1.1	0.9	5.8	6.3
Dab	15.3	1.4	2.8	0.5
Bullrout	3.3	6.5	0.0	0.3
Sprat	0.0	0.0	8.9	2.7
Unidentified Salmonid	0.7	5.8	0.0	0.0
Loligo	2.4	1.0	0.0	0.0

D) Orkney

Species	**Summer**	**Autumn**	**Spring**
Cod	**22.5**	**26.0**	4.1
Haddock	0.7	3.3	0.5
Saithe	2.5	2.0	**24.1**
Ling	2.6	3.0	0.0

Sandeel	**49.6**	**13.3**	**61.8**
Plaice	2.4	1.0	0.0
Flounder (Butt)	2.2	0.0	0.0
Dab	1.4	3.8	0.0
Dragonet	1.2	3.0	0.0
Sea Scorpion	2.4	0.1	0.0
Mackerel	0.9	7.4	2.3
Herring	6.0	**32.8**	0.9

E) Shetland

Species	**Summer**	**Autumn**	**Spring**
Saithe	4.0	**21.9**	**12.9**
Ling	**12.1**	0.7	1.7
Rockling	0.9	0.0	8.7
3-bearded rockling	0.0	0.0	2.2
Poor cod	1.7	5.1	0.7
Norway pout	7.8	0.5	4.2
Sandeel	**33.4**	**29.7**	5.9
Plaice	2.0	0.2	0.0
Lemon sole	0.0	2.7	0.0
Dragonet	0.0	0.8	**20.5**
Mackerel	0.7	**10.3**	1.9
Herring	**35.1**	**14.3**	**39.4**
Garfish	0.0	9.4	0.0

F) Outer Hebrides

Species	**Summer**
Cod	3.5
Whiting	2.2
Ling	2.6
Rockling	3.8
Poor cod	4.1
Norway pout	**19.3**

Sandeel	**12.7**
Dragonet	2.7
Unidentified *Cottidae*	**15.8**
Mackerel	**12.3**
Herring	7.3
Horse mackerel (Scad)	2.7
Eledone	3.7

G) West coast – north

Species	**Summer**	**Spring**
Cod	**12.9**	4.9
Whiting	8.6	2.0
Saithe	8.8	7.6
Ling	8.6	**16.1**
Rockling	0.0	5.5
Blue whiting	7.0	0.5
Poor cod	8.5	5.8
Norway pout	9.9	**16.0**
Norway pout / Poor cod	2.3	0.0
Sandeel	2.4	9.6
Mackerel	5.6	**11.8**
Herring	**15.1**	9.4
Loligo	0.5	5.6

H) West coast - central

Species	**Summer**	**Autumn**	**Winter**	**Spring**
Cod	1.8	4.0	3.9	7.7
Whiting	**14.9**	1.5	9.3	1.0
Haddock	0.5	2.6	2.0	9.7
Saithe	0.0	1.8	5.7	7.1
Ling	1.2	1.5	7.5	3.3
Unidentified gadid	4.6	0.5	2.7	1.2
Saithe or Pollock	0.0	0.3	3.3	0.0

Hake	2.2	0.0	1.1	0.9
Blue whiting	**17.2**	0.7	**16.7**	**18.6**
Poor cod	7.9	3.3	**12.6**	3.2
Norway pout	**10.8**	1.5	5.1	1.8
Sandeel	5.9	7.0	2.9	3.7
Plaice	0.2	2.1	0.0	0.6
Lemon sole	0.5	0.2	0.0	2.5
Dab	0.0	3.2	0.2	0.6
Dragonet	0.8	**20.1**	**15.4**	0.6
Unidentified *Cottidae*	**18.6**	1.8	0.0	0.0
Mackerel	5.8	**28.1**	0.2	**25.5**
Herring	3.8	**13.1**	4.2	5.4
Horse mackerel (Scad)	0.0	4.1	1.4	0.1
Eledone	1.2	0.6	0.0	2.2

I) West coast – south

Species	Summer	Autumn	Winter	Spring
Cod	4.9	6.4	**19.7**	**21.7**
Whiting	**23.6**	6.8	**19.0**	**13.6**
Haddock	**16.3**	**21.2**	**13.4**	**26.5**
Saithe	1.1	1.0	**13.5**	3.4
Ling	0.9	1.9	6.9	0.0
Rockling	0.2	3.0	0.0	0.1
Unidentified gadid	7.3	2.0	3.3	5.3
Blue whiting	5.0	0.3	0.8	3.5
Poor cod	4.0	4.8	7.2	5.1
Norway pout	4.0	0.1	0.6	3.4
Witch	0.8	0.9	0.0	2.1
Dragonet	**12.7**	9.6	6.1	1.6
Mackerel	**10.8**	5.3	2.0	3.9
Herring	2.4	**26.2**	4.0	4.6

A) Outer Hebrides

Species	**Summer**
Cod	3.6
Whiting	2.2
Ling	2.6
Rockling	3.8
Poor cod	4.1
Norway pout	**19.3**
Sandeel	**12.7**
Dragonet	2.7
Unidentified *Cottidae*	**15.8**
Mackerel	**12.3**
Herring	7.3
Horse mackerel (Scad)	2.7
Eledone	3.7

B) West coast – north

Species	**Summer**	**Spring**
Cod	**12.9**	4.9
Whiting	8.6	2.0
Saithe	8.8	7.6
Ling	8.6	**16.1**
Rockling	0.0	5.5
Blue whiting	7.0	0.5
Poor cod	8.5	5.8
Norway pout	9.9	**16.0**
Norway pout or Poor cod	2.3	0.0
Sandeel	2.4	9.6
Mackerel	5.6	**11.8**
Herring	**15.1**	9.4
Loligo	0.5	5.6

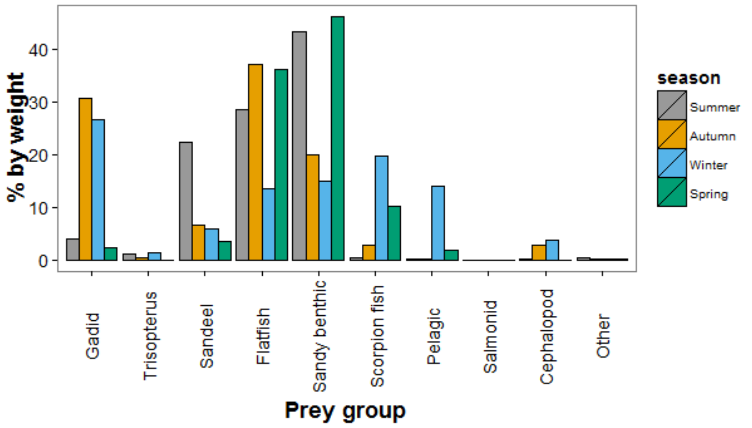
C) West coast - central

Species	**Summer**	**Autumn**	**Winter**	**Spring**
Cod	1.8	4.0	3.9	7.7
Whiting	**14.9**	1.5	9.3	1.0
Haddock	0.5	2.6	2.0	9.7
Saithe	0.0	1.9	5.7	7.1
Ling	1.2	1.5	7.5	3.3
Unidentified gadid	4.6	0.5	2.7	1.2
Saithe or Pollock	0.0	0.3	3.3	0.0
Hake	2.2	0.0	1.1	0.9
Blue whiting	**17.2**	0.7	**16.7**	**18.6**
Poor cod	7.9	3.3	**12.6**	3.2
Norway pout	**10.8**	1.5	5.1	1.8
Sandeel	5.9	7.0	2.9	3.7
Plaice	0.2	2.1	0.0	0.6
Lemon sole	0.5	0.2	0.0	2.5
Dab	0.0	3.2	0.2	0.6
Dragonet	0.8	**20.1**	**15.5**	0.6
Unidentified *Cottidae*	**18.6**	1.8	0.0	0.0
Mackerel	5.8	**28.1**	0.2	**25.5**
Herring	3.8	**13.1**	4.2	5.4
Horse mackerel (Scad)	0.0	4.2	1.4	0.1
Eledone	1.2	0.6	0.0	2.2

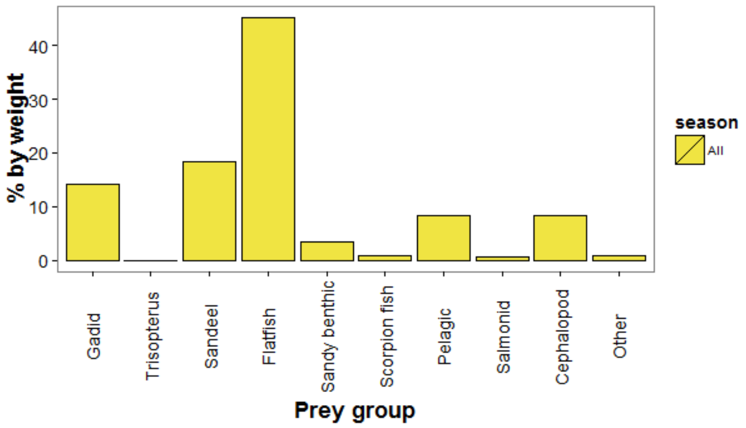
D) West coast - south

Species	**Summer**	**Autumn**	**Winter**	**Spring**
Cod	4.9	6.4	**19.7**	**21.7**
Whiting	**23.6**	6.8	**19.1**	**13.6**
Haddock	**16.3**	**21.2**	**13.4**	**26.5**
Saithe	1.1	1.0	**13.5**	3.4
Ling	0.9	1.9	6.9	0.0
Rockling	0.2	3.0	0.0	0.1
Unidentified gadid	7.3	2.0	3.3	5.3
Blue whiting	5.0	0.3	0.8	3.5
Poor cod	4.0	4.8	7.2	5.1
Norway pout	4.0	0.1	0.6	3.4
Witch	0.8	0.9	0.0	2.1
Dragonet	**12.7**	9.6	6.1	1.6
Mackerel	**10.8**	5.3	2.0	3.9
Herring	2.4	**26.2**	4.0	4.6

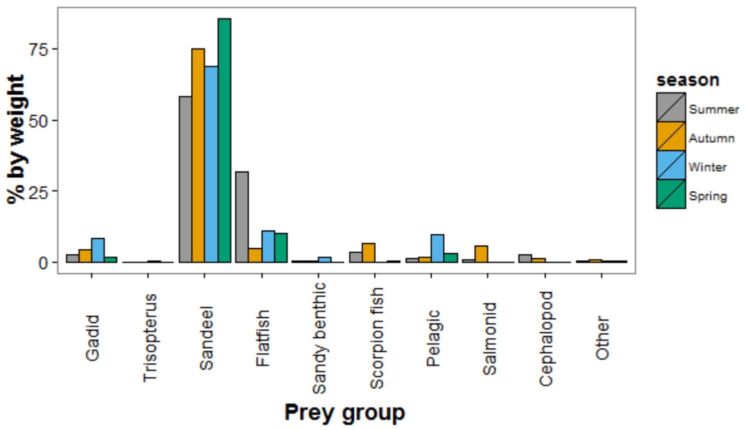
A) The Wash



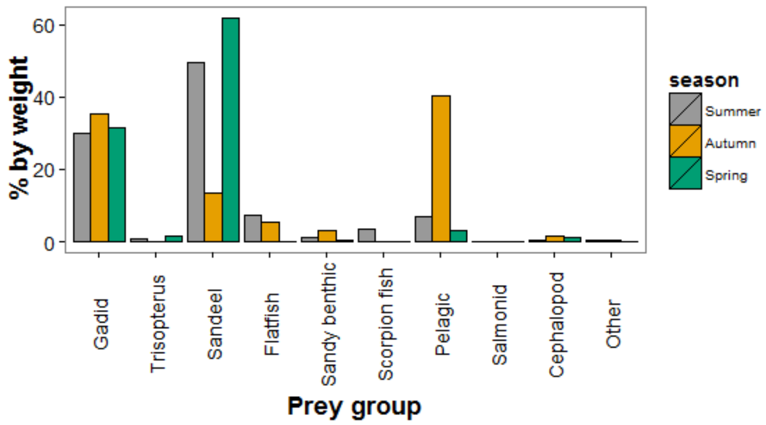
B) SE Scotland



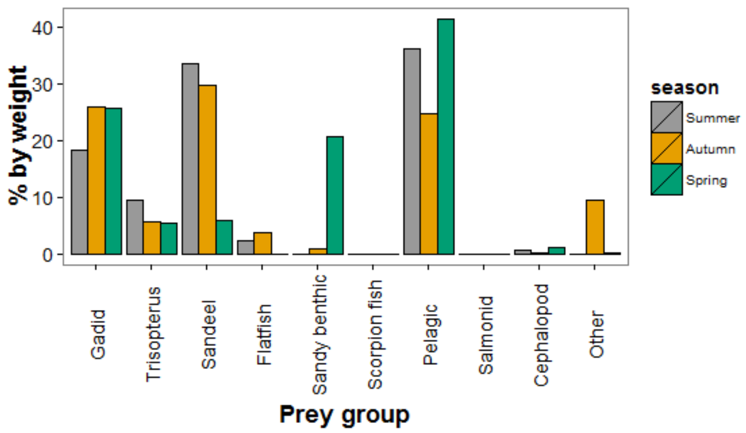
C) Moray Firth



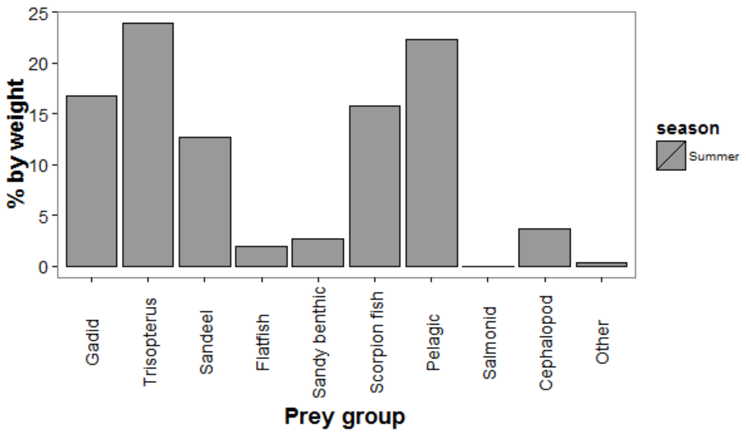
D) Orkney



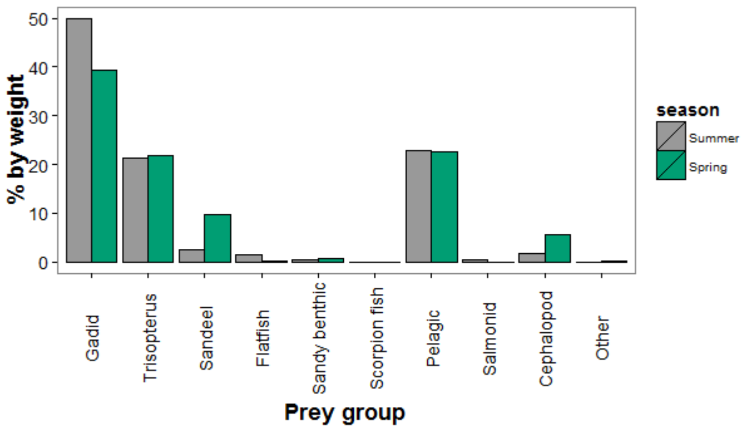
E) Shetland



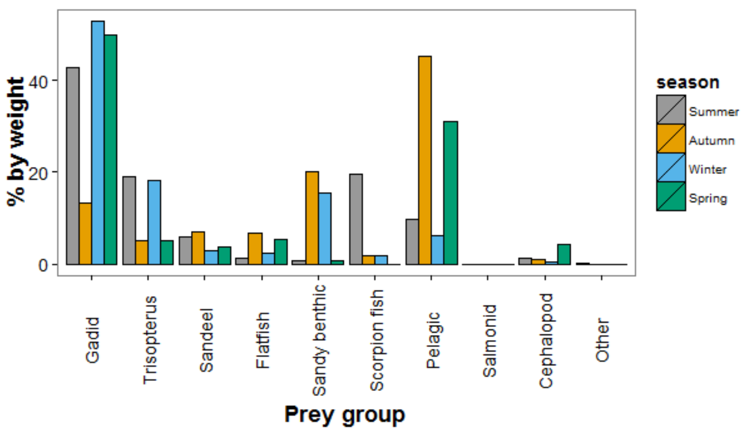
F) Outer Hebrides



G) West coast – north



H) West coast – central



G) West coast – south

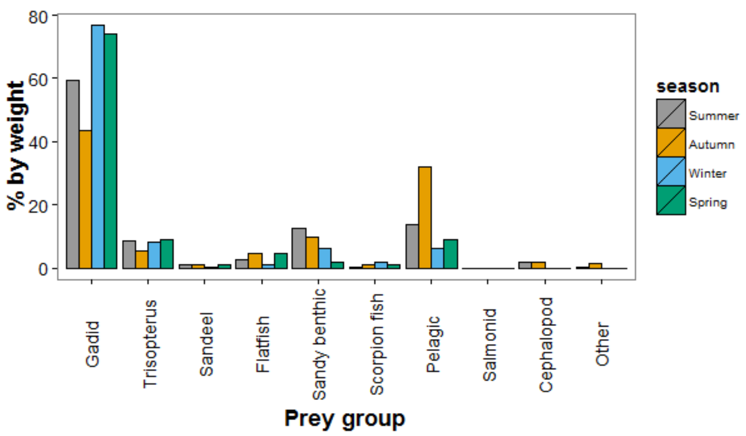


Figure 3.4: Seasonal variation in the diet of harbour seals around the UK. Diet is expressed as the percentage of each prey group in the diet, by weight.

3.3.4 Diet quality

The mean energy densities of the diet for each region/ season ranged from 905 to 1313 (cal.g^{-1}, Table 3.9).

Table 3.9: Mean energy density of the diet (cal.g^{-1}) ± SE of harbour seals around the UK in summer, autumn, winter and spring.

A) Summer

Region	Calorific density (cal.g-1)	SE
The Wash	1008	13
Moray Firth	1142	28
Orkney	1114	22
Shetland	1221	37
Outer Hebrides	1118	26
WC – north	1114	28
WC – central	1026	25
WC – south	906	23

B) Autumn

Region	Calorific density (cal.g-1)	SE
The Wash	928	14
Moray Firth	1189	49
Orkney	1156	30
Shetland	1113	25
Outer Hebrides	-	-
WC – north	-	-
WC – central	1152	26
WC – south	1025	27

C) Winter

Region	Calorific density (cal.g-1)	SE
The Wash	1125	32
Moray Firth	1203	40
Orkney	-	-
Shetland	-	-
Outer Hebrides	-	-
WC – north	-	-
WC – central	957	20
WC – south	936	38

D) Spring

Region	Calorific density (cal.g-1)	SE
The Wash	1142	44
Moray Firth	1259	23
Orkney	1057	46
Shetland	1132	52
Outer Hebrides	-	-
WC – north	1102	33
WC – central	1091	34
WC – south	915	18

Region had the lowest AIC, though the two way interaction between region and season was within 1 unit. Based on the principle that increasing the number of parameters in the model always improves the goodness of the fit, region was selected as the best model for describing differences in harbour seal diet quality (Table 3.10 A). The diet of harbour seals in the Moray Firth was significantly better quality than average ($t = 2.5$, $p = 0.01$), the lowest quality diets were consumed by harbour seals in the West coast – south ($t = -8.2$, $p < 0.001$), The Wash ($t = -5.97$, $p < 0.001$) and West coast – central ($t = -2.95$, $p = 0.003$, Table 3.10 B).

Table 3.10: Summary results of the GLMs to investigate differences in diet quality across regions and seasons and their relationship. A) Model diagnostics and AIC values. B) Parameter estimates for each region.

A)

Model	**Null deviance**	**Null DF**	**Residual deviance**	**Residual DF**	**AIC**	
Region	165607267	2241	151587970	7	31315	*
Season	165607267	2241	165562890	3	31505	
Region+Season	165607267		151258451	10	31316	

* indicates the lowest AIC

B)

Model = Region	**Value**	**SE**	**t-value**	**P**
Coefficient				
Intercept (Shetland)	1140.64	18.19	62.7	<0.001
The Wash	-131.58	22.04	-5.97	<0.001
Moray Firth	62.37	24.2	2.57	0.01
Orkney	-14.68	23.29	-0.63	
Outer Hebrides	-12.71	30.61	-0.42	
WC – north	-31.92	28.04	-1.14	
WC – central	-66.78	22.66	-2.95	0.003
WC – south	-186.74	22.57	-8.27	<0.001

3.3.5 Size of prey consumed by seals

Fish length-frequency distributions across all seasons and regions were constructed for those species which were major contributors to the diet: cod, whiting, haddock, poor cod, Norway pout, plaice, dab, mackerel, herring, sandeel and dragonet (Appendix 3.6). As the lengths are estimated caution should be used interpreting the tails of the distributions as these likely represent associated error. Overall size range of the main prey are summarised in Table 3.11.

The distributions of prey lengths show that seals predated mainly on small fish < 30 cm. The mean size of: large gadoids consumed ranged between 17.4 and 24.3 cm, *Trisopterus* spp. 12.4 – 14 cm, flatfish 14.2 – 17.4 cm, pelagic fish 26.6 – 32.6, sandeel 15.5 cm and dragonet 19.2 cm (Table 3.11). Fish length ranged from minimum -3.2 cm (dragonet, see *below Table 3.11) to maximum 56.8 cm (mackerel). Mackerel had the largest minimum fish size eaten (15.54 cm).

Table 3.11: Estimated lengths of the main prey eaten by harbour seals.

	Estimated ingested fish length (cm)				**Number**
Species	**Minimum**	**Maximum**	**Mean**	**± SD**	**of fish**
Cod	4.2	55.0	23.6	11.3	730
Whiting	3.3	40.0	17.4	5.5	2871
Haddock	5.2	44.7	24.3	5.3	953
Poor cod	1.4	26.0	12.4	3.8	3119
Norway pout	6.0	40.9	14.0	2.8	3458
Plaice	2.5	51.4	14.2	6.7	1673
Dab	3.1	49.9	17.4	6.4	757
Mackerel	15.5	56.8	32.6	6.8	343
Herring	8.2	43.2	26.6	5.9	863
Sandeel	1.0	42.4	15.5	4.6	11195
Dragonet	0.01*	37.0	19.2	4.8	1334

* For dragonet some of the otoliths recovered were very small, and some estimated minimum length values were negative, so the minimum length has been set to zero in

this table. This occurrence is not unexpected when fish lengths were estimated using equations relating otolith width/ length to fish length and from otolith measurements corrected for digestion.

Both regional and seasonal variation was evident in the mean size of the main prey eaten by harbour seals (Appendix 3.6 and Table 3.12). The largest cod were eaten by harbour seals on the west coast of Scotland and the smallest in the Wash, England. Haddock were largest in Shetland and Whiting largest from Orkney and Shetland, the smallest fish of both species were consumed in south east Scotland. The smallest flatfish (dab and plaice) were also eaten in the sandy bottomed central and southern North Sea (southeast Scotland and the Wash) and the largest fish were eaten in the West coast north (plaice) and central (dab) regions. Poor cod were largest from the Wash and the smallest from the Moray Firth and Norway pout largest from the Outer Hebrides and smallest from the West coast –south region. Mackerel were largest from the Moray Firth and in southeast Scotland. Contrastingly the smallest herring were eaten in the Moray Firth and southeast Scotland regions and the largest fish eaten in the Outer Hebrides, Orkney and Shetland. The largest sandeel were eaten in the Wash, Outer Hebrides, Orkney and West coast - north and central regions and the smallest in southeast Scotland. The smallest dragonet were eaten in Shetland and the largest in the Moray Firth and West coast – north regions.

In spring the largest cod, poor cod, Norway pout, mackerel and herring were eaten and the smallest dragonet, dab and sandeel (Appendix 3.6). Large cod were also eaten in autumn, along with whiting, dab, plaice and dragonet. The smallest cod, whiting and haddock (main large gadoid prey) were eaten in summer. The smallest Norway pout were eaten in autumn and the smallest poor cod and mackerel and herring were eaten in winter.

The GLM results show that the length of fish eaten by harbour seals is significantly related to region and time of year. The results were highly significant for the individual variables and region + season (Table 3.12). For all species the best model with the lowest AIC contained both region and season as covariates.

Table 3.12: Summary of the generalised linear models for estimating differences in the length of fish eaten by season and region, showing the; null and residual deviance, null and residual degrees of freedom and AIC for each model.

Model	Null deviance	Null DF	Residual deviance	DF	AIC	∆ AIC	
Cod							
Season	92404	729	76409	3	5476.7	170.7	
Region	92404	729	75334	8	5476.4	170.4	
Season+Region	92404	729	59163	11	5306		*
Haddock							
Season	26530	952	24013	3	5789.6	36.6	
Region	26530	952	25110	7	5840.2	87.2	
Season+Region	26530	952	22771		5753		*
Whiting							
Season	85590	2870	76650	3	17588	780	
Region	85590	2870	59550	8	16873	65	
Region+Season	85590	2870	58090	11	16808		*
Poor cod							
Season	44039	3118	41352	3	16923	188	
Region	44039	3118	40826	7	16891	156	
Region+Season	44039	3118	38758	10	16735		*
Norway Pout							
Season	27194	3457	26804	3	16905	1264	
Region	27194	3457	19499	6	15811	170	
Region+Season	27194	3457	18536	9	15641		*
Mackerel							
Season	15792	342	13901	3	2253.2	5.9	
Region	15792	342	15018	7	2287.7	40.4	
Season+Region	15792	342	13117	10	2247.3		*
Herring							
Season	30123	862	28891	3	5489	122.7	
Region	30123	862	25010	8	5374.5	8.2	
Region+Season	30123	862	24603	11	5366.3		*
Sandeel							
Season	239925	11194	237223	3	65964	4471	
Region	239925	11194	159972	8	61563	70	
Region+Season	239925	11194	158884	11	61493		*
Plaice							
Season	74922	1672	73908	3	11095	532	
Region	74922	1672	56281	8	10650	87	
Region+Season	74922	1672	53260	11	10563		*
Dab							
Season	30620	756	28921	3	4916	297.2	

Region	30620	756	22759	6	4740.6	121.8	
Region+Season	30620	756	19224	9	4618.8		*
Dragonet							
Season	31257	1333	29446	3	7923.6	73.6	
Region	31257	1333	28087	8	7870.6	20.6	
Region+Season	31257	1333	27533	11	7850		*

* indicates the lowest AIC for each model

3.4. Discussion

3.4.1 Assessing harbour seal diet from scat analysis

The estimation of seal diet composition from the analysis of fish otoliths and cephalopod beaks recovered from scats collected at haul-out sites is an established technique (Pierce *et al.*, 1991c; Bowen and Harrison, 1994; Hammond *et al.*, 1994b; Cottrell *et al.*, 1996; Thompson *et al.*, 1996a; Tollit and Thompson, 1996; Brown and Pierce, 1998; Hall *et al.*, 1998; Fea *et al.*, 1999; Wilson *et al.*, 2002; Hume *et al.*, 2004; Hammond and Harris, 2006; Phillips and Harvey, 2009). However, it is important to minimise sources of bias and uncertainty (Pierce and Boyle, 1991; Bowen, 2000; Tollit *et al.*, 2003; Bowen and Iverson, 2013).

3.4.1.1 Scat collection bias

Like any sampling method scat analysis assumes that the data are representative of the population to which the results are extrapolated. This means that the faeces recovered from haul-out sites should be representative of the population diet.

Mixed haul-outs of harbour and grey seals. Potential mismatches from allocating scats to particular seal species at haul-out sites based on counts and behavioural observations were reduced in this study by the use of species identification using molecular analysis. If ≥ 80% of the animals at the haul-out site were observed to be harbour seals the misclassification rate for collected scats was very low (3%). qPCR is the best technique to use when the DNA sample is small or degraded which is to be expected when using faecal samples (Matejusová *et al.*, 2013).

At mixed haul-out sites where the proportion of harbour seals at the haul-out site was ≥ 20% and <80% the misclassification rate was 17% which is similar to that presented by

Masland *et al.*, (2010) who found that 13% of scats originated from grey seals in mixed haul-out sites with an average 1:1 species ratio. Reed *et al.*, (1997) reported that, 12% of the scats collected were misclassified with respect to species (Reed *et al.*, 1997).

Based on this study it should be possible for researchers to increase the number of scats available for reliable harbour seal diet analysis. Previously scats collected at sites where the harbour seal count was < 90% of the total were discarded from any analysis or scat collections were not attempted (*e.g.*, Pierce *et al.*, 1991c; Tollit and Thompson, 1996). However, when targeting haul-out sites which are expected to contain predominantly harbour seals, based on up-to-date abundance and distribution maps, and where behavioural observations and species counts are conducted prior to disturbing seals from the haul-out site, misclassification rates of scats should be very low.

Seasonal and regional variation in diet. Because diet can vary in space and time the collections and analysis in this study were stratified according to harbour seal life history and regional management regions.

Scats represent recent or coastal feeding. Scats typically represent recent feeding (2-3 days, see Chapter 2). This is expected to introduce bias in diet estimates for wide-ranging species such as elephant seals (*Mirounga angustirostris*). In this species only a small portion of foraging effort is expected to be near haul-out sites as faecal samples rarely contain otoliths, indicating that otoliths are completely digested or excreted before animals come ashore (Harvey and Antonelis, 1994). However, telemetry studies have shown that harbour seals around the UK have a mainly coastal distribution (Cunningham *et al.*, 2009; Sharples *et al.*, 2012; Jones *et al.*, 2013) and bias should be small.

3.4.1.2 Sampling Bias

How many scats should be collected? When using scats to estimate diet it is important to ensure that sufficient samples are collected so that the sampling error that results from differences in diet among individual faeces does not become too large. Using grey seals diet as a model Hammond and Rothery (1996) suggested that approximately 100 scats should be enough. Depending on the diversity of prey in the samples Trites and Joy (2005) estimated that between 59 and 179 scats would be necessary to statistically distinguish between populations. The target for collections in this study was 100 harbour seal scats per region and season; however success was limited by weather conditions and animal behaviour. Where sample sizes were very low for a particular region/ season it was removed from further analysis.

Identification of prey hard remains. Scat analysis assumes that all prey consumed have recoverable remains. In particular, seals must eat the whole prey including the heads of fish for the analysis of otoliths. In this study otoliths and beaks alone were used for prey identification. The inclusion of other diagnostic skeletal structures has been shown to increase the detection rate for some prey species, particularly those with fragile otoliths such as salmon (*e.g.*, Olesiuk *et al.*, 1990; Tollit *et al.*, 2003; Phillips and Harvey, 2009; Gosch *et al.*, 2014). However, a high detection rate is not a requirement as long as detection has been estimated (recovery rates) and is accounted for in diet reconstruction.

Effects of digestion. If the effects of partial and complete digestion are not taken into account seal diet reconstruction using otoliths and beaks is subject to bias. Application of DCFs provides the best estimate of size and number of prey eaten. By not taking account of otolith recovery rate the number of fish eaten (particularly fish with fragile otoliths) will be underestimated and application of grey seal specific digestion coefficients may overestimate the size of prey eaten as these have been shown to be generally larger than for harbour seals (Chapter 2). These methods use comprehensive and robust estimates of digestion coefficients and recovery rates to eliminate any biases resulting from these effects; as such there is no need to consider other hard remains from prey.

Secondary prey. The presence of otoliths or beaks in seal scats which were not eaten by the seal but come from the stomachs of large fish is possible – so called secondary prey. However, the contribution of secondary prey to the estimates of diet composition is considered to be minimal – much less than 1 % (Hammond and Grellier, 2006). Other potential prey which do not possess otoliths and beaks; for example *Crustacea* are fully expected to be secondary prey as personal observations from the harbour seal feeding experiments showed that 50 % of scats contained crustacean remains, though none were ever fed to the seals while in the captive facility (Chapter 2).

3.4.2 Diversity of prey in harbour seal diet

It is commonly accepted that the dietary diversity of consumers increases as food becomes limiting (*e.g.*, Krebs *et al.*, 1977; Thompson and Colgan, 1990). I used species richness and evenness to examine the structure and dynamics of the diet of harbour seals around Britain, where the individual seal is used as the sampling unit and each scat represents a combination of what prey was available to the seal and what the individual chose to eat. I used rarefied estimates of the diversity indices, allowing for meaningful standardisation and comparison of datasets (Gotelli and Colwell, 2001).

Using prey remains to study diversity in diet is common across a variety of species *e.g.*, hen harriers (Redpath *et al.*, 2001), Steller sea lions (Merrick *et al.*, 1997), greater horseshoe bats (*Rhinolophus ferrumequinum,* Jones, 1990) and has even been used to monitor the richness and composition of prey communities (Torre *et al.*, 2004; McDowell and Medlin, 2009; Torre *et al.*, 2013). Diversity comprises two components, species richness and species evenness, and though they can be combined in some indices, this is believed to potentially obscure useful information (Magurran and McGill, 2011). A recent study of harbour seal diet in the Gulf of Alaska revealed differences in diet diversity linked to the annual life cycle. Geiger et al., (2013) found significant differences in harbour seal diet diversity between the breeding season and the moult. They proposed that both females and males restricted their foraging trips during breeding thereby potentially limiting them to a less diverse array of prey due to dependent pups and attempts to maximise mating opportunities.

In this study differences in species richness showed no relationship with harbour seal population trajectories. There was little difference in species richness across most regions, except for the west coast of Scotland (particularly in the south and central regions) where harbour seals ate a greater number of species than in other regions.

However, this study did reveal greater evenness in the diet of harbour seals from stable or increasing populations (Figure 3.5). In the Outer Hebrides, West coast – north, central and south regions (stable populations) and in The Wash (increasing population) Pielou's evenness index (PIE) was greater than 0.7. There were however, two exceptions to this pattern; the very uneven diet observed in all seasons in the stable population of Moray Firth harbour seals (PIE <0.2, diet was heavily dominated by sandeel) and the spring diet of harbour seals in the Wash (PIE = 0.45) which was reasonably evenly split between dragonet and Dover sole. The increase in the proportion of sole in the Wash diet in spring was also seen by Hall *et al.*, (1998) and was noted as being coincident with the movement of this species into waters less than 30 m deep to spawn in the southern North Sea (Rijnsdorp *et al.*, 1992).

Species evenness in the diet of harbour seals in regions of population decline varied by season. In the summer the diet was reasonably specialised (PIE <0.4) and in the autumn diet was moderately split (PIE = 0.48 and 0.49). However, in the spring the diet between the two regions was different. In Orkney the proportion of different species in the diet was very uneven (PIE = 0.19) while in Shetland the diet was more even (PIE = 0.69).

Though recent biological opinion reports (NOAA Fisheries, 2010; Bowen, 2012; Stewart, 2012; Stokes, 2012; NOAA Fisheries, 2014) have contested the findings, strong correlations between diet diversity and regional population decline have been described in Steller sea lions: as diet diversity decreased, populations decreased (Merrick *et al.*, 1997; Trites *et al.*, 2007a) and more recently areas which showed the greatest increase in diversity of prey have been linked to those of the strongest population growth since 1999 (Sinclair *et al.*, 2013). I have also shown that species abundance is less evenly spread in the diet of harbour seals from declining populations. However, declines in sea lion abundance have been associated with diet samples consisting mostly of a single prey type; walleye pollock or atka mackerel (*Pleurogrammus monopterygius*, Merrick *et al.*, 1997).

Harbour seals in the Moray Firth showed the most extreme case of diet unevenness in this study, with samples consisting mostly of sandeel. This population is currently considered to be stable following a period of decline 1995 – 2010 (Figure 3.6 and SCOS, 2013). Merrick *et al.*, (1997) suggested that a variety of prey in the diet is important and that walleye pollock or atka mackerel are not profitable to the sea lions. The current stability of the Moray Firth harbour seal population suggests that a diet consisting of a single prey type can be profitable for pinnipeds; however, this is likely dependent on the calorific quality of that prey species.

The energy density (quality) of the diet has been shown to have large effects on the amount of food that Steller sea lions need to consume (Winship and Trites, 2003). For pinnipeds therefore advantages may be made by feeding on several prey species. Merrick *et al.*, (1997) suggested that a varied diet may increase foraging efficiency as diverse prey are easier to find, capture and handle due to the increased likelihood of locating a prey patch of a suitable density and with prey of the correct size. Alternatively a diverse diet may buffer against significant changes in the abundance in a single prey species (Merrick *et al.*, 1997). However, despite changes in diet composition and diversity between breeding and moult seasons the gross energy content of the average diet of harbour seals has been shown not to vary significantly indicating that harbour seals are capable of maintaining their energetic intake despite changes in prey consumption (Geiger *et al.*, 2013).

3.4.3 Diet of harbour seals in the North Sea including Orkney and Shetland

In this study I used biomass reconstruction to estimate the diet of harbour seals around Britain. Sampling was stratified to compare diets regionally and seasonally. Comparisons were also made to previous work to examine possibilities for interannual variation. This discussion focuses on whether regional and seasonal differences observed in the diet of harbour seals around Britain supports the accepted wisdom that harbour seals are generalistg predators and that variation in diet reflects the relative availability of prey (Tollit and Thompson, 1996; Brown and Pierce, 1998; Hall *et al.*, 1998).

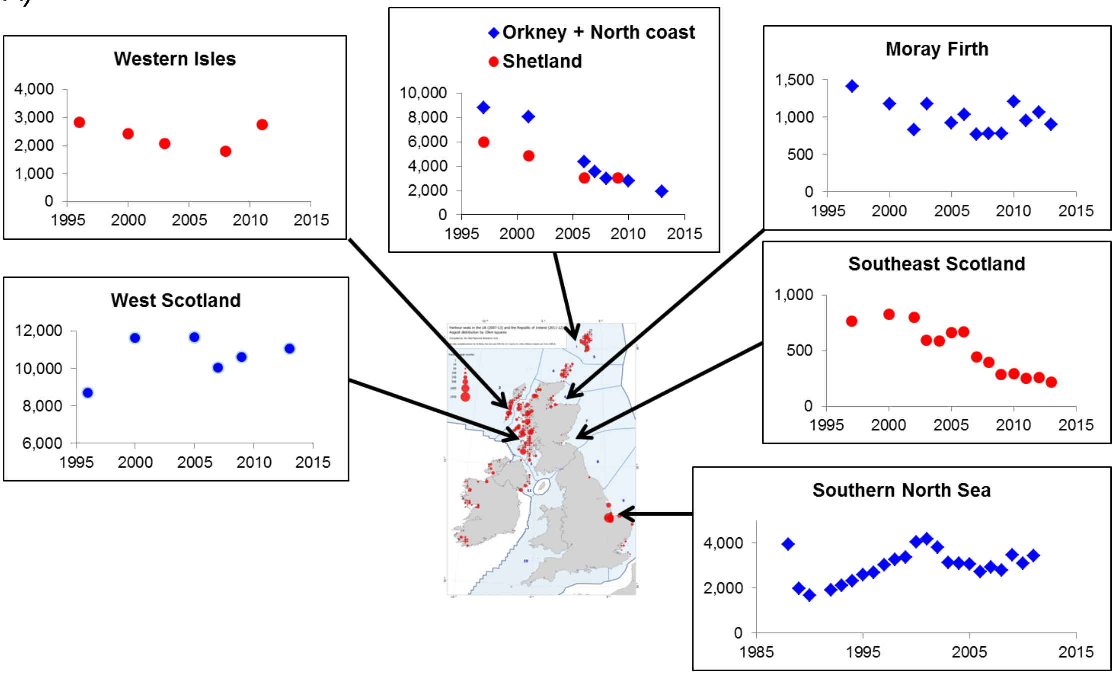
3.4.3.1 Southern North Sea

In the southern North Sea monthly scat collections (1990-1992) showed that fifty percent of the diet was composed of whiting and flatfish, around one third of the diet was made up of dragonet, sand goby and bullrout and gadoids (other than whiting) constituted around 12% (Hall *et al.*, 1998). Consistent seasonal changes in diet were also observed; with whiting, bib and bullrout dominant in winter, sand goby and Dover sole in spring and other flatfish and dragonet in summer (Hall *et al.*, 1998).

The progression of dominant species in the diet observed in this study was similar to that described by Hall *et al.*, (1998) of; whiting, bib and bullrout in winter, through sand goby and Dover sole in spring to other flatfish and dragonet in summer. However, complete digestion of otoliths was not accounted for by Hall *et al.*, (1998) and so the importance of some prey species *e.g.,* sandeel, herring and lemon sole will be underestimated in the diet. However, this explanation would not account for the large difference seen between the low contribution of sandeel (<4%) in summer reported by Hall *et al.,* (1998) and the high contribution observed in this study (>20%).

The diet of seals in the Wash appears to closely reflect the most abundant prey including; dragonet, plaice, Dover sole and whiting (Callaway *et al.*, 2002). Seasonally important was the movement of Dover sole into shallow waters to spawn in spring time (Rijnsdorp *et al.*, 1992) and peak feeding of dragonet in shallow waters over sand and mud in the April-October (Wheeler, 1978; Van der Veer *et al.*, 1990).

A)



B)

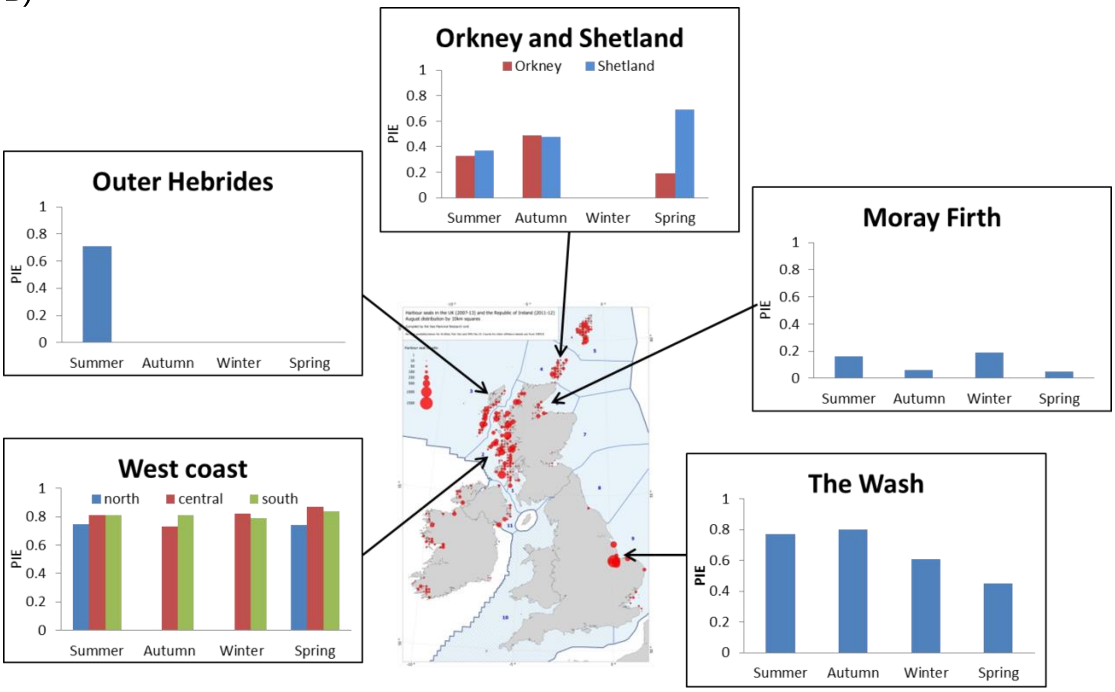


Figure 3.5: Regional patterns around Britain are shown for A) harbour seal population trajectories (SCOS, 2013) and B) Pielou's evenness index (PIE) which provides a measure of how different the abundances of the species in the diet (*i.e.*, evenness is highest when species abundance is evenly spread and a sample is not dominated by one or a few species with high abundance).

3.4.3.2 Southeast Scotland

Seasonal investigation of the diet of harbour seals in SE Scotland was not possible in this study as such diet was examined for this region over all the seasons combined. Flatfish were the main contributors to the diet. Plaice was the dominant prey species overall (28.1%) and sandeel were the second most important prey type (18.4%) followed by large gadoid fish (14.1%). The dominant prey identified in the most recent fisheries assessments covering southeast Scotland were flatfish, gadoids and sandeel (Callaway *et al.*, 2002; ICES, 2011b). The overall diet of southeast Scotland harbour seals reflects the fish species considered dominant in the region in the most recent fisheries assessments; flatfish, gadoids and sandeel (Callaway *et al.*, 2002; ICES, 2011b).

Studies of the diet of harbour seals in southeast Scotland previously focused on the Firth of Tay and Eden Estuary SAC between 1998 and 2003 (Sharples *et al.*, 2009). In the Eden estuary the diet was heavily dominated by sandeel, especially in winter and spring (69.5% annual mean). Gadoids (mainly whiting and cod, 10.6%) and flatfish (dab, plaice and flounder, 8.1%) were the other main prey. In the Firth of Tay salmonid prey dominated the diet spring – summer and were important in autumn (38.4% annual mean) and sandeel were important in autumn and winter (44.9% annual mean, Sharples *et al.*, 2009).

The sample size in the Sharples *et al.*, (2009) study was much larger than in the present study (n = 749 and n = 75 respectively) and used the most current DCFs available to estimate the diet of harbour seals in southeast Scotland. However the dominance of flatfish in the diet in this study is unlikely to be explained by the use of some grey seal DCFs by Sharples *et al.*, (2009). And though sandeel remains an important prey species the contribution to the diet of harbour seals in this region has significantly reduced.

This Firth of Tay and Eden Estuary population of harbour seals has been declining dramatically, with an estimated 89% decrease in the population since 2000, and an average rate of decline of 20% p.a. over the last 10 years (SCOS, 2013) . Fewer than 100 adult harbour seals now populate this area which used to hold around 2% of the

UK population (around 600 adults, SCOS, 2013). It is not possible to draw inferences from this study about why the differences in diet might have occurred. What is clear is that the proportions of different prey in the diet have changed and that more poor quality prey with lower individual calorific densities (Murray and Burt, 1977) are being eaten.

3.4.3.3 Moray Firth

Sandeel dominated the diet of harbour seals in the Moray Firth in this study. Notable seasonal contributions included: flatfish in summer, bullrout, salmonids, flatfish and large gadoids in autumn, pelagic and large gadoid prey in winter and flounder in spring.

Sandeel have typically dominated the diet of harbour seals in the Moray Firth even without the application of DCFs (*e.g.*, Tollit and Thompson, 1996). Important contributions of other prey have included: lesser octopus, large gadoids (whiting and cod) flatfish and pelagic species (Pierce *et al.*, 1990a; Thompson *et al.*, 1996a; Tollit and Thompson, 1996; Tollit *et al.*, 1997a). Between year and seasonal patterns in the diet have revealed significant fluctuations in the contributions of these prey; 20-86% sandeel contribution in summer and 49-91% in winter, lesser octopus contributed 0-62% in summer and <5% in winter and whiting and cod contributed 2-34% in winter and 1-4% in summer (Thompson *et al.*, 1996b). Significant peaks in pelagic prey in the winter have also been described (Pierce *et al.*, 1990a; Thompson *et al.*, 1991b).

The importance of flatfish in the diet in this study was higher than previously reported and though a seasonal peak was observed in the contribution of pelagic prey in the winter, the proportion in the diet was not dominant (10%), nor were cephalopod prey important in the diet in this study.

There was no recent detailed fish abundance data available for the region but comprehensive surveys were conducted in 1992-1994 (Greenstreet *et al.*, 1998). The diet of harbour seals in the Moray Firth still closely reflects the fish abundance previously described by Greenstreet *et al.*, (1998) where: herring, sprat, sandeel, haddock, whiting, Norway pout, poor cod, cod, dab, long rough dab, plaice and lemon sole were the twelve most abundant fish species.

Sandeel are largely stationary after settlement and are dependent on suitable sediment types (Lewy *et al.*, 2004). They emerge infrequently from the sea bed September-March except during spawning (December-January, Wright and Begg, 1997). The appearance of sandeel in the diet of grey seals year-round led Grellier (2006) to infer that grey seals are able to disturb and prey upon buried sandeel. The behaviour must also be assumed for harbour seals at least in the Moray Firth, as sandeel are abundant in the diet of at all times of the year.

It is possible that harbour seals could be adversely affected by changes in the availability of their dominant prey type: sandeel. Declines in Steller sea lion abundance have been associated with diet samples consisting mostly of a single prey type (Merrick *et al.*, 1997) and a more diverse diet is considered to be important to buffer predators against significant changes in the abundance in a single prey species (Merrick *et al.*, 1997). Diversity in prey would also buffer against fluctuations in the energy content of fish which has been shown to fluctuate widely and have population level consequences (Wanless *et al.*, 2005). For example, low energy values for sandeel and sprats is considered the probable cause of a major seabird breeding failure in the North Sea in 2004 (Wanless *et al.*, 2005)

Neither diet nor fishery studies have been conducted in the Moray Firth during the period of harbour seal decline in that region 1995-2010 (SCOS, 2013). As such the abundance of sandeel in the diet of harbour seals and the availability and quality of sandeels to harbour seals is unknown.

3.4.3.4 Orkney

In Orkney, in summer and spring harbour seal diet was made up of ≥ 50% sandeel. In autumn sandeel constituted < 15% of the diet and pelagic prey peaked at 40.2%. Large gadoids made up minimum 30% of the diet in summer, autumn and spring. The winter diet was not estimated due to small sample size.

During 1986-1988 the diet of harbour seals in Orkney (based on frequency of occurrence) was sandeels, followed by herring and gadoid fish (whiting, Trisopterus, ling/rockling, haddock/saithe/pollack, Pierce *et al.*, 1990a). Though still dominant the proportion of sandeel in the diet was less in July-September than in April-June and a corresponding increase in the proportions of herring, mackerel, scad and flatfish was observed (Pierce *et al.*, 1990a).

The dominance of sandeel in the diet in spring and summer is coincident with the season of active feeding for this taxa (April-September). There is a very large spawning area for sandeel to the north and west of Orkney with very limited fishing presence in the area due to the mixed ground type. Due to the area size and the importance of the breeding stock this area has been proposed as a possible Marine Protected Area for sandeels (MSS, 2012).

At times when sandeel are not actively feeding and available above the substrate, harbour seals in Orkney switched to highly calorific pelagic fish (in autumn). The seasonal importance of pelagic prey in the diet coincides with the autumn migrations and the main fishery catches for these species (Baxter *et al.*, 2011; Marine Scotland, 2014b). The autumn diet has not previously been studied and the dominance of pelagic fish cannot be compared.

3.4.3.5 Shetland

Pelagic and large gadoid fish were important in the diet of harbour seals in Shetland in summer, autumn and spring. Sandeel was also important in summer and autumn but not in spring when sandy benthic prey showed seasonal importance.

Brown and Pierce (1998) described the diet in Shetland in 1995-96 to consist of mostly gadoids (including *Trisopterus* species). Though, sandeels dominated in the spring and were important in the summer and pelagic prey were important in summer and autumn. Marked between-year variation in the relative importance of prey at one haul-out location; Mousa, Shetland has also been reported during the summer months, 1994-97; Whiting varied between 16-34% of the diet, herring 12-28% and sandeel 7-18 % (Brown *et al.*, 2001).

In this study (2010-11) the main prey types were the same but the seasonal pattern of dominance and importance by weight had changed. Sandeel were important but not dominant prey in summer and autum and constituted much less of the diet in spring when sandy benthic prey peaked in the diet. Whiting (25.3%) and saithe (11.1%) were the main gadoid prey in the mid-90s (Brown and Pierce, 1998) and though the proportions of saithe in the diet remained roughly the same whiting made up less than 1% of the diet. The change of importance by weight is probably coincident with the application of Number Correction Factors to account for the completed digestion of otoliths; species with fragile otolith such as sandeel and herring have poor recovery rates and so will have been underestimated in the diet presented by Brown *et al.*, (1998).

Sandeels are an important component of the Shetland coastal ecosystem for both seals (Brown and Pierce, 1997; Brown and Pierce, 1998; Brown *et al.*, 2001) and seabirds (*e.g.*, Furness, 1990; Furness and Tasker, 2000). The commercial sandeel fishery in Shetland has previously been described as focusing its efforts during spring and summer and it has therefore been assumed that sandeel availability to seals was highest at this time (Brown and Pierce, 1998) but in this study sandeel made up one third of the diet in autumn and consumption was low in spring.

The abundance of herring in the diet does however, reflect the herring ground fishing season around Shetland; May-September which ties in to the spring and autumn spawning stocks distributed across the west and north of Scotland (Hatfield and Simmonds, 2002) and may indicate a preference for pelagic prey in the diet.

3.4.4 West of Scotland

3.4.4.1 Outer Hebrides and West coast – north

Trisopterus species and pelagic prey dominated the summer diet of harbour seals in the Outer Hebrides. Large gadoids, scorpion fish and sandeel also made important contributions to the diet. In the West coast – north region large gadoids, pelagic fish and *Trisopterus* species dominated. To date there has been no other description of the diet of harbour seals in the Outer Hebrides or in the West coast – north region.

3.4.4.2 West coast – central

In winter, spring and summer large gadoid fish dominated the diet of West coast central harbour seals while in autumn pelagic prey dominated. Blue whiting was the dominant gadoid prey and mackerel the dominant pelagic prey. Other seasonally important prey included *Trisopterus* species, *Cottidae* species and dragonet. The maximum seasonal contribution of sandeel contributed was 7% in autumn.

The diet of harbour seals in the West coast – central region was previously studied on the Isle of Skye in 1993 – 1994 (Pierce and Santos, 2003). Large gadoid prey dominated the diet (particularly whiting) with pulses of haddock/pollack in summer and ling/rockling in September. Herring was important June-November and Scad (*Decapterus macarellus*) in September. Sandeel were a very minor part of the diet (Pierce and Santos, 2003).

Large gadoid prey also dominated the diet in this most recent study with whiting remaining important in the diet. However, scad were not as important, replaced in the diet in 2010-11 by pelagic and sandy benthic species. The sample sizes presented by Pierce and Santos (2003) were small in two seasons October-November 1993, n = 17 and June-August 1994, n = 12 and so the importance of species in these seasons may not be representative of the population as a whole.

The importance of pelagic fish in the diet was most prominent in the West coast – central region though important seasonal pulses were detected in the diet of the entire west of Scotland. Mackerel was the dominant prey type, though herring and horse mackerel (scad) were also seasonally important. There is also seasonality to the fishery for mackerel based on the migrations of the species. West of Scotland catches occur mainly January-March and north and east of Scotland catches are in October-December (Baxter *et al.*, 2011). Autumn and spring peaks in mackerel contribution to harbour seal diet appear coincide with the main fishery catches for the species in the West coast – central region.

3.4.4.3 West coast - south

Large gadoid prey were dominant in the diet of West coast – south harbour seals and sandeels contributed very little; less than 2 % in most seasons. Whiting and haddock dominated in summer, herring and haddock in autumn and in winter and spring cod, whiting and haddock were all important contributors.

The diet of harbour seals in the west – coast central region was dominated by gadoids in a study conducted on the Isle of Mull 1993 – 1994 (Pierce and Santos, 2003). Whiting was the dominant prey type and the second most important prey were pelagic fish particularly in autumn when the incidence of gadoids was lowest in the diet (pelagic prey was mainly scad). The importance of other prey varied seasonally with scad (*Decapterus macarellus*) dominating in September and *Trisopterus* species in May. Flatfish and *Eledone* species were of lesser importance in May and sandeels were a very minor part of the diet (Pierce and Santos, 2003).

Large gadoid prey continued to dominate the diet in this study and whiting remained important in the diet of West coast – south harbour seals. However, scad and *Trisopterus* species were not as important, replaced in the diet in 2010-11 by pelagic and sandy benthic species. The sample sizes for the Isle of Mull study were small September n = 17 and May n = 10 and from only one location (Pierce and Santos, 2003) and so the estimated diet in 1993 - 1994 may not reflect the wider population.

Trisopterus species are migratory fish with spawning grounds located around NW Scotland and Shetland (Cohen *et al.*, 1990) and a spawning period which extends from January to July. The importance of *Trisopterus* species was principally seen in the diet of harbour seals in the Outer Hebrides and West coast north and central regions in this study. There is little information available about the stock but it is considered to be an important food source for other predators *e.g,.* saithe, haddock, cod and mackerel as well as squids, flatfish and gurnards (ICES, 2009).

Gadoid fish were important prey throughout the year for harbour seals in the Inner Hebrides. The spawning stock of cod on the west of Scotland is increasing from an all-time low in 2006 (ICES, 2009). There are important spring time spawning areas across the west of Scotland (ICES Division Via) and the diet in the West coast – south reflected a peak in contribution during the cod spawning season (spring).

Despite the wide distribution of haddock across the west and north of Scotland (ICES, 2009) and a similar spawning period to cod this species was only really important in the diet of West coast – south harbour seals. Whiting appeared to be more important in the diet of West coast – central and south harbour seals though this was not linked to spring time spawning. This species occurs throughout the northeast Atlantic but seals may have been targeting juvenile fish which dominate inshore areas (ICES, 2009).

3.4.5 Diet Quality

Spitz *et al.*, (2012) showed that for cetaceans a significant relationship exists between diet quality and metabolic cost of living and they proposed that on an ecological time scale the costs of living reflects and dictates the quality of foods they consume *e.g.*, species with lower costs need only feed on lower quality prey. This framework was suggested to apply equally well for understanding the dietary choices and needs of other animals such as birds, small terrestrial mammals or reptiles (Spitz *et al.*, 2012). In this study I examined the diet quality within a species not across species and considered if variation in the quality of seal diets may be a consequence of their costs of living at a regional level.

The role of diet quality in addition to prey abundance and availability is considered to be important for sustaining healthy populations of marine top predators (Österblom *et al.*, 2008). The diet of seals is made up of mobile prey and seals must use energy to find, pursue, catch and handle them. Harbour seals tend to have heterogeneous at-sea usage which is proposed to reflect seasonal variation in foraging areas and is also related to seasonal changes in terrestrial haul-out distribution (Thompson *et al.*, 1996a). This is supported by fine scale observations of environmental and anthropogenic influences on the distribution of harbour seals which have shown that high abundance and proximity to the haul-out site of prey was strongly associated with the spatial distribution of individuals (Grigg *et al.*, 2012).

The regional differences in diet revealed in this Chapter, show that seals in the Moray Firth have the best diet quality (consuming the highest calorific diet) and seals in the West coast – south and central and Wash regions have the lowest quality (consuming a lower calorific diet). Excepting the Moray Firth, this result is perhaps counterintuitive when considering the population trajectories of the different regions; one might expect seals with stable or increasing populations to have higher quality diets and seal populations which are declining to have lower quality diets, *i.e.*, be struggling to consume enough calories to maintain fitness. However, regions with declining populations had an average diet quality and those which are stable had diet qualities which were; high, low or average and the population which is increasing had a significantly lower diet quality.

Alongside the pursuit of prey seals spend time in other activities including resting, travelling, predator avoidance and provisioning of young. Individuals are expected to adjust their activity budgets if it is in their best interests to do so due to changes in ecological and social circumstances (Mooring and Rominger, 2004). Russell *et al.*, (In Review) recently used behavioural and movement data from telemetry tags to define population level activity budgets for UK harbour seals. No link was found between regional activity budgets and regional population trajectories and the authors cautioned against using activity budgets as indicators of population heath. They did find regional variation in the proportion of time seals spent resting at sea or on land, with the lowest proportion of time spent resting at-sea and overall in western Scotland (Russell *et al.*, In Review). Resting at-sea offshore is proposed to occur to facilitate digestion (Sparling *et al.*, 2007) and is expected to occur more often on longer trips, while inshore resting was more common in tidal areas (eastern UK) where animals wait for a haul-out to become exposed (Russell *et al.*, In Review). In western Scotland, overall time spent resting can be reduced as haul-outs are largely non-tidal and resting at-sea between low tides is not necessary (Russell *et al.*, In Review).

Strong regional differences in the foraging behaviour of harbour seals have been revealed through large scale electronic tagging programs around Britain (Sharples *et al.*, 2012). Seals in the Outer Hebrides, Shetland and Orkney generally made short distance (11-21 km), short duration (1-2 days) foraging trips, while North Sea harbour seals in the Moray Firth, southeast Scotland and the Wash regions made much longer distance (*e.g.*, the Wash mean 86 km) and duration (1-6 days) foraging trips (Sharples *et al.*, 2012). However, harbour seal foraging trips in the West coast - central and southern regions are short. Mean travel-trip extent was 10.5 km and 50% of trips were within 25 km of the haul-out site and mean trip duration was 25 h and 35 h in West coast – south and central regions respectively (Cunningham *et al.*, 2009). Though some individuals made long distance transits, > 100 km and 9 days these trips were rare (Cunningham *et al.*, 2009).

The telemetry data imply that seals in the North Sea have to travel further to find productive foraging areas than seals on the west of Scotland and in the Northern Isles. At sites where the local habitat provides prey refugia close to the haul-out site prey may be less depleted than at North Sea sites where prey are more accessible over soft bottom habitats (Sharples *et al.*, 2012).

If foraging trip parameters can be used as an indicator of the cost of living of seals then the framework suggested by Spitz *et al.*, (2012) may explain some of the variation in regional energy requirements of seals around the UK. Seals on the west of Scotland feed on lower quality prey than in other regions but this would match a lower cost of living indicated by shorter foraging trips and recovery periods (Cunningham *et al.*, 2009; Russell *et al.*, In Review). Based on foraging trip parameters the cost of living in the Moray Firth is high as seals there made the longest average foraging trips (100.6 km and 4.5 days, Sharples *et al.*, 2012) and have a low probability of being hauled-out, favouring resting at-sea. The high proportion of high caloric density prey (principally sandeel) in the diet of Moray Firth harbour seals supports this energetic requirement. However, any relationship between trip duration and metabolic cost of living is not proven nor is it possible to conclude from this study if seals target certain prey types or if this is all that is available to them. The possibility of such behaviour and relationships warrants further investigation.

Seals in the Wash have a similar cost of living to animals in the Moray Firth; however the quality of diet (based on calories consumed) is lower than that eaten in the Moray Firth. Harbour seals in the Wash make some of the longest foraging trips in the UK, with some individuals travelling more than 200 km (Sharples *et al.*, 2012). However, the relationship between the quality of their food and the cost of living for these seals does not appear to be detrimental to the population. The population suffered a 22% drop during the 2002 PDV epidemic from which no recovery was recorded until 2008 (SCOS, 2013). Since 2008 the population has increased by 12% p.a. between 2008 and 2012 (SCOS, 2013).

Other measures of diet quality could be assessed and may include; protein content, vitamins and micronutrient composition. However, energy density is thought to offer a more quantitative proxy of diet quality, with the added benefit that it can be easily measured in a wide range of prey items (Spitz *et al.*, 2012). Captive feeding experiments conducted with Steller sea lions focused on the energy density of prey with diets of high and low energy density food fed over a period of 14 days. Despite ingested food mass remaining the same sea lions lost an average 1.1 kg/d totalling 12.2.% of their initial body mass on a low energy density diet (Rosen and Trites, 1999). Furthermore, decreases in metabolism were observed in animals eating a low energy diet leading Rosen and Trites (1999) to suggest that sea lions can depress their resting metabolism in response to decreases in energy intake or body mass. More recently the nutritional profile of harbour seal diets has been studied from scats collected at Tugidak Island, Alaska. Using a ration formulation software program designed for the agricultural industry the quality of harbour seal diets was evaluated with respect to crude protein, lipid, ash and gross energy content (Geiger *et al.*, 2013). Based on split-sample frequency of occurrence and biomass reconstruction the importance of some prey items were significantly different; however, there were no significant differences in the overall estimated protein, lipid or gross energy composition of the diets during summers 2001 – 2009 (Geiger *et al.*, 2013).

These results show that the diet of harbour seals around Scotland do have varying qualities. However, there was no evidence for seasonal variation in diet quality suggesting that the energy needs of harbour seals do not change in relation to their biological life cycle. This is consistent with the findings of Geiger et al., (Geiger *et al.*, 2013) who showed that despite seasonal differences in diet composition and diversity the gross energy content of the diet of harbour seals did not vary, indicating that harbour seals are capable of maintaining their energetic intake despite changes in the abundance and species of ingested prey. Seasonal patterns in energy requirement have been shown for adult female grey seals through examination of resting rates of oxygen consumption as a proxy for metabolic rate (Sparling *et al.*, 2006). Metabolic rates were highest in spring (moult) and declined through the summer into autumn during this same period adults increased in total body mass and fat content (Sparling *et al.*, 2006). The variation was not related to changes in water temperature and was not seen in juveniles. In Chapter 4 sex differences in the diet of harbour seals is examined and may reveal differences in seasonal energy needs reflecting periods of reproduction, parental care or moult.

3.4.6 Size of prey consumed by seals

The size of individual fish species has been shown to vary markedly between stocks and it is not surprising therefore that significant regional differences were found in the size of fish eaten around Britain. For example, pronounced regional differences in sandeel length have been recorded in the North Sea (Boulcott *et al.*, 2007), sole at higher latitudes have a smaller asymptotic size than southern populations (Mollet *et al.*, 2013) and haddock from the western North Sea are smaller than those from the east (Wright *et al.*, 2011). Abundance-at-age has also been shown to vary seasonally *e.g.*, pollack in western Norway peak in spring to summer during the period of most growth and decline in autumn and winter (Heino *et al.*, 2012). Additionally, size dependency on migration timing is also evident with larger mackerel arriving earlier to spawning grounds and leaving later than small fish in the Kattegat and Skagerrak (Jansen and Gislason, 2011).

The majority (95.0%) of fish eaten in this study were small (<30 cm in estimated length) and the mean size of each species was mostly below the minimum landing size for commercial fisheries of cod (35 cm), haddock (30 cm), whiting (27 cm) and plaice (27 cm). It is important to take a conservative approach to estimated fish length comparisons due to the variability in fish weight-otolith size relationships and the use of different digestion coefficients. However in general terms, the estimated sizes of fish eaten are in-line with those estimated in the Wash (<30 cm, Hall *et al.*, 1998) though larger fish sizes were estimated in this study for; cod, plaice and sole. Hall *et al.*,

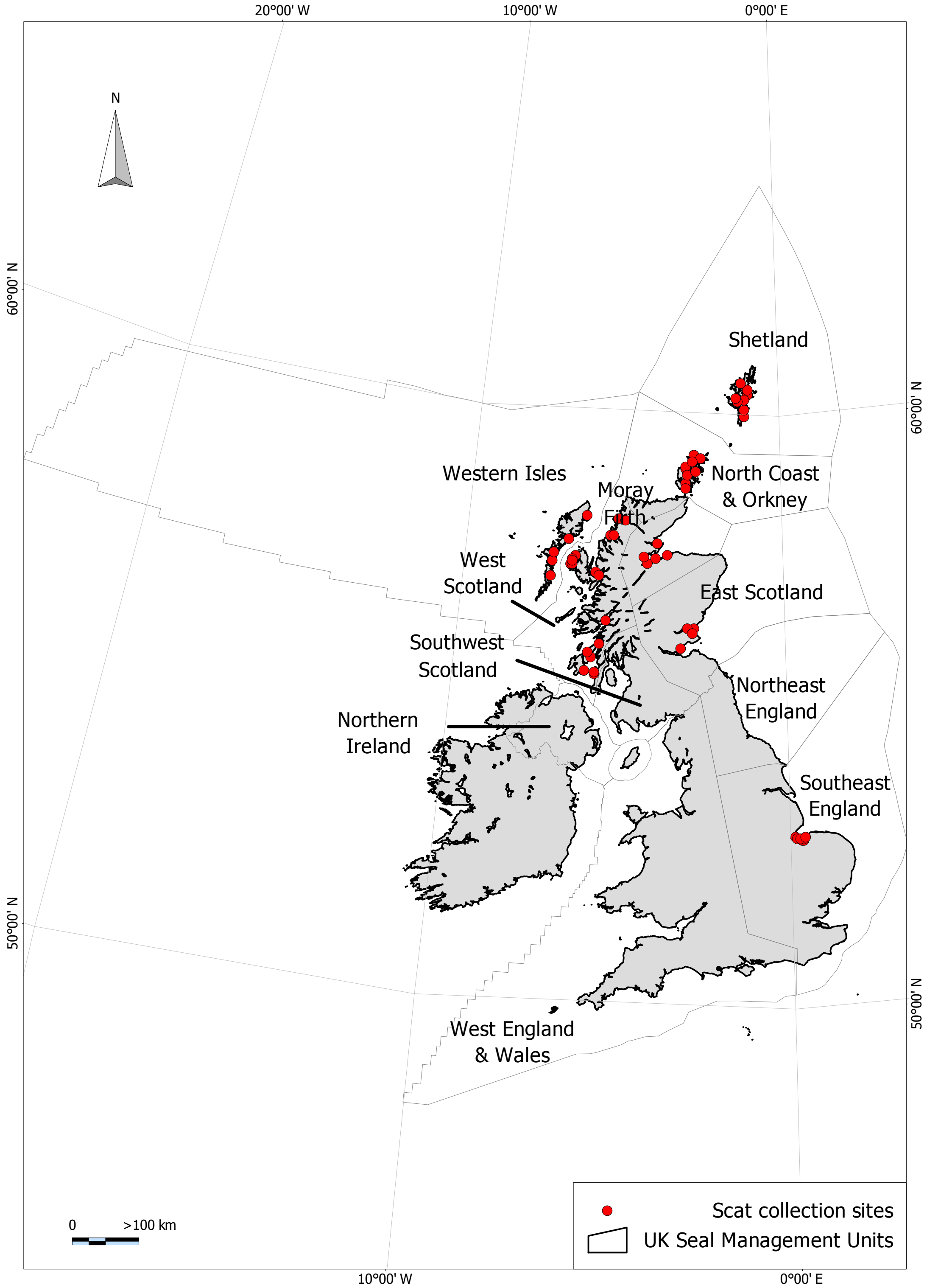
(1998) reported that: approximately 95% of Dover sole eaten were less than 35 cm, greater than 90% of the plaice were less than 18 cm and greater than 90% of the cod was below 35 cm estimated length. In this study 87.9% of the Dover sole were less than 35 cm, 78.3% of the plaice were less than 18 cm and 80.7% of the cod were less than 35 cm estimated length. The majority of sandeels taken in both studies were in the range 8-24 cm estimated length (93.2% in this study) (93.2% in this study and Hall *et al.*, 1998). Sandeel estimates were also similar to those reported for southeast Scotland (Sharples *et al.*, 2009) and the Moray Firth (Tollit *et al.*, 1997a).

Since the collapse of the sandeel stock around Shetland in the mid-1980s sandeel availability has fluctuated in this area. Seabird breeding success or failure has been closely linked to the availability of sandeel in Shetland (*e.g.*, Hamer *et al.*, 1993; Furness and Tasker, 2000) and a precautionary ban was imposed on the Shetland fishery in 1990-95. Catches subsequently have been limited to low levels, with a voluntary ban around south Shetland in 2004 (Mitchell, 2006). Furthermore, significant depression of black-legged kittiwake survival and breeding success was linked to the sandeel fishery in southeast Scotland (Frederiksen *et al.*, 2008) and the fishery was closed in 2000. The population size of sandeel in Shetland and southeast Scotland increased substantially within a few years of the fishery closures (Wright, 1996; Greenstreet *et al.*, 2006) and the average size of sandeels consumed by harbour seals in southeast Scotland following the closure of the fishery was seen to significantly increase (Sharples *et al.*, 2009). Reduced localised fishing efforts may therefore effect the size distribution of prey available to marine predators.

3.4.7 Final Remarks

I explored the diet of harbour seals around Britain to try and determine if reduced availability of suitable prey is a potential cause of harbour seal declines in some regions. However, no consistent pattern emerged linking the quality and/ or quantity of prey in the diet of harbour seals with their population trajectories. Regional and seasonal differences in the diet of harbour seals around Britain appeared to reflect the distribution, abundance and seasonal patterns (feeding, spawning and migrations) of their prey. On the east coast of Scotland sandeel and flatfish were the most important prey in the diet with sandeel dominating in the north and flatfish in the south. In the southern North Sea sandy benthic, flatfish, gadoids and sandeel were important seasonal prey. In the northern isles; sandeel or scorpion fish dominated the diet depending on the season with large gadoids as important supporting prey. In Orkney and in Shetland sandeel peaked in summer and pelagic prey in Orkney in autumn. Large gadoid prey were consistently important in the diet in the Northern Isles as were pelagic prey in the diet in Shetland. In summer, in the Outer Hebrides *Trisopterus* species, pelagic, gadoid, scorpion fish and sandeel were all important prey. In the Inner Hebrides (west coast – north, central and south) diet was dominated by gadoids throughout most of the year with important seasonal contributions of pelagic species. Against my expectations, diversity in the number and abundance of prey consumed was not linked to population trajectories, nor was the quality of the diet in the different regions around Britain. In regions which are currently undergoing serious population declines only limited changes in the diet were observed between this and previous studies undertaken at times of high harbour seal abundance. Based on these analyses and if measures of diet such as diversity, composition, quality and size of prey consumed are associated with levels of food intake then it does not appear that harbour seals in regions of population decline are experiencing negative physiological and/or behavioural states triggered by sub-optimal quantity or quality of food.

Appendix 3.1: Map and table documenting the principal haul-out sites where successful scat collections took place.



Region	**Location**	**Haul-out**
England	The Wash and north Norfolk coast SAC	Fleethaven
England	The Wash and north Norfolk coast SAC	Kenzie Creek
England	The Wash and north Norfolk coast SAC	Evans Creek
England	The Wash and north Norfolk coast SAC	Daseleys Sand
England	The Wash and north Norfolk coast SAC	Hull Sand
England	The Wash and north Norfolk coast SAC	Pandora Sand
England	The Wash and north Norfolk coast SAC	Seal Sand
England	The Wash and north Norfolk coast SAC	Thief Sand
England	The Wash and north Norfolk coast SAC	Stylemans Middle
SE Scotland	Firth of Tay and Eden Estuary SAC	Abertay sands
SE Scotland	Firth of Tay and Eden Estuary SAC	Naughtons Bank
SE Scotland	Firth of Tay and Eden Estuary SAC	River Eden
SE Scotland	Firth of Forth	Seafield Tower, Kirkcaldy
Moray Firth	Moray Firth	Ardesier
Moray Firth	Moray Firth	Findhorn
Moray Firth	Dornoch Firth and Morrich More SAC	Whiteness
Moray Firth	Dornoch Firth and Morrich More SAC	Gizzen Briggs
Moray Firth	Beauly Firth	Torrgorn Bank
Moray Firth	Cromarty Firth	Bridge
Orkney	Scapa Flow	Barrel of Butter
Orkney	Eynhallow sound	Burgar Farm
Orkney	Eynhallow sound	Eynhallow
Orkney	Finstown Bay	Damsay
Orkney	Westray	Papa Westray, Holm of Papay
Orkney	Westray	Papa Westray, Weelie's Taing
Orkney	Sanday SAC	Holms of Ire
Orkney	Shapinsay	Shapinsay, Broch
Orkney	Scapa Flow	Switha
Orkney	Westray	Skerry of Wastbist
Shetland	Lunning sound	Lunning sound Islands

Shetland	Mousa SAC	Mousa
Shetland	SE Shetland	Voe of Sound
Shetland	South Nesting	Skudills Wick
Shetland	West mainland	Bixter voe
Shetland	West mainland	Vementry
Shetland	Yell Sound Coast SAC	Lunna Ness, sand skerry
Shetland	Yell Sound	Lunna Ness, Little holm
Outer Hebrids	Stornoway	Broad Bay, Sgeir Leathann
Outer Hebrids	South Uist	Loch Aineort
Outer Hebrids	Benbecula	Flodaigh
Outer Hebrids	Harris east	East Loch Tarbert
Outer Hebrids	Loch Maddy	Loch Maddy
WC - north	Summer Isles	Sgeirean Glasa
WC - north	Summer Isles	Carn naan Sgier
WC - north	Oldany Islands	Oldanay Islands
WC - north	Loch Glen Coul Islands	Loch Glen Coul Islands
WC - central	Inner Sound	Crowlin Islands
WC - central	Ascrib, Isay and Dunvegan SAC	Ascrib Islands
WC - central	Ascrib, Isay and Dunvegan SAC	Dunvegan Castle Islands
WC - central	Ascrib, Isay and Dunvegan SAC	Dunvegan west Islands
WC - central	Loch Dunvegan	Loch Bay, Mingay
WC - central	Loch Dunvegan	Loch Bay, Sgeir nam Biast
WC - central	Plock of Kyle	Skye Bridge skerries
WC - south	Ardfern	Eiean na Cillie
WC - south	Gigha	Cara Reef
WC - south	Gigha	Caolas Gigalum
WC - south	South-East Islay Skerries SAC	Plod Sgeirean
WC - south	South-East Islay Skerries SAC	Loch a'Chnuic
WC - south	Jura	Lowlandsman Bay
WC - south	Jura	West Loch Tarbert
WC - south	Eileanan agus Sgeiran Lios mór SAC	Eilean Dubh skerry

Appendix 3.2: Seasonal and regional variation in the number of otoliths and beaks recovered for the 20 most abundant species or higher taxon prey.

A) England

Species	Spring	Summer	Autumn	Winter	Total
Goby	500	1268	132	998	2898
Sandeel	12	588	135	94	829
Plaice	16	611	127	16	770
Dragonet	31	463	167	23	684
Whiting	5	29	523	80	637
Unidentified flatfish	9	169	119	10	307
Dab	9	211	51	8	279
Dover sole	20	60	36	6	122
Sprat	4			102	106
Flounder (Butt)		33	8		41
Lemon sole		10	24	4	38
Pout whiting (Bib)		14	5	8	27
Lesser weever		14	11		25
Bullrout	5		4	13	22
Cod		14	1	6	21
Sea Scorpion		1	1	18	20
Herring			1	17	18
Smelt		12	1		13
Unidentified roundfish		7		6	13
Sepiolids		9	1	1	11
Other		21	24	9	57
Total	614	3534	1371	1419	6938

B) SE Scotland

Species	All seasons
Goby	2522
Sandeel	1261
Plaice	1022
Whiting	641

Unidentified flatfish	359
Dab	186
Sprat	96
Loligo	34
Cod	27
Flounder (Butt)	23
Haddock	11
Dragonet	10
Unidentified gadid	8
Saithe	6
Eelpout	3
Lemon sole	3
Mackerel	3
Long rough dab	2
Sea trout	2
Snake blenny	2
Other	5
Total	6226

C) Moray Firth

Species	**Spring**	**Summer**	**Autumn**	**Winter**	**Total**
Sandeel	6237	8906	1960	1208	18311
Plaice	20	753	19	9	801
Unidentified flatfish	95	316	7	16	434
Dab	24	321	5	9	359
Sprat	75			93	168
Cod	1	50	25	6	82
Flounder (Butt)	39	20	1	7	67
Whiting	3	29	12	11	55
Saithe	13	8	9	21	51
Unidentified gadid	3	14	15	5	37
Bullrout	2	20	3		25
Loligo		21	3		24

Goby	2	1	14	1	18
Haddock		17		1	18
Poor cod	1	1		11	13
Flounder or Plaice	2	9			11
Eelpout	5	1	1	2	9
Long rough dab	1	8			9
Herring	1	1	1	3	6
Dragonet		2		2	4
Other	4	11	3	1	19
Total	6528	10509	2078	1406	20521

D) Orkney

Species	**Spring**	**Summer**	**Autumn**	**Total**
Sandeel	632	2835	888	4355
Cod	8	570	94	672
Unidentified gadid	13	245	31	289
Herring	2	35	152	189
Saithe	45	93	31	169
Poor cod	31	77	20	128
Dab		47	16	63
Plaice		51	9	60
Dragonet		29	22	51
Haddock	1	11	38	50
Unidentified *Trisopterus* spp.	15	19	11	45
Sea Scorpion		38	3	41
Unidentified flatfish		29	6	35
Mackerel	2	3	29	34
Rockling	15	4	2	21
Ling		10	6	16
Butterfish	12	2		14
Whiting	4	2	7	13
Flounder (Butt)		12		12
Goby		9		9

Other	10	21	12	43
Total	790	4142	1377	6309

E) Shetland

Species	Spring	Summer	Autumn	Total
Sandeel	76	1016	1415	2507
Saithe	20	21	651	692
Norway pout	158	362	49	569
Poor cod	17	55	228	300
Herring	44	71	45	160
Unidentified gadid	1	72	65	138
Dragonet	124		7	131
Unidentified *Trisopterus* spp.	40	4	54	98
Garfish			37	37
Mackerel	3	1	24	28
Cod		12	10	22
Plaice		18	2	20
Ling	2	9	4	15
Whiting		2	6	8
Dab		1	4	5
Lemon sole			5	5
Goby		3	1	4
Unknown Species		1	3	4
Eledone		1	2	3
Rockling	2	1		3
	4	4	10	18
Total	491	1654	2622	4767

F) Outer Hebrides

Species	Summer
3-bearded rockling	
Norway pout	798
Sandeel	250

Poor cod	201
Unidentified *Trisopterus* spp.	54
Unidentified gadid	45
Whiting	34
Cod	33
Dragonet	28
Horse mackerel (Scad)	22
Mackerel	20
Norway pout or Poor cod	19
Herring	17
Unidentified *Cottidae*	16
Haddock	14
Eledone	10
Plaice	7
Saithe	3
Wrasse	3
Ling	2
Other	8
Total	1584

G) West coast – north

Species	**Spring**	**Summer**	**Total**
Norway pout	261	745	1006
Poor cod	52	442	494
Whiting	16	469	485
Norway pout or Poor cod		442	442
Unidentified *Trisopterus* spp.	7	393	400
Blue whiting	2	160	162
Unidentified gadid	1	145	146
Sandeel	57	58	115
Herring	7	65	72
Cod	9	58	67
Saithe	13	35	48

Ling	6	14	20
Mackerel	7	13	20
Haddock	5	9	14
Horse mackerel (Scad)		14	14
Loligo	6	3	9
Plaice		8	8
Argentine	3	4	7
Rockling	5	2	7
Norwegian topknot	4	1	5
Other	7	15	22
Total	468	3095	3563

H) West coast – central

Species	**Spring**	**Summer**	**Autumn**	**Winter**	**Total**
Poor cod	100	307	832	695	1934
Norway pout	61	607	275	509	1452
Whiting	18	407	88	355	868
Blue whiting	183	271	38	275	767
Sandeel	47	90	421	114	672
Dragonet	4	7	232	103	346
Unidentified gadid	17	82	30	90	219
Unidentified *Trisopterus* spp.	16	45	81	72	214
Mackerel	30	8	159	1	198
Herring	16	8	131	25	180
Norway pout or Poor cod			166	3	169
Silvery pout	3	71	2	47	123
Haddock	52	7	45	14	118
Horse mackerel (Scad)	1		52	8	61
Saithe	20		20	20	60
Cod	10	3	32	13	58
Unidentified *Cottidae*		24	12		36
Plaice	7	1	23		31
Long rough dab	20	1	2	1	24

Dab	5		14	1	20
Other	46	24	38	53	161
Total	656	1963	2693	2399	7711

I) West coast – south

Species	**Spring**	**Summer**	**Autumn**	**Winter**	**Total**
Whiting	227	1148	185	99	1659
Poor cod	160	317	672	135	1284
Norway pout	197	569	14	15	795
Haddock	142	287	268	14	711
Unidentified gadid	90	365	114	32	601
Dragonet	5	152	165	12	334
Blue whiting	56	218	11	5	290
Herring	17	27	189	4	237
Unidentified *Trisopterus* spp.	31	104	31	8	174
Sandeel	12	90	31	4	137
Cod	21	20	40	44	125
Witch	15	21	27	1	64
Mackerel	5	28	16	1	50
Plaice	5	15	25		45
Rockling	2	2	40		44
Saithe	9	9	6	7	31
Sepiolids	1		22		23
Goby	5	4	1	10	20
Dab	3	6	8	1	18
Long rough dab	2	2	14		18
Other	19	37	92	6	154
Total	1024	3421	1971	398	6814

Appendix 3.3: Harbour seal diet (expressed as the percentage of each prey type in the diet by weight) listed according to prey type for each region and season.

A) The Wash

Prey group	Summer	Autumn	Winter	Spring
Gadid	3.9	30.5	26.6	2.2
Trisopterus spp.	1.2	0.3	1.3	0.0
Sandeel	22.2	6.6	5.9	3.4
Flatfish	28.4	37.1	13.5	36.2
Sandy benthic	43.3	19.8	15.0	46.0
Scorpion fish	0.3	2.7	19.8	10.2
Pelagic	0.1	0.2	14.1	1.8
Salmonid	0.0	0.0	0.0	0.0
Cephalopod	0.0	2.6	3.8	0.0
Other	0.5	0.2	0.0	0.1

B) SE Scotland

Prey group	All
Gadid	14.1
Trisopterus spp.	0.0
Sandeel	18.4
Flatfish	45.1
Sandy benthic	3.4
Scorpion fish	0.8
Pelagic	8.3
Salmonid	0.7
Cephalopod	8.4
Other	0.8

C) Moray Firth

Prey group	Summer	Autumn	Winter	Spring
Gadid	2.4	4.2	8.0	1.6
Trisopterus spp.	0.0	0.0	0.5	0.0
Sandeel	58.3	75.1	69.0	85.4

Flatfish	31.4	4.7	10.9	9.8
Sandy benthic	0.2	0.4	1.6	0.0
Scorpion fish	3.3	6.5	0.0	0.3
Pelagic	1.1	1.7	9.8	2.8
Salmonid	0.7	5.8	0.0	0.0
Cephalopod	2.4	1.0	0.0	0.0
Other	0.0	0.7	0.3	0.1

D) Orkney

Prey group	**Summer**	**Autumn**	**Spring**
Gadid	30.0	35.4	31.6
Trisopterus spp.	0.9	0.2	1.5
Sandeel	49.6	13.3	61.8
Flatfish	7.3	5.5	0.0
Sandy benthic	1.2	3.0	0.5
Scorpion fish	3.4	0.1	0.1
Pelagic	7.0	40.2	3.2
Salmonid	0.0	0.0	0.0
Cephalopod	0.3	1.7	1.0
Other	0.3	0.5	0.2

E) Shetland

Prey group	**Summer**	**Autumn**	**Spring**
Gadid	18.2	26.0	25.6
Trisopterus spp.	9.5	5.6	5.5
Sandeel	33.4	29.7	5.9
Flatfish	2.2	3.7	0.0
Sandy benthic	0.0	0.8	20.5
Scorpion fish	0.0	0.0	0.0
Pelagic	36.1	24.6	41.3
Salmonid	0.0	0.0	0.0
Cephalopod	0.6	0.2	1.1
Other	0.0	9.4	0.1

F) Outer Hebrides

Prey group	Summer
Gadid	16.7
Trisopterus spp.	23.9
Sandeel	12.7
Flatfish	1.9
Sandy benthic	2.7
Scorpion fish	15.8
Pelagic	22.3
Salmonid	0.0
Cephalopod	3.7
Other	0.3

G) West coast - north

Prey group	Summer	Spring
Gadid	49.8	39.3
Trisopterus spp.	21.2	21.9
Sandeel	2.4	9.6
Flatfish	1.4	0.3
Sandy benthic	0.3	0.6
Scorpion fish	0.0	0.0
Pelagic	22.8	22.6
Salmonid	0.3	0.0
Cephalopod	1.7	5.6
Other	0.0	0.0

H) West coast - central

Prey group	Summer	Autumn	Winter	Spring
Gadid	42.6	13.2	52.7	49.9
Trisopterus spp.	19.0	5.1	18.1	5.1
Sandeel	5.9	7.0	2.9	3.7
Flatfish	1.2	6.7	2.2	5.4

Sandy benthic	0.8	20.1	15.5	0.6
Scorpion fish	19.4	1.8	1.9	0.0
Pelagic	9.6	45.3	6.2	31.1
Salmonid	0.0	0.0	0.0	0.0
Cephalopod	1.2	0.8	0.4	4.2
Other	0.3	0.0	0.0	0.0

I) West coast - south

Prey group	**Summer**	**Autumn**	**Winter**	**Spring**
Gadid	59.2	43.3	76.7	74.0
Trisopterus spp.	8.5	5.4	8.0	8.9
Sandeel	0.9	1.1	0.3	0.9
Flatfish	2.5	4.6	0.9	4.8
Sandy benthic	12.7	9.7	6.1	1.7
Scorpion fish	0.0	1.0	1.9	1.0
Pelagic	13.9	31.9	6.0	8.8
Salmonid	0.0	0.0	0.0	0.0
Cephalopod	1.9	1.7	0.0	0.0
Other	0.2	1.3	0.0	0.0

Appendix 3.4: 95% Confidence Limits (CL) for harbour seal diet composition expressed as the percentage of each prey type in the diet by weight (Appendix 3.3).

A) The Wash

	95% CL			
Prey type	**Summer**	**Autumn**	**Winter**	**Spring**
Gadid	0.6-8.9	16.3-45.6	15.1-40	0-8.7
Trisopterus spp.	0-3.4	0-0.7	0-4.7	
Sandeel	6.3-41.5	1.4-16.4	1.0-15.3	0.7-11.0
Flatfish	15.8-40.4	21.6-51.3	5.0-26.5	12-63.8
Sandy benthic	29.9-63.1	12.2-34.7	7.4-25.5	14.8-72.8
Scorpion fish	0-0.8	0.5-6.6	3.1-38.4	0-37.2
Pelagic	0-0.4	0-0.5	4.2-30.1	0-8.2

Salmonid				
Cephalopod	0-0.1	0-6.7	0-12.0	
Other	0-1.3	0-1.0	0-0.1	0-0.5

B) SE Scotland

Prey type	95% CL All seasons
Gadid	5.8-27.9
Trisopterus spp.	
Sandeel	2.7-38.8
Flatfish	22-66.2
Sandy benthic	0.2-8.8
Scorpion fish	0-3.4
Pelagic	2-22.5
Salmonid	0-2.3
Cephalopod	0-23.4
Other	0-2.9

C) Moray firth

	95% CL			
Prey type	**Summer**	**Autumn**	**Winter**	**Spring**
Gadid	1.1-4.8	1.0-13.3	1.7-30.6	0.3-9
Trisopterus spp.	0-0.1		0-1.5	0-0
Sandeel	37.1-75.8	41.1-95.2	41.1-84.8	68.2-93.7
Flatfish	16.1-50.2	1.1-10.1	3.7-23.8	3.0-21.8
Sandy benthic	0-0.9	0-1.3	0-7.4	0-0
Scorpion fish	0.3-9.9	0-20.8		0-1.0
Pelagic	0-4.7	0-7.7	2.3-25.8	0.9-7.5
Salmonid	0-2.6	0-20.0		
Cephalopod	0-7.6	0-3.5		
Other	0-0.2	0-2.3	0-1.0	0-0.3

D) Orkney

	95% CL		
Prey type	**Summer**	**Autumn**	**Spring**
Gadid	16.5-48	22.1-51.3	4.9-84.8
Trisopterus spp.	0.4-1.8	0.1-0.4	0-6.5
Sandeel	28.0-70.0	5.2-26.2	11.6-90.5
Flatfish	2.1-14.5	1.2-13.0	
Sandy benthic	0.5-2.9	0.4-8.4	0-1.6
Scorpion fish	0.4-12.8	0-0.5	0-0.7
Pelagic	1.5-16.4	24.9-56.1	0-11.4
Salmonid			
Cephalopod	0-1.1	0-3.5	0-5.2
Other	0-0.8	0-2.3	0-0.9

E) Shetland

	95% CL		
Prey type	**Summer**	**Autumn**	**Spring**
Gadid	5.2-39.4	7.8-64.7	4.9-68.1
Trisopterus spp.	4.2-16.6	1.3-11.7	0.6-13.1
Sandeel	12.1-58	10.7-51	0.2-20.4
Flatfish	0-7.0	0.6-11	
Sandy benthic	0-0	0-2.6	6.0-49.2
Scorpion fish			
Pelagic	15.2-61.5	9.4-45.6	10.5-64.9
Salmonid			
Cephalopod	0-1.9	0-0.7	0-3.8
Other	0-0	1.6-24.6	0-0.3

F) Outer Hebrides

	95% CL
Prey type	**Summer**
Gadid	7.1-33.6
Trisopterus spp.	12.7-36.6

Sandeel	1.4-32.7
Flatfish	0.1-5.9
Sandy benthic	0-10.2
Scorpion fish	1-36.6
Pelagic	10-44.1
Salmonid	
Cephalopod	0.3-10
Other	0-0.8

G) West coast - north

	95% CL	
Prey type	**Summer**	**Spring**
Gadid	33.8-73.4	13.8-64.9
Trisopterus spp.	10.3-29.3	9.9-38.2
Sandeel	0.7-6.4	1.7-27.2
Flatfish	0-4.8	0.1-0.7
Sandy benthic	0-1.4	0-2.8
Scorpion fish		0-0
Pelagic	10.1-40.6	8.7-42.7
Salmonid	0-1.3	
Cephalopod	0.1-4.4	0-16.1
Other	0-0	0-0.1

H) West coast - central

	95% CL			
Prey type	**Summer**	**Autumn**	**Winter**	**Spring**
Gadid	24.4-61.5	6.7-24.7	35.3-72.4	25.7-72.8
Trisopterus spp.	9.3-30.1	2.2-9.2	7.1-28.0	1.8-9.6
Sandeel	2.1-13.2	0.6-17	1.1-11.7	1.1-9.5
Flatfish	0.2-3.3	1.3-14.9	0.7-5.1	1.5-11.6
Sandy benthic	0.2-2.1	4.7-43.2	1.3-36.1	0-2.1
Scorpion fish	0.9-46.3	0.2-5.6	0.1-3.9	
Pelagic	3-24.1	24-68.2	1.1-17.1	10.9-59.6

Salmonid				
Cephalopod	0-4.4	0.1-1.9	0-1.6	0.7-9.4
Other	0-0.9	0-0		0-0

I) West coast - south

	95% CL			
Prey type	**Summer**	**Autumn**	**Winter**	**Spring**
Gadid	42.7-71.6	29.7-55.9	59-91.1	62.6-83.6
Trisopterus spp.	5.4-12.2	2.2-9.4	3.1-12.7	3.8-14.0
Sandeel	0.3-1.9	0.2-3.2	0-0.8	0.1-2.3
Flatfish	1.1-4.5	2.1-7.4	0-3.6	2.0-8.3
Sandy benthic	3.7-25.3	4.4-20.0	0.1-19.1	0.2-5
Scorpion fish	0-0.2	0-3.7	0-6.6	0-4.1
Pelagic	5.4-32.5	18.7-48	0-17.6	2.8-18.2
Salmonid				
Cephalopod	0-6.1	0.2-4.3		0-0
Other	0-0.5	0-3.1		

Appendix 3.5: 95% Confidence Limits (CL) for harbour seal diet composition expressed as the percentage of each species in the diet by weight (Table 3.8). Prey species listed are those that contributed >2% in any season

A) The Wash

	95% CL			
Species	**Summer**	**Autumn**	**Winter**	**Spring**
Cod	0-6.5	0-0.8	0-11.6	0-17
Whiting	0.4-2.7	16.3-45.6	12.3-34.6	0.2-2.3
Sandeel	6.3-41.5	1.4-16.4	1.0-15.3	1.1-9.5
Plaice	2.6-19.4	3.3-21.1	0.1-5.6	0-2.1
Lemon sole	0.3-5.7	0.7-16.0	0-19.2	0.5-7.1
Unidentified flatfish	1-4.2	2.1-9.3	0.1-1.8	0-1.3
Dover sole	2.3-11.0	0.9-22.7	0.2-4.5	
Flounder (Butt)	1.1-7.7	0-3.3		
Dab	1.9-8.7	1.6-7.5	0-2.9	0-1.7

Dragonet	25.7-58.9	11.3-34	2.1-19.5	0-2.1
Goby	1.8-7.1	0.1-1.5	1.6-13.2	0-0.2
Bullrout		0-5.8	0.4-34.1	
Sea Scorpion	0-0.7	0-1.9	0.4-20.1	
Herring		0-0.5	0-19.4	0.5-13.3
Sprat			2.0-18.3	
Loligo		0-3.4	0-12	0-5.2

B) Southeast Scotland

	95% CL
Species	**All Seasons**
Cod	1.0-8.0
Whiting	1.0-20.0
Sandeel	3.0-39.0
Plaice	9.0-49.0
Unidentified flatfish	2.0-6.0
Flounder (Butt)	1.0-13.0
Dab	3.0-13.0
Goby	0-7.0
Mackerel	0-14.0
Sprat	0-15.0
Loligo	0-23.0

C) Moray Firth

	95% CL			
Species	**Summer**	**Autumn**	**Winter**	**Spring**
Saithe	0-1.7	0.1-9.4	0-28.7	0.1-8.3
Sandeel	37.1-75.8	41.1-95.2	41.1-84.8	68.2-93.7
Plaice	5.2-20.9	0.5-4	0.1-2.3	0.2-1.5
Unidentified flatfish	1.3-6.7	0-2.4	0.2-3.3	0.5-4.9
Flounder (Butt)	0.2-3.1	0-2.9	0.9-16.8	1.2-15.5
Dab	6.3-27.8	0.1-3.5	0.6-7.5	0-1.8
Bullrout	0.3-9.9	0-20.8		0-1.0

Sprat			1.7-23.7	0.8-7.3
Unidentified Salmonid	0-2.6	0-20.0		
Loligo	0-7.6	0-3.5		

D) Orkney

	95% CL		
Species	**Summer**	**Autumn**	**Spring**
Cod	10.9-35.4	13.7-39.1	0-16.2
Saithe	0.3-14.7	0.2-13.5	1.3-79.4
Haddock	0-2.2	0.8-6.7	0-2.4
Ling	0.7-5.4	0.1-10.3	
Sandeel	28-70	5.2-26.2	11.6-90.5
Plaice	0.7-5.4	0.2-2.3	
Flounder (Butt)	0-6.9		
Dab	0.3-3	0.2-10.5	
Dragonet	0.4-2.8	0.4-8.4	
Sea Scorpion	0-11.4	0-0.4	
Mackerel	0-4.1	1.7-20.8	0-9.9
Herring	0.7-14.9	17.4-47.9	0-4.8

E) Shetland

	95% CL		
Species	**Summer**	**Autumn**	**Spring**
Saithe	0.5-21.3	3.7-62.2	0.4-61.6
Ling	1.4-30.1	0-2.0	0-6.3
Rockling	0-3.2		0-24.1
3-bearded rockling			0-7.9
Poor cod	0.4-3.4	1.1-11.1	0.1-1.6
Norway pout	2.9-14.7	0-1.4	0.1-10.5
Sandeel	12.1-58	10.7-51	0.2-20.4
Plaice	0-6.6	0-0.5	
Lemon sole		0-9.8	
Dragonet		0-2.6	6-49.2

Mackerel	0-4.3	2.2-28.4	0-9.2
Herring	14.7-60.3	4.7-27.7	10.5-62.7
Garfish		1.6-24.5	

F) Outer Hebrides

	95% CL
species	**Summer**
Cod	1.1-8.7
Whiting	0.9-4
Ling	0-8.9
Rockling	0-12.5
Poor cod	1.7-7.1
Norway pout	9.5-30.9
Sandeel	1.4-32.7
Dragonet	0-10.2
Unidentified *Cottidae*	1-36.6
Mackerel	3.2-32.8
Herring	2.1-15.4
Horse mackerel (Scad)	0.3-6.6
Eledone	0.3-10

G) West coast - North

	95% CL	
species	**Summer**	**Spring**
Cod	5.1-21.2	0-12.0
Whiting	1.8-18.1	0.4-4.7
Saithe	0.7-50.0	0.7-39.8
Ling	2.2-16.8	0.6-34.5
Rockling	0-0.1	0-17.1
Blue whiting	2.1-15	0-1.6
Poor cod	3.2-14.1	2.4-11.2
Norway pout	4.7-14.6	5.6-30.9
Norway pout / Poor cod	0.8-4.0	

Sandeel	0.7-6.4	1.7-27.2
Mackerel	0.8-17.9	1.7-33.8
Herring	5.9-29.1	1.8-18.7
Loligo	0-1.7	0-16.1

H) West coast - central

	95% CL			
Species	**Summer**	**Autumn**	**Winter**	**Spring**
Cod	0-5.3	1.1-7.4	0.2-13.4	0-12.0
Whiting	7.4-23.8	0.6-2.6	2.9-15.7	0.4-4.7
Haddock	0.1-1.1	1-4.5	0.3-4.6	0-5.3
Saithe		0.1-13.3	0.5-33.9	0.7-39.8
Ling	0-3.7	0.1-3.8	0.4-18.0	0.6-34.5
Unidentified gadid	2-8.1	0.1-1.1	0.9-4.4	0-0
Saithe or Pollock		0-2.3	0-31.0	
Hake	0.4-5.5		0-3.1	
Blue whiting	5.4-35.9	0-1.9	6.4-27.8	0-1.6
Poor cod	3-14.6	1.2-6.7	4.9-19.7	2.4-11.2
Norway pout	4.4-19.1	0.6-2.6	1.6-8.5	5.6-30.9
Sandeel	2.1-13.2	0.6-17	1.1-11.7	1.7-27.2
Plaice	0-0.8	0.5-4.7		
Lemon sole	0-1.9	0-0.7		0-0.3
Dab		0.3-8.9	0-0.5	
Dragonet	0.2-2.1	4.7-43.2	1.3-36.1	0-2.8
Unidentified *Cottidae*	0-45.2	0.2-5.6		
Mackerel	0-20.2	8.6-55	0-0.9	1.7-33.8
Herring	0.6-9.8	5.4-22.9	0-14.4	1.8-18.7
Horse mackerel (Scad)		1.5-7.5	0.4-3.0	
Eledone	0-4.4	0-1.5		

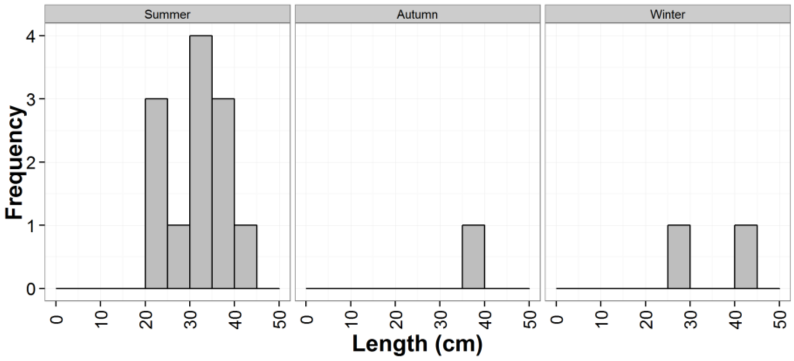
I) West coast - south

	95% CL			
Species	**Summer**	**Autumn**	**Winter**	**Spring**
Cod	0.6-12.0	2.0-12.8	3.3-41.2	8.2-38.2
Whiting	15.3-30.7	3.6-10.5	5.2-36.6	7.8-19.0
Haddock	9.8-23.1	12.3-31	3.9-24.8	14.2-41.3
Saithe	0-8.2	0-7.5	0.5-63.9	0.1-23.4
Ling	0-3.2	0-4.3	0-20.4	
Rockling	0-0.5	0.5-7.0		0-0.3
Unidentified gadid	3.5-12.2	0.4-4.7	0.7-6.6	1.7-9.2
Blue whiting	2.2-8.8	0-0.6	0.1-2.2	1.3-6.6
Poor cod	2.3-6.2	1.9-8.5	2.7-11.5	2.1-8.7
Norway pout	2.6-5.6	0-0.2	0.1-1.4	1.4-5.3
Witch	0.1-2.1	0.1-2.4	0-0	0.5-4.5
Dragonet	3.7-25.3	4.2-20.0	0-18.9	0-4.9
Mackerel	2.7-29.7	1.0-17.4	0-10.4	0-12.5
Herring	0.4-6.0	13.9-40.5	0-11.8	1-11.6

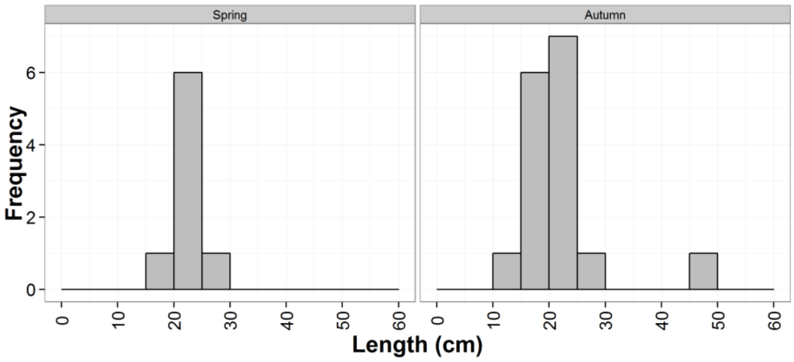
Appendix 3.6: Length-frequency histograms for 9 major prey species in harbour seal diet in each region and season where prey remains were available.

Cod

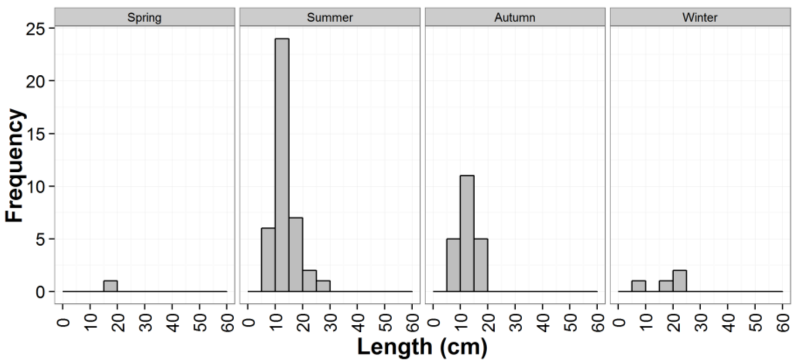
A) England



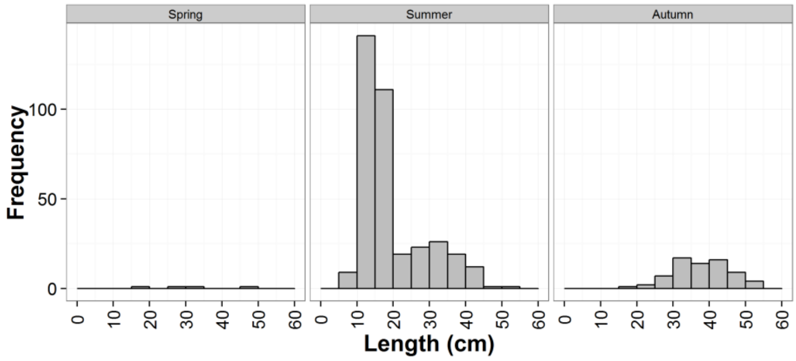
B) SE Scotland



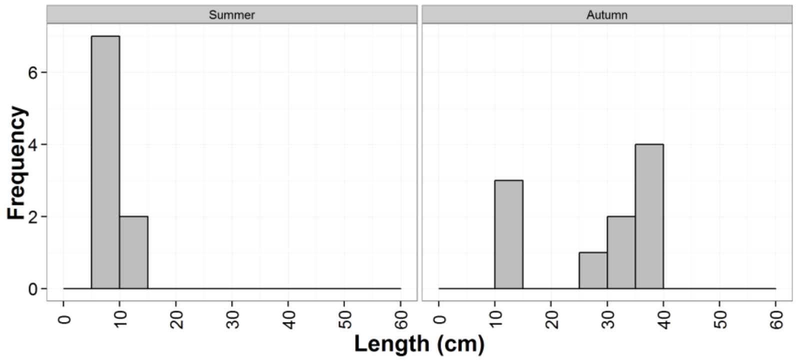
C) Moray Firth



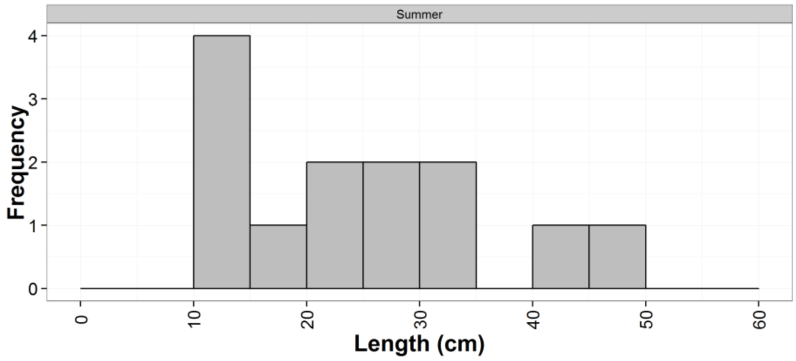
D) Orkney



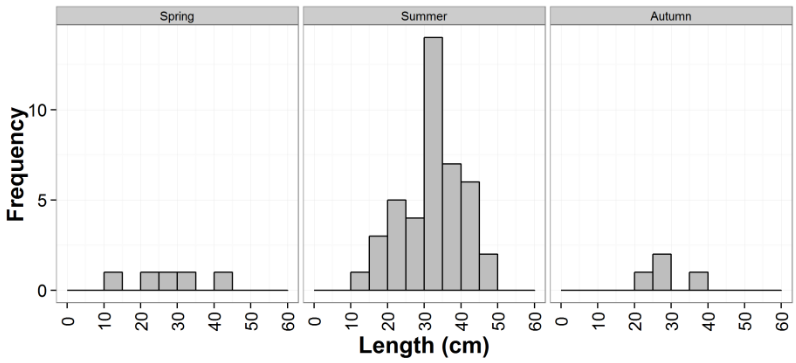
E) Shetland



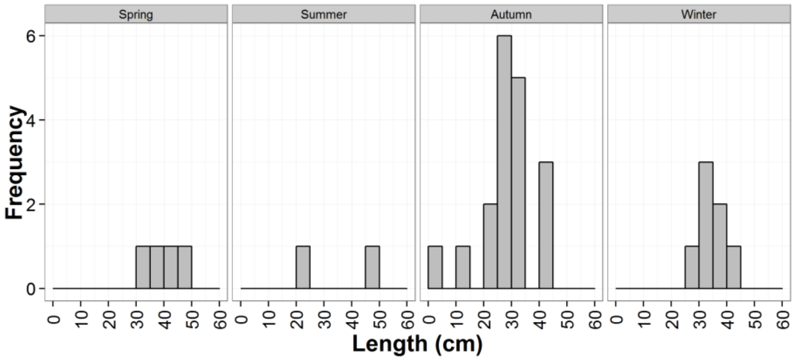
F) Outer Hebrides



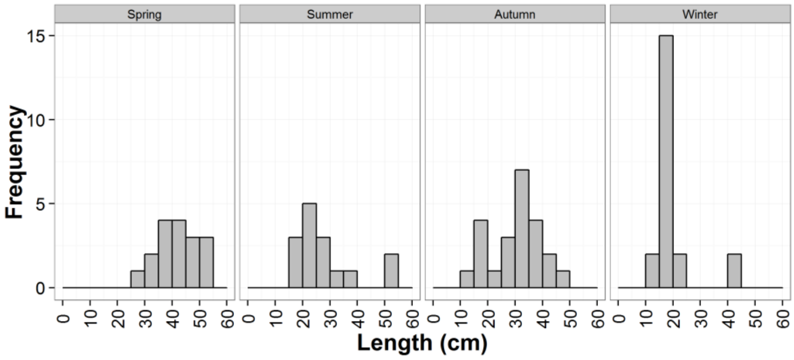
G) West coast – north



H) West coast – central

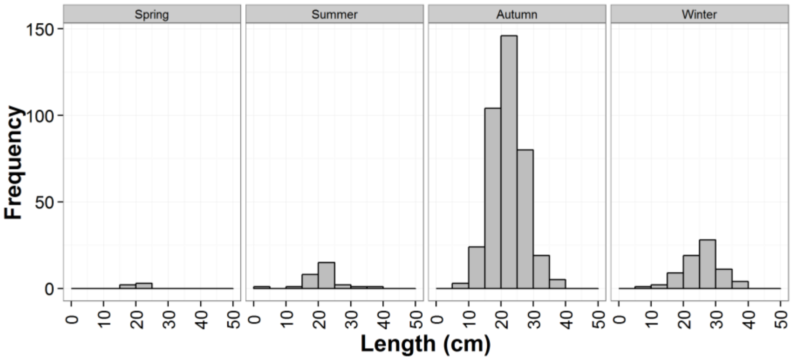


I) West coast – south

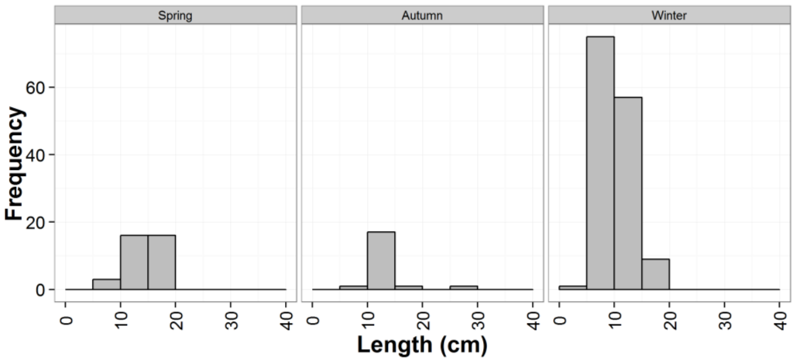


Whiting

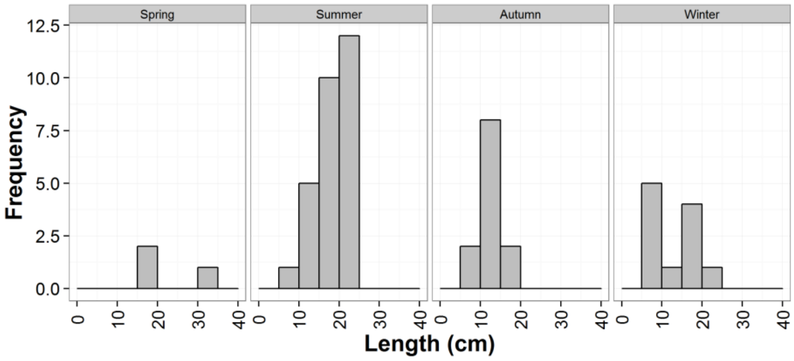
A) England



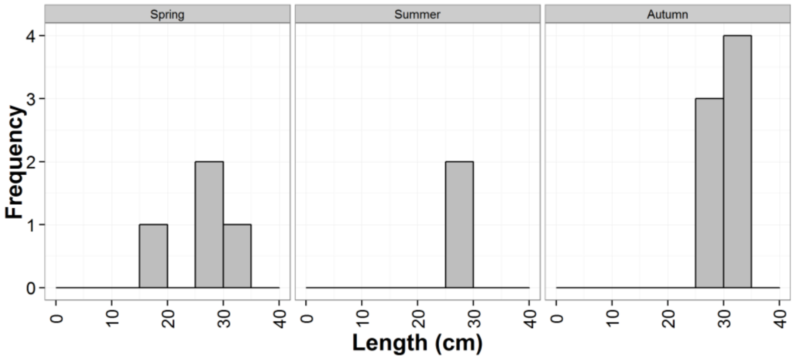
B) SE Scotland



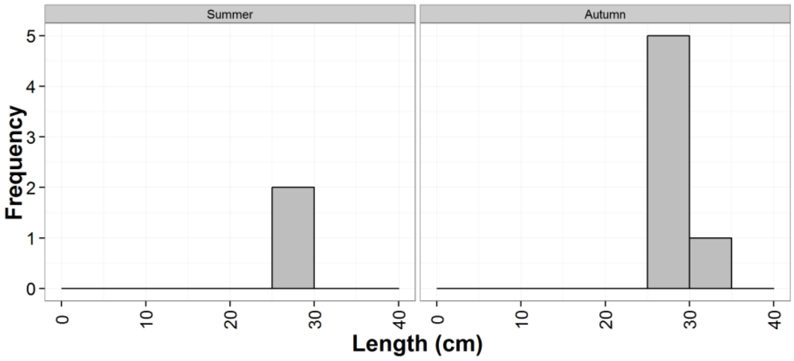
C) Moray Firth



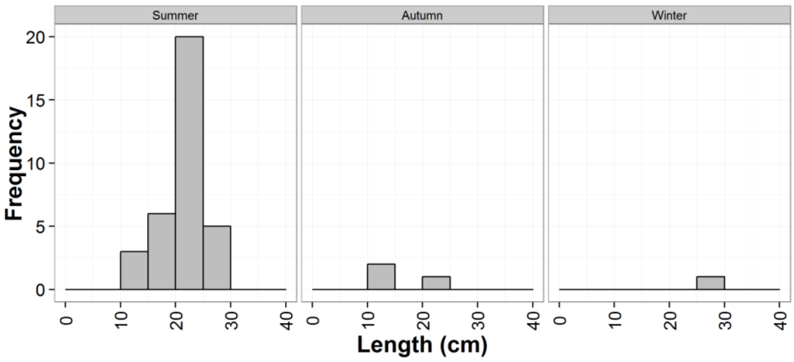
D) Orkney



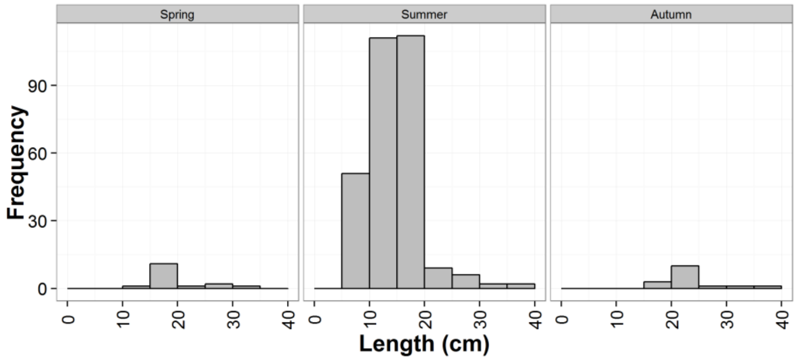
E) Shetland



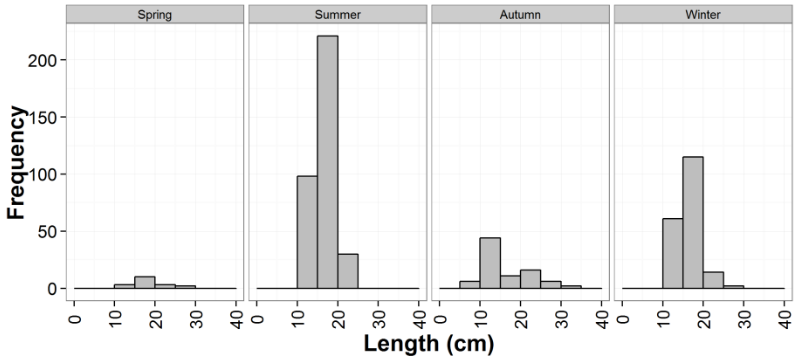
F) Outer Hebrides



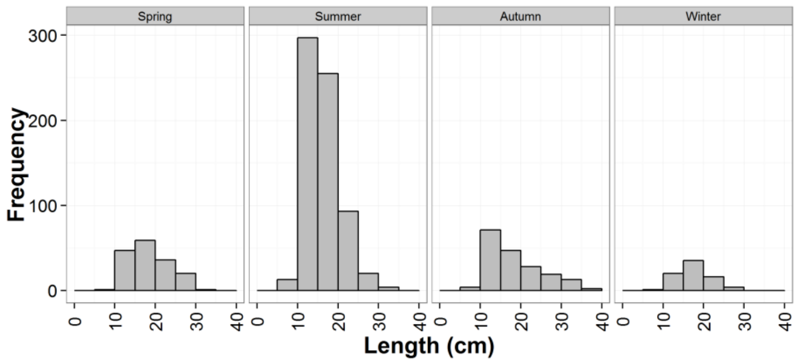
G) West coast – north



H) West coast – central

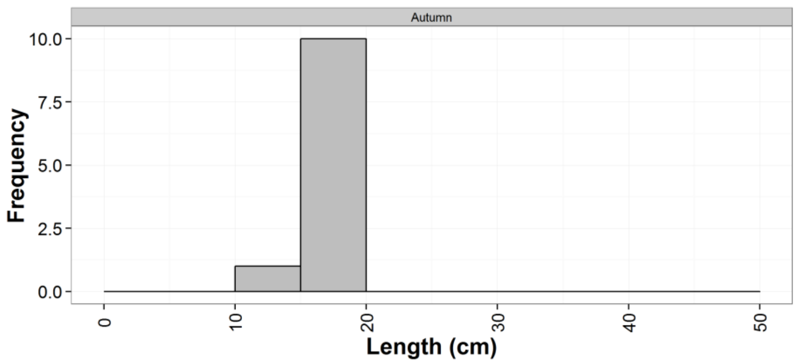


I) West coast – south

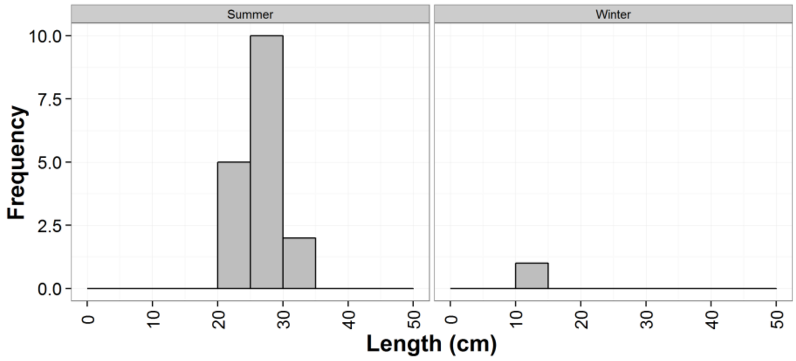


Haddock

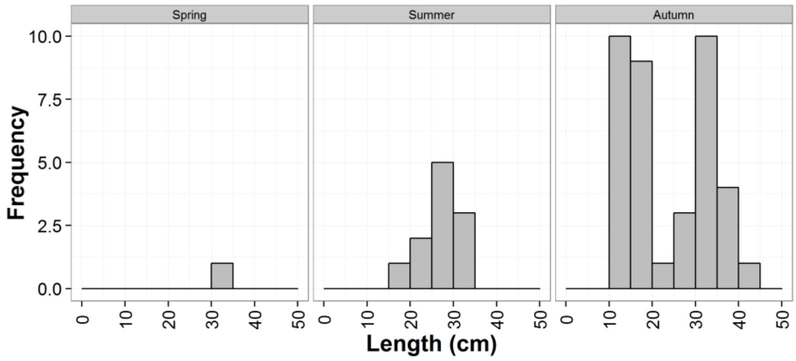
A) SE Scotland



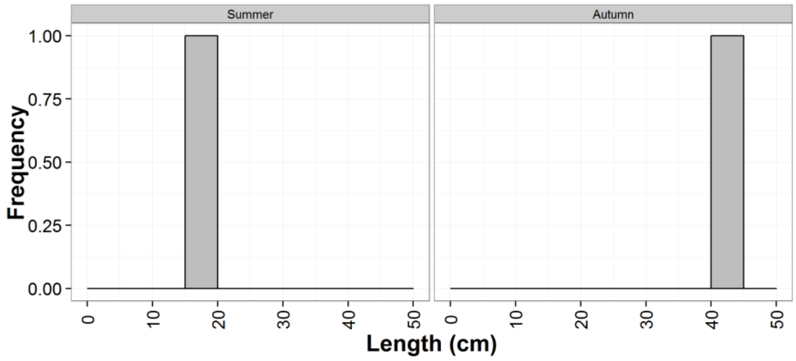
B) Moray Firth



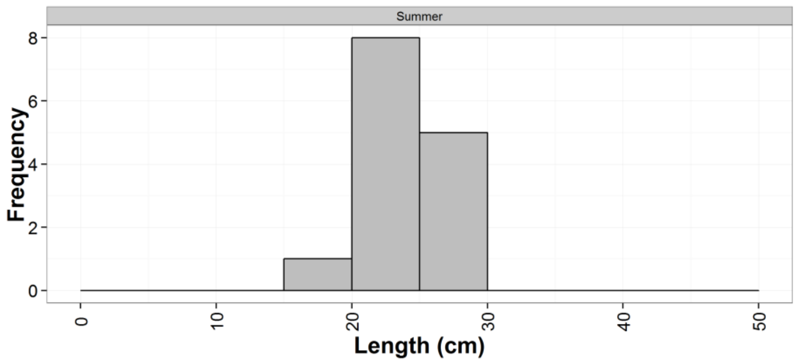
C) Orkney



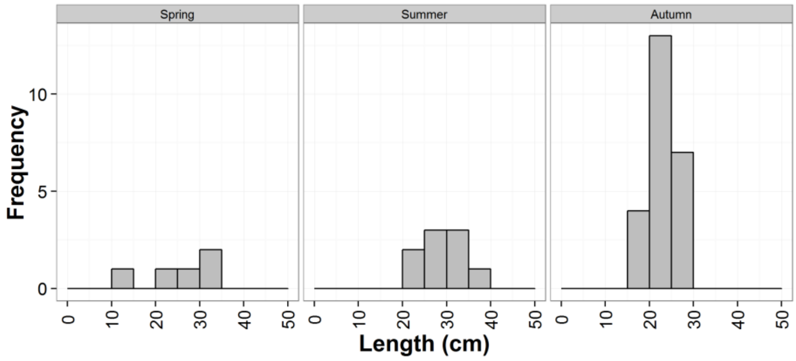
D) Shetland



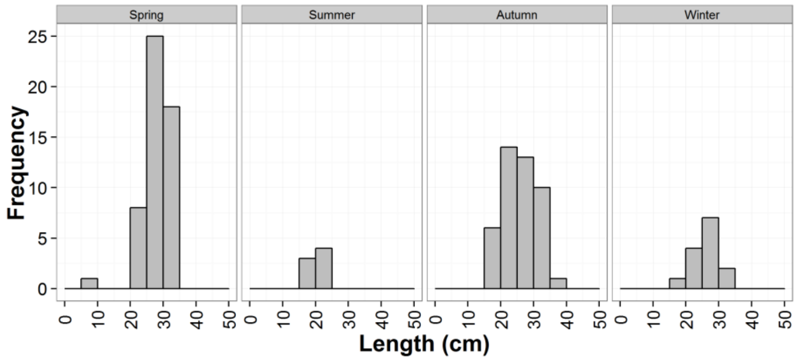
E) Outer Hebrides



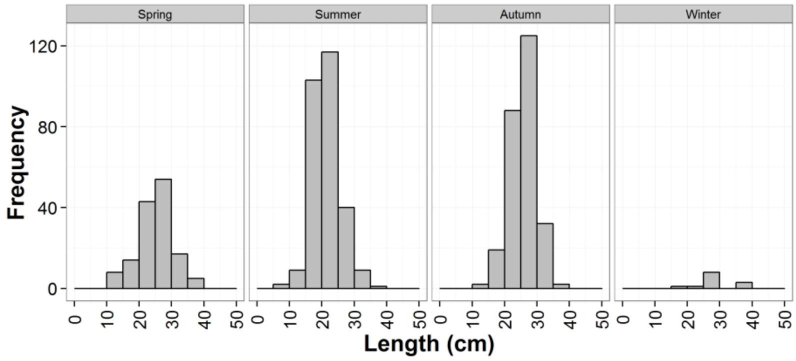
F) West coast – north



G) West coast – central

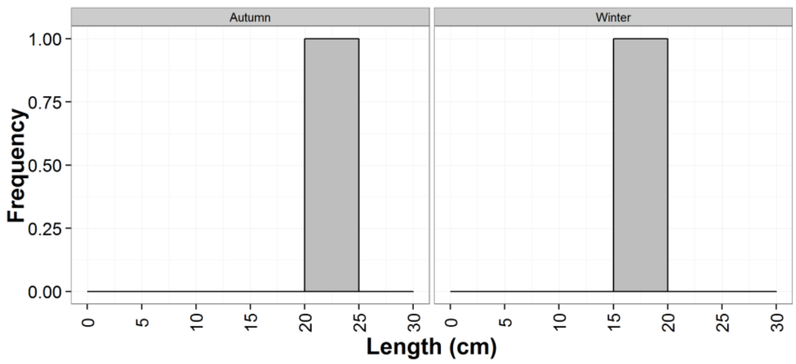


H) West coast – south

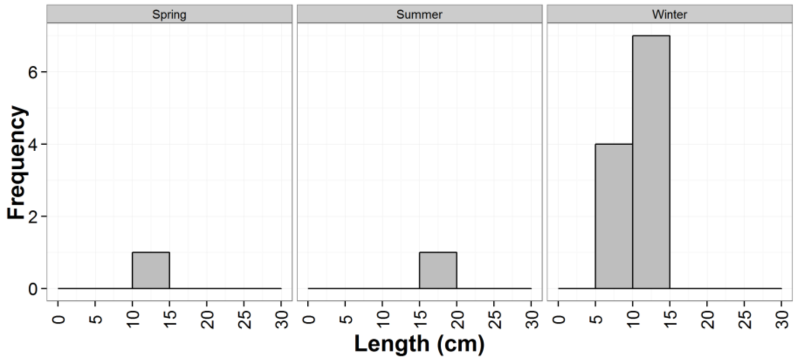


Poor cod

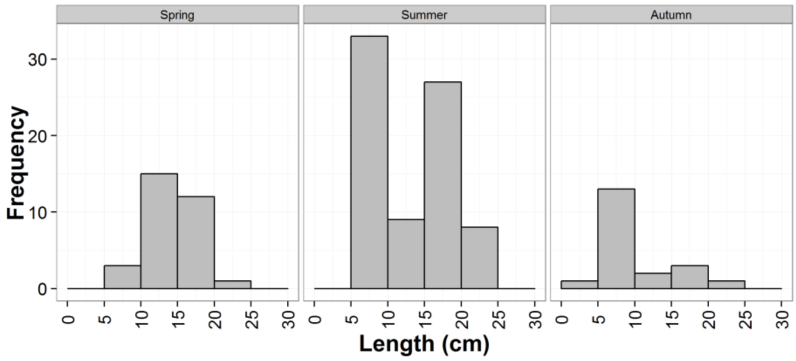
A) England



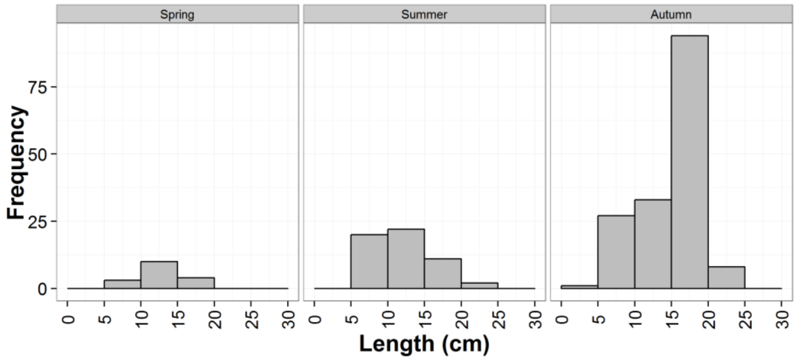
B) Moray Firth



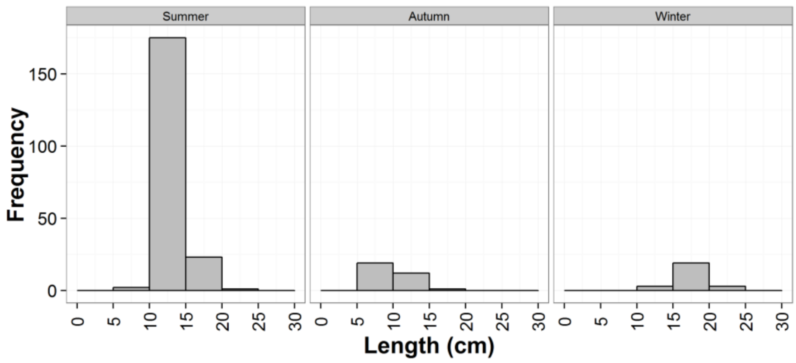
C) Orkney



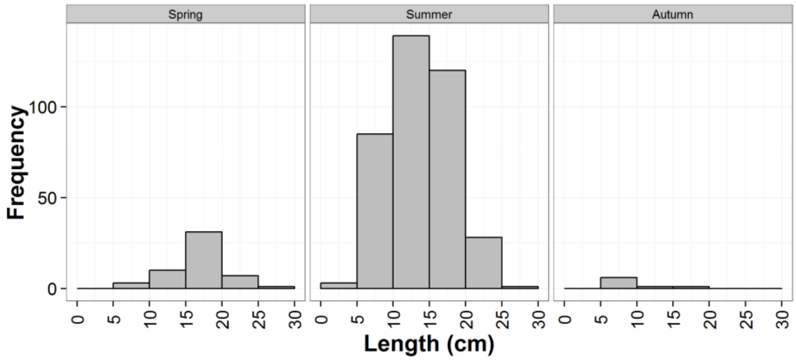
D) Shetland



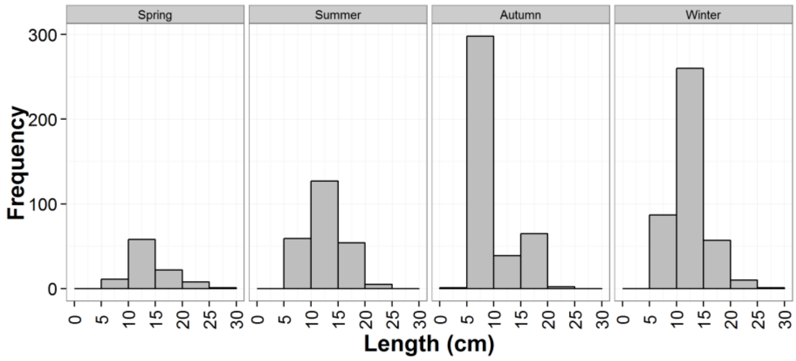
E) Outer Hebrides



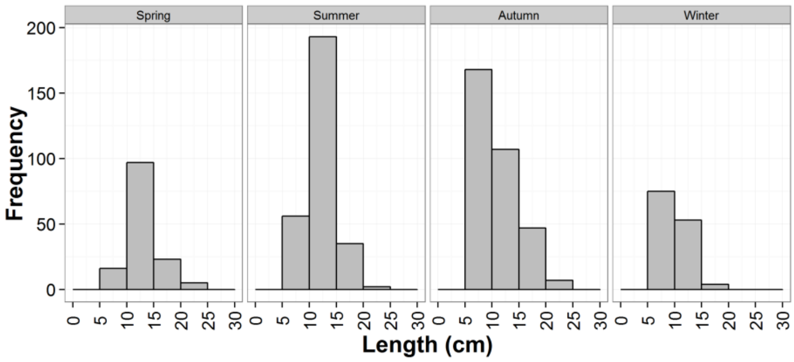
F) West coast – north



G) West coast – central

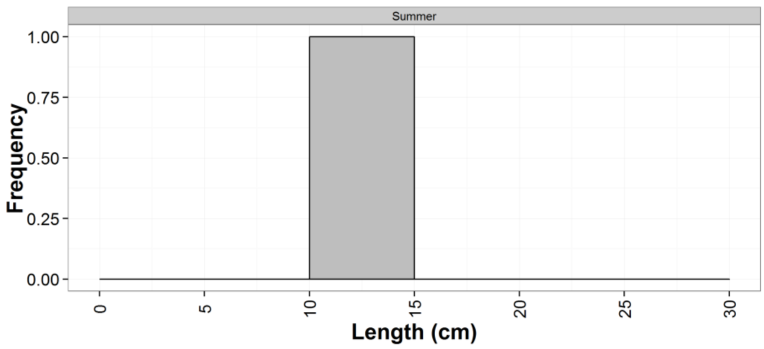


H) West coast – south

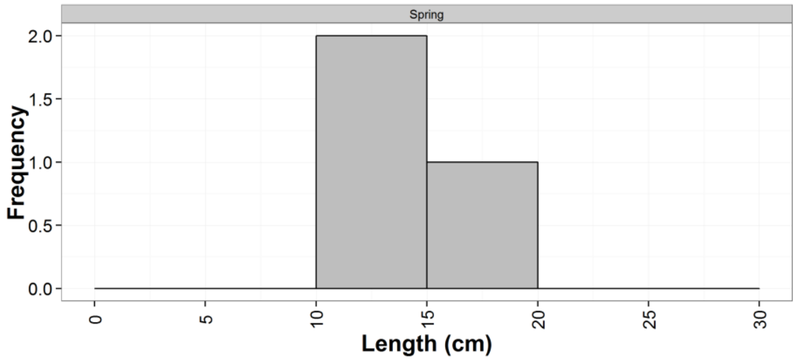


Norway pout

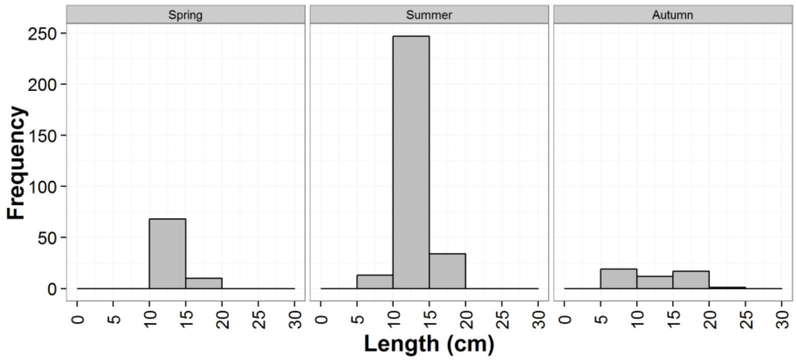
A) Moray Firth



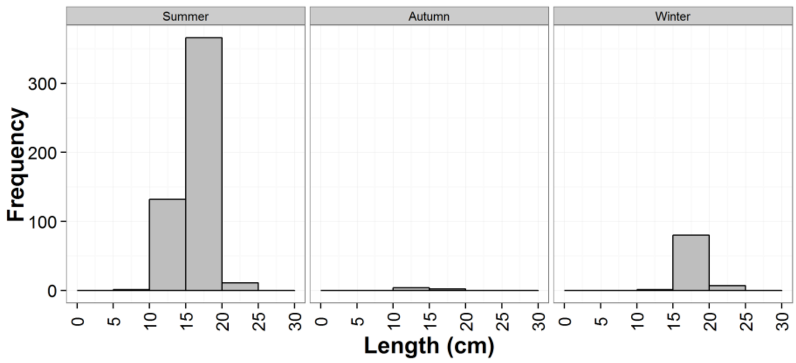
B) Orkney



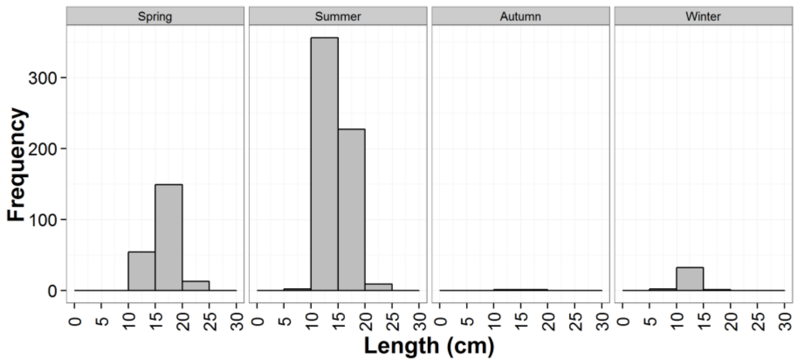
C) Shetland



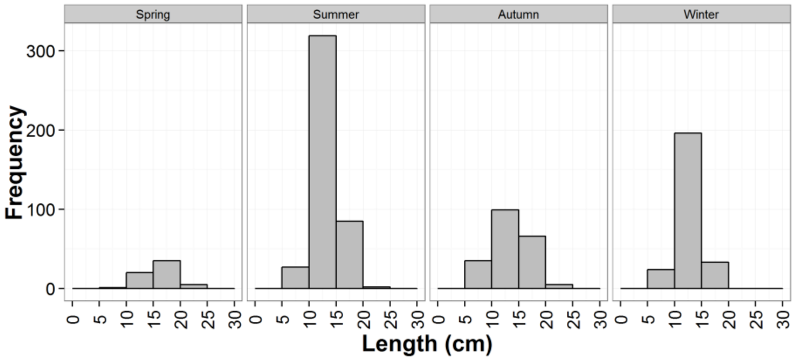
D) Outer Hebrides



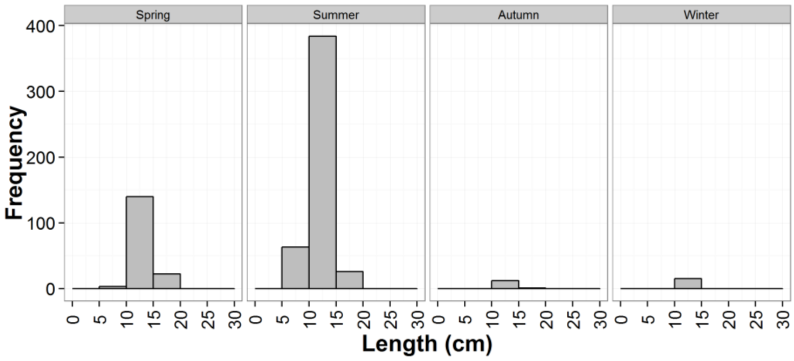
E) West coast – north



F) West coast – central

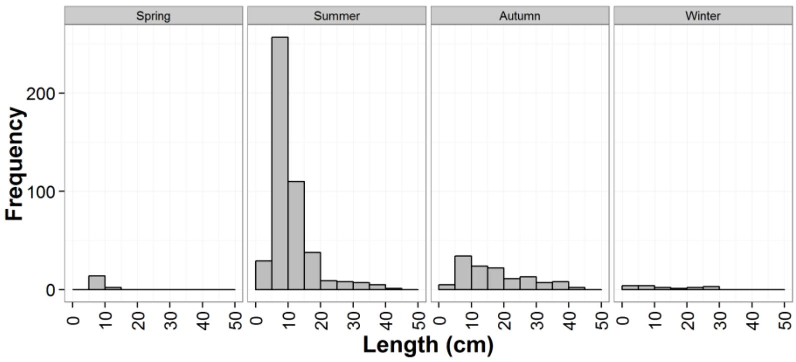


G) West coast – south

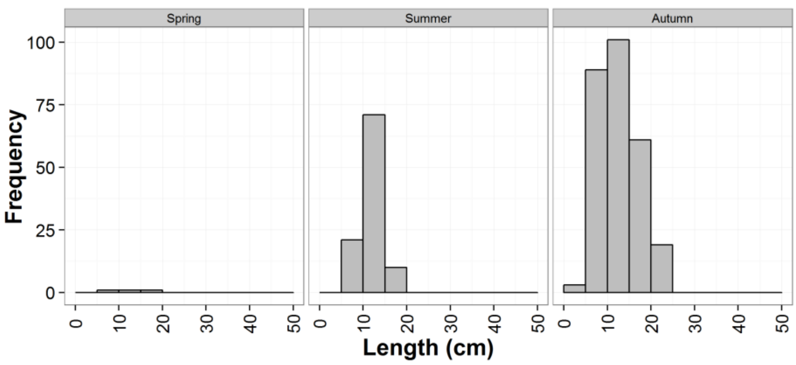


Plaice

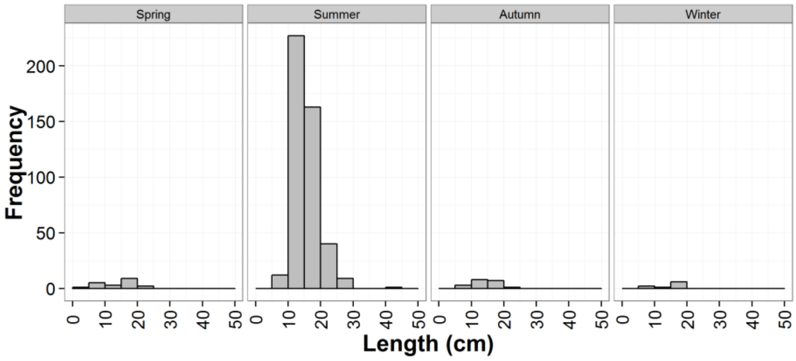
A) England



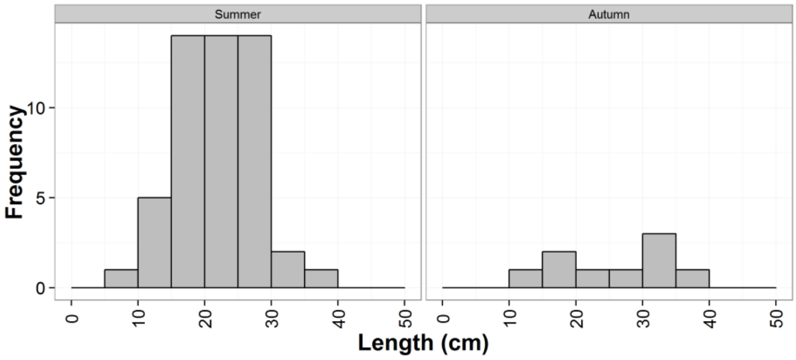
B) SE Scotland



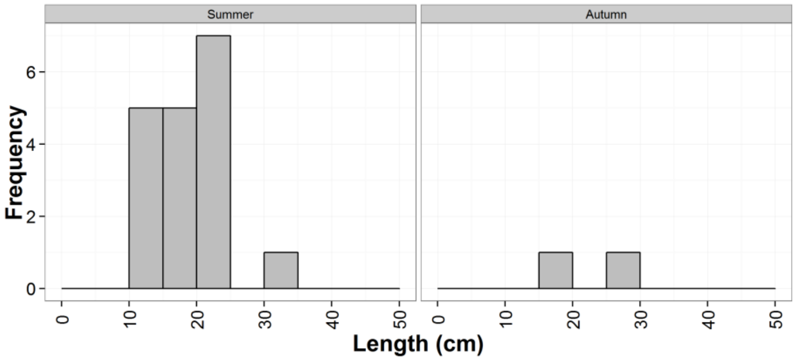
C) Moray Firth



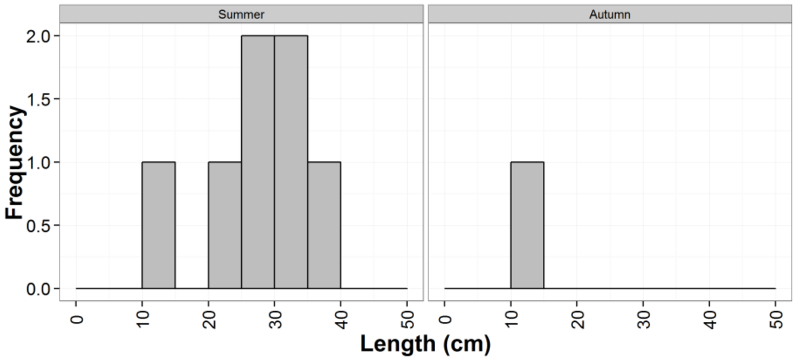
D) Orkney



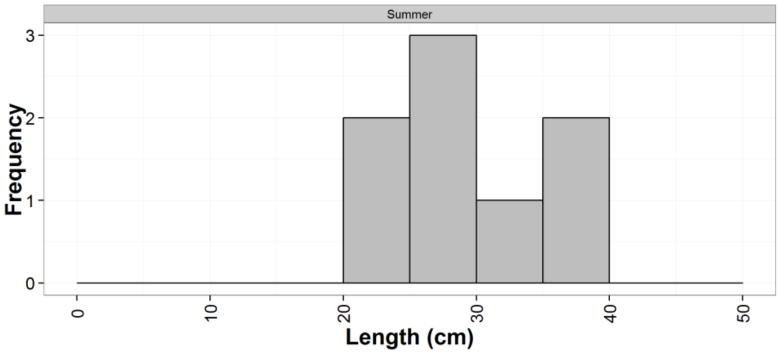
E) Shetland



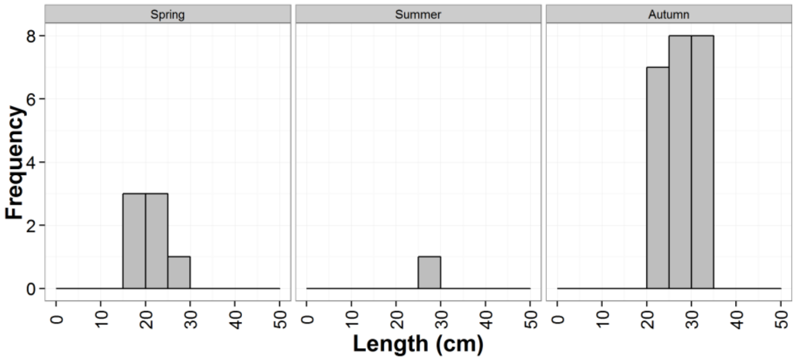
F) Outer Hebrides



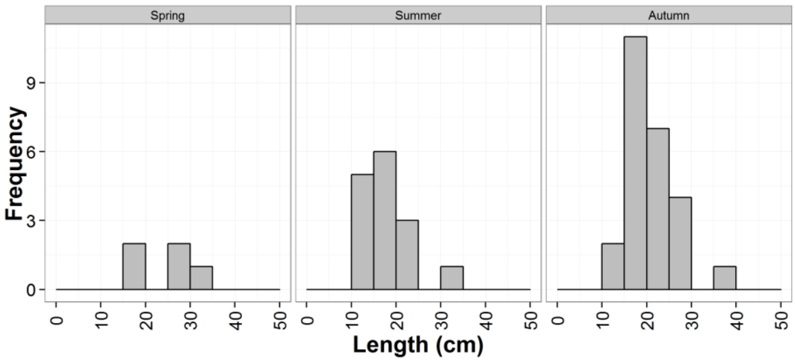
G) West coast – north



H) West coast – central

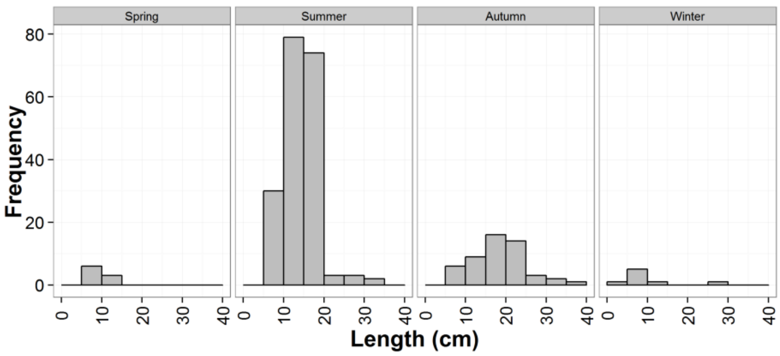


I) West coast – south

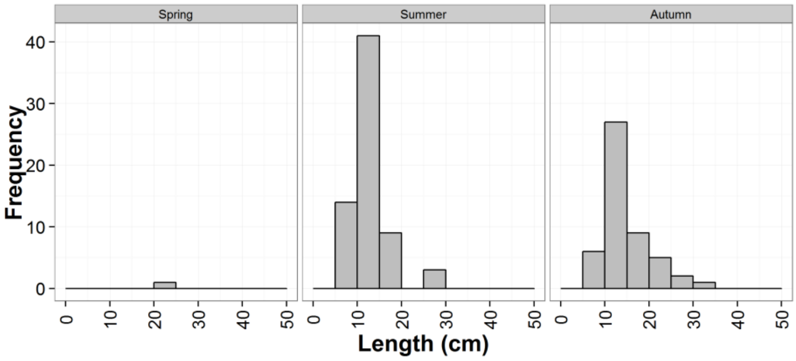


Dab

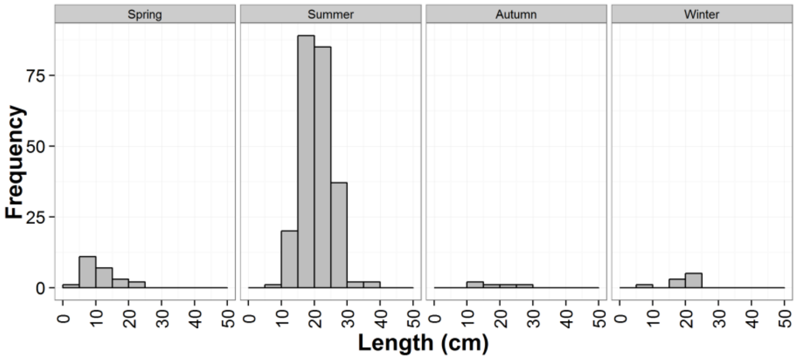
A) England



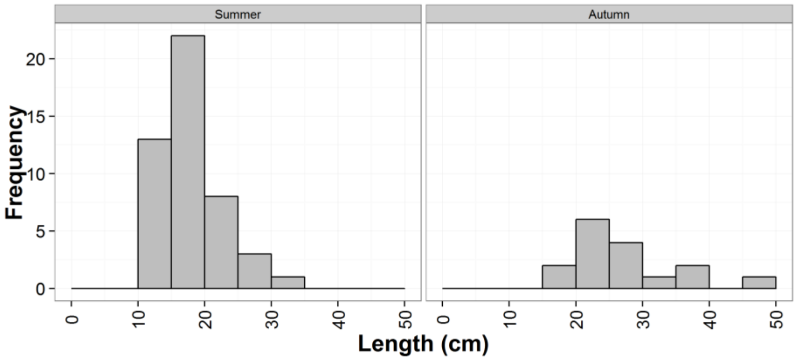
B) SE Scotland



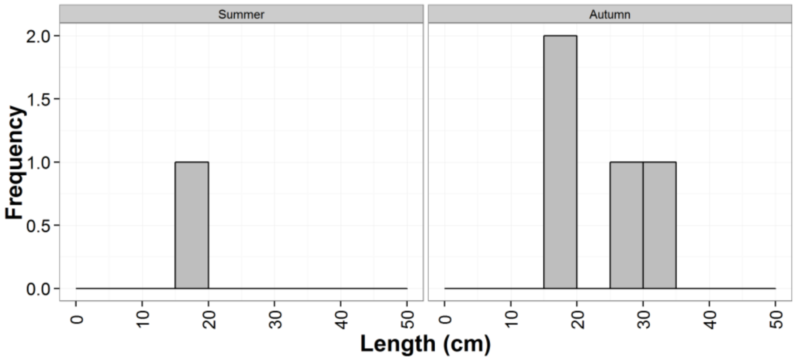
C) Moray Firth



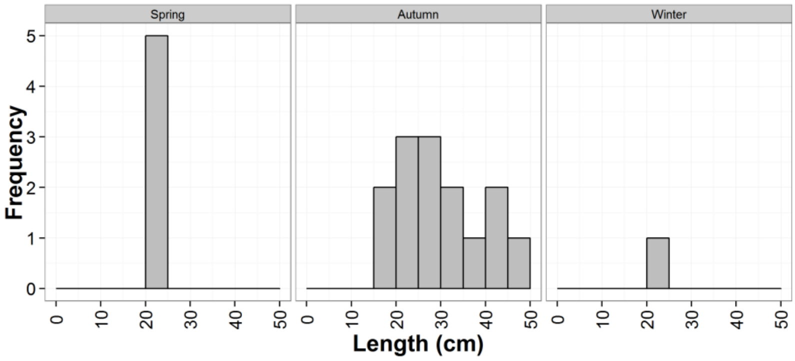
D) Orkney



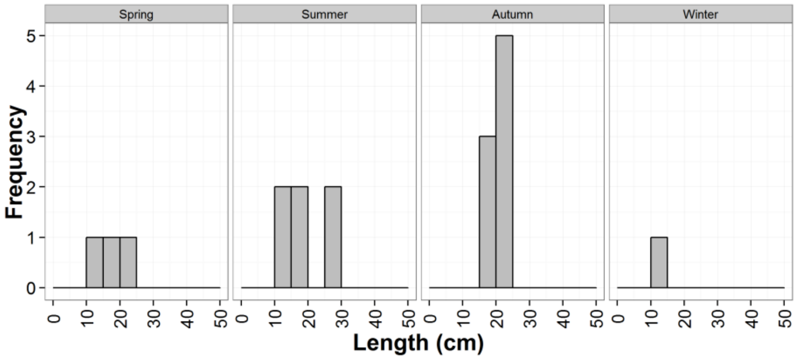
E) Shetland



F) West coast – central

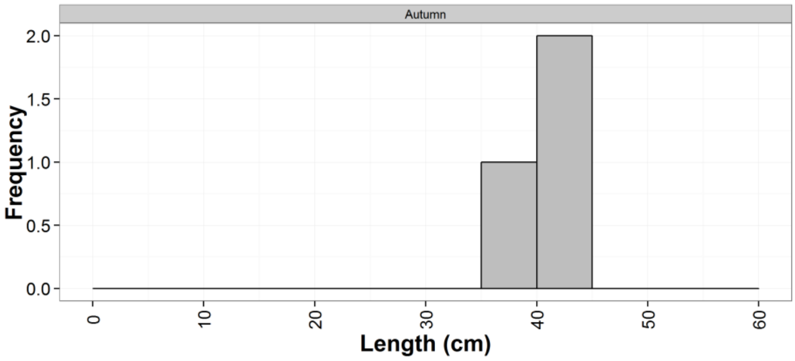


G) West coast – south

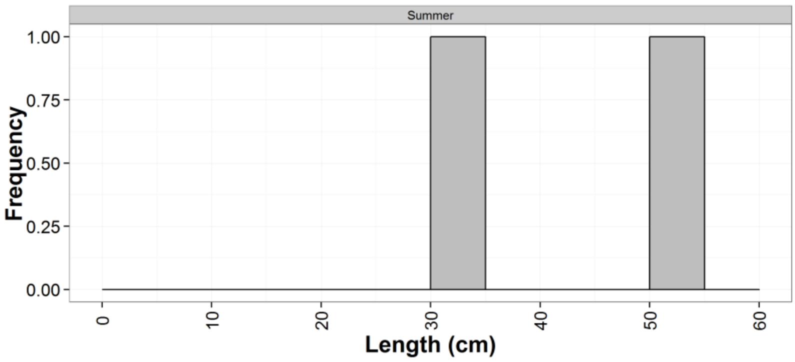


Mackerel

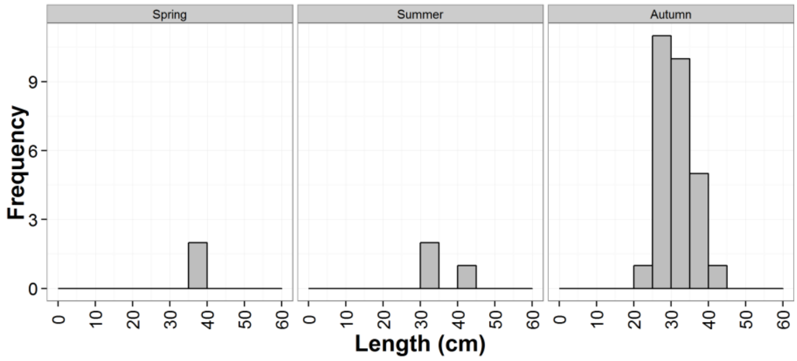
A) SE Scotland



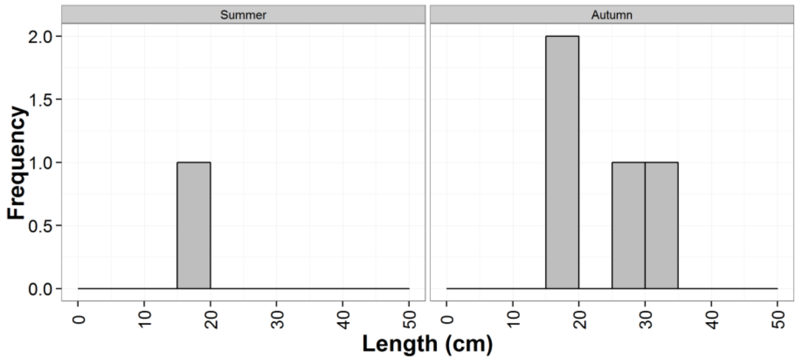
B) Moray Firth



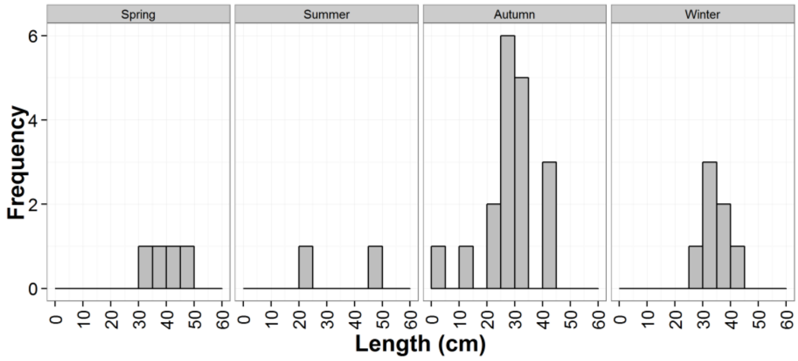
C) Orkney



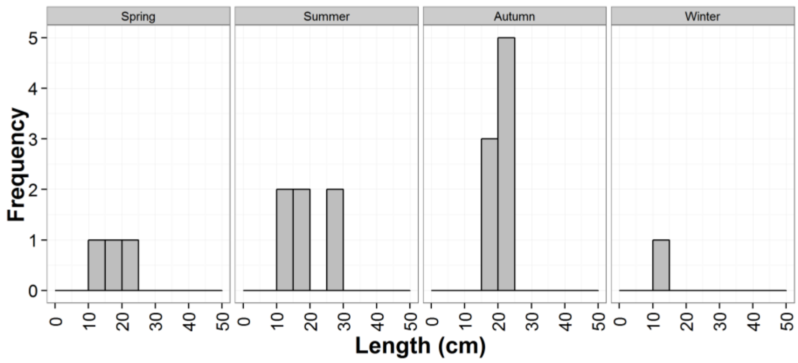
D) Shetland



E) West coast – central

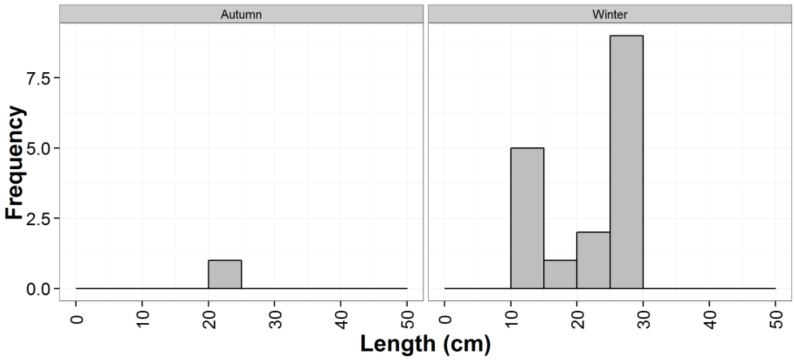


F) West coast – south

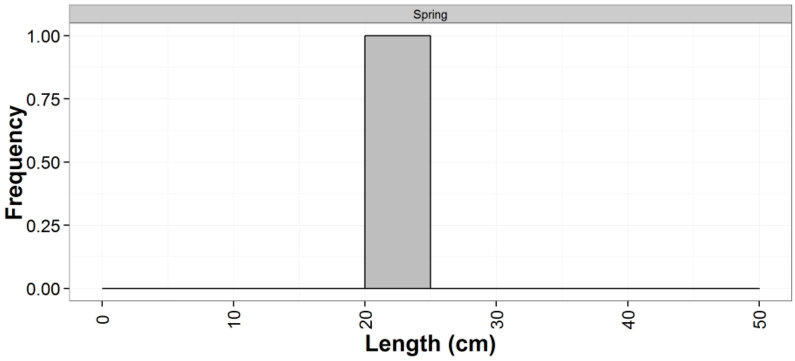


Herring

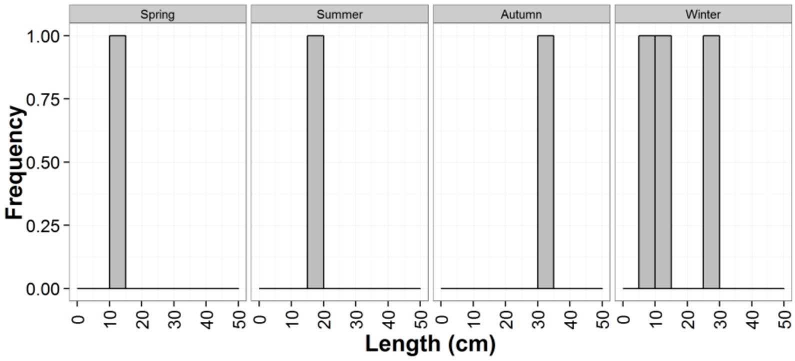
A) England



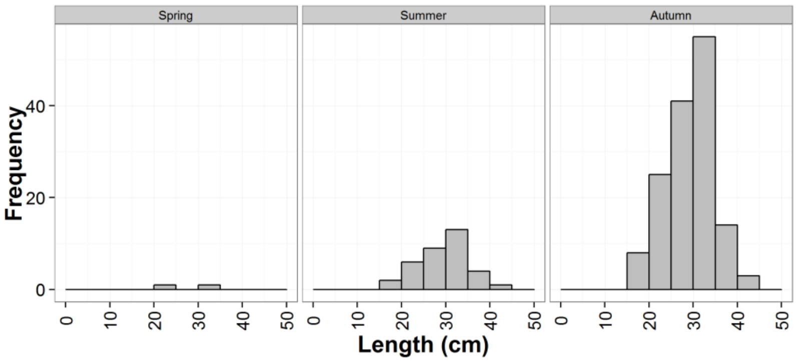
B) SE Scotland



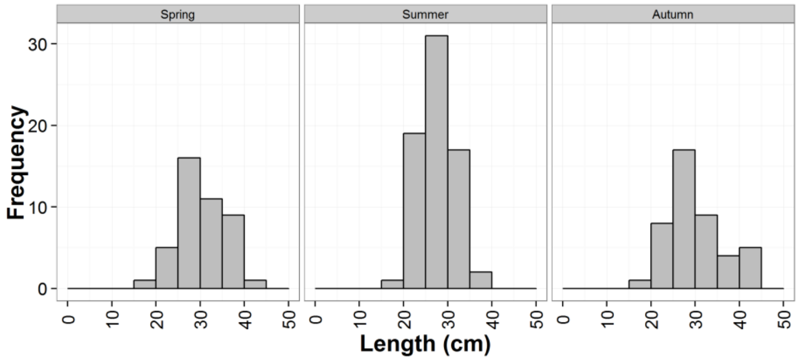
C) Moray Firth



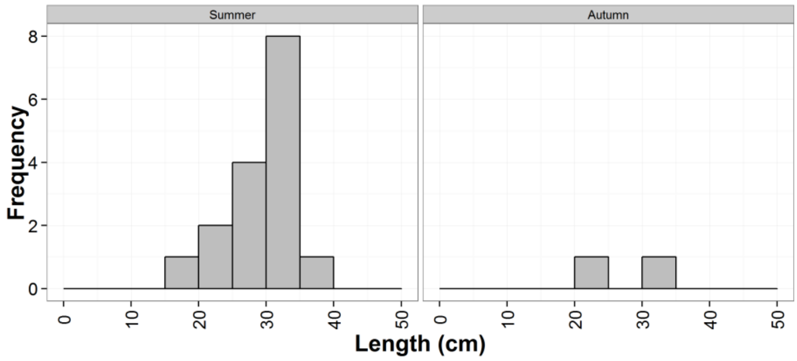
D) Orkney



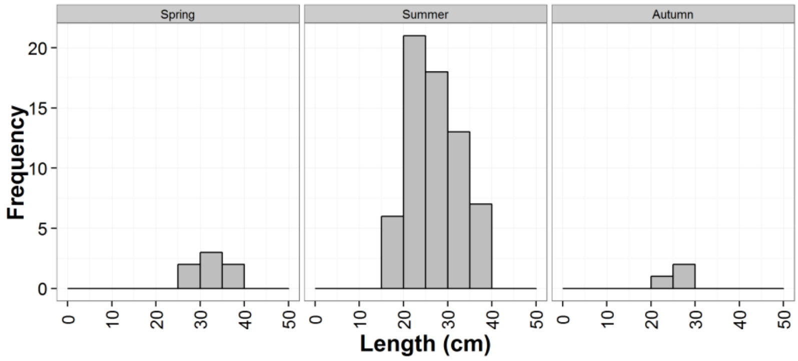
E) Shetland



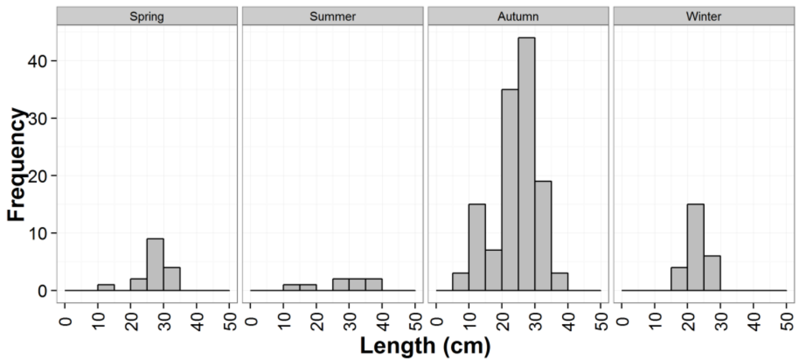
F) Outer Hebrides



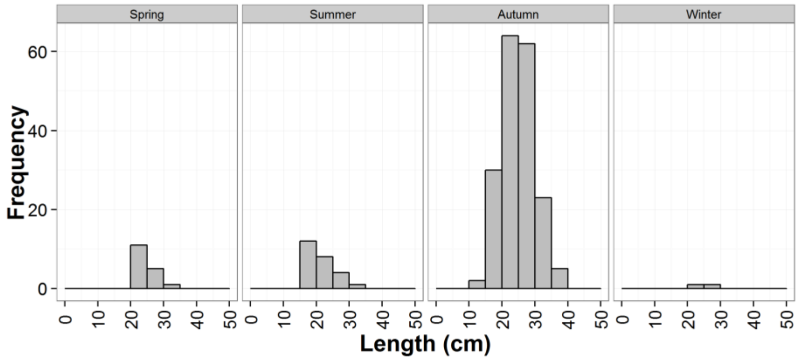
G) West coast – north



H) West coast – central

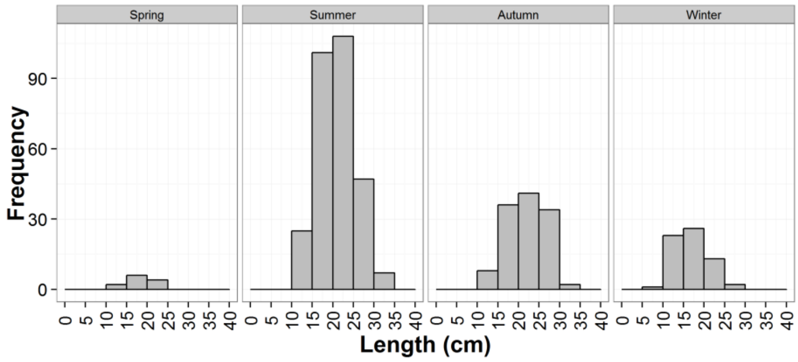


I) West coast – south

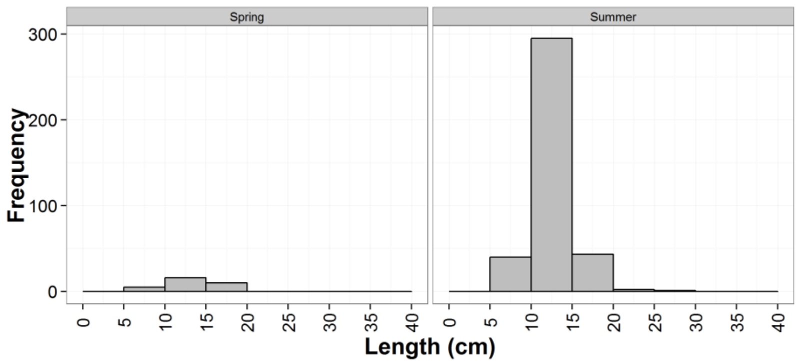


Sandeel

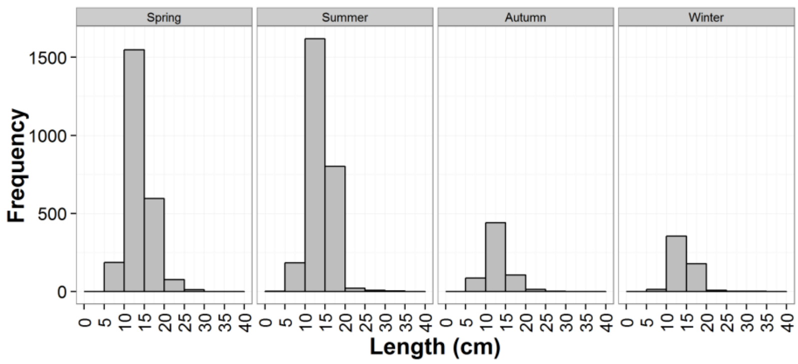
A) England



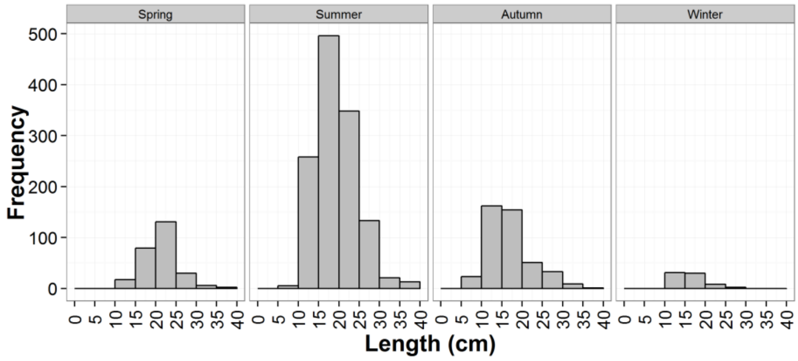
B) SE Scotland



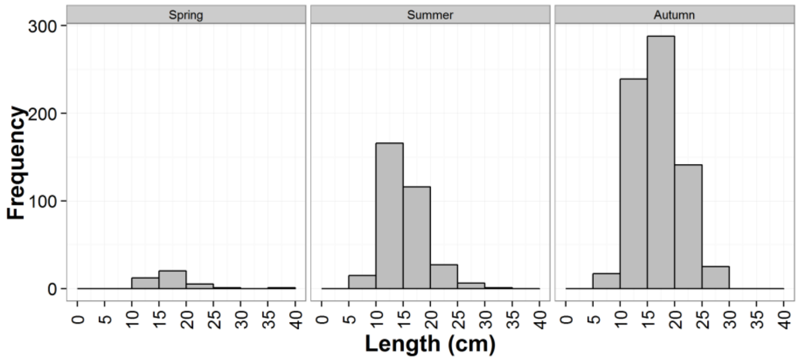
C) Moray Firth



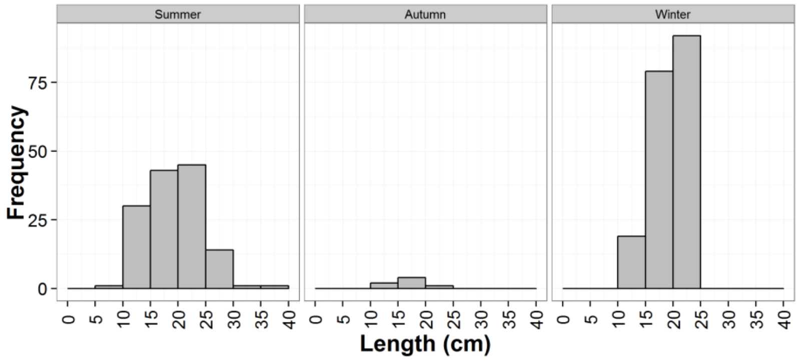
D) Orkney



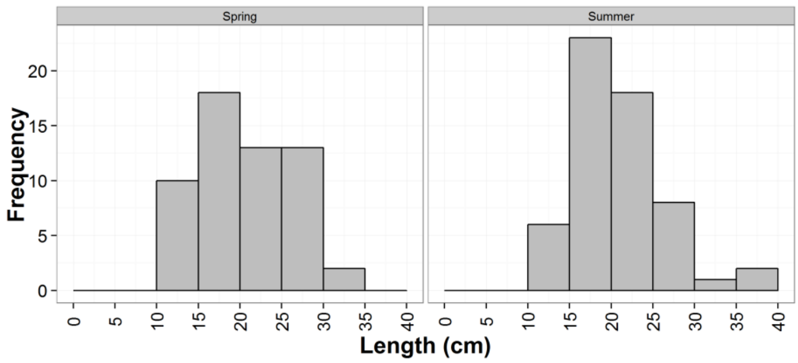
E) Shetland



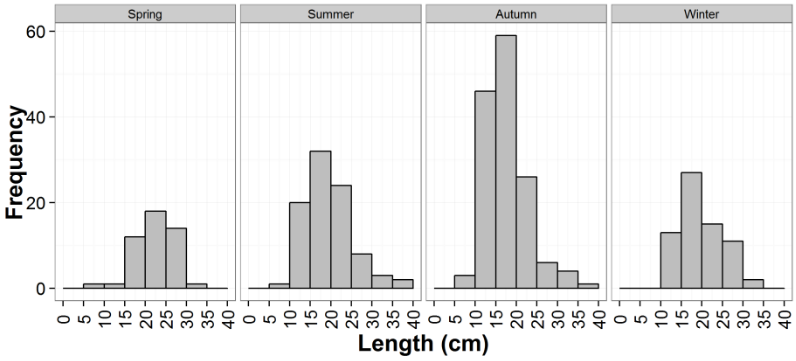
F) Outer Hebrides



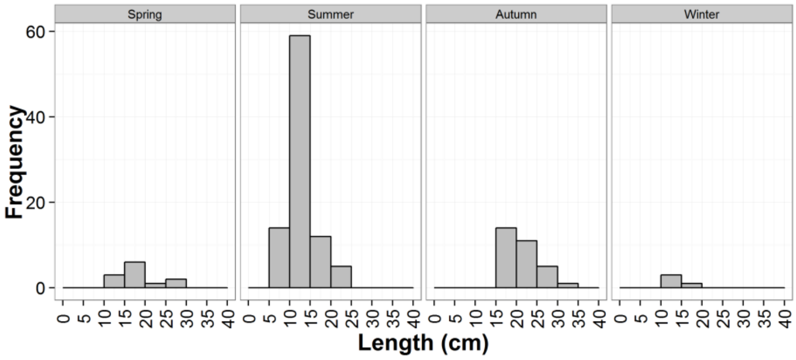
G) West coast – north



H) West coast – central

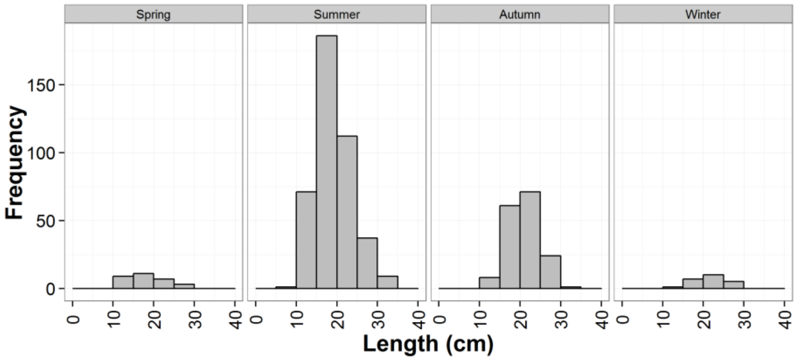


I) West coast – south

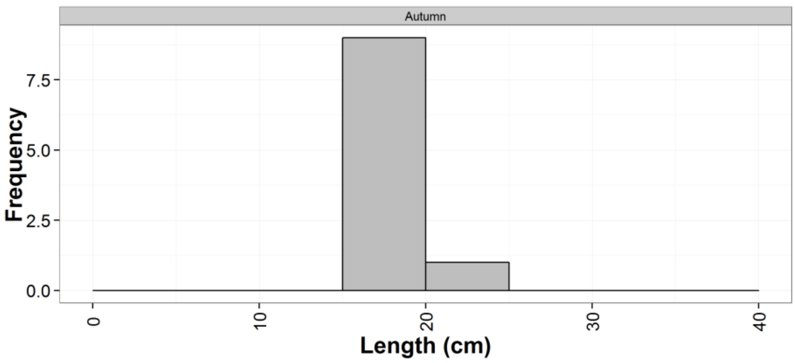


Dragonet

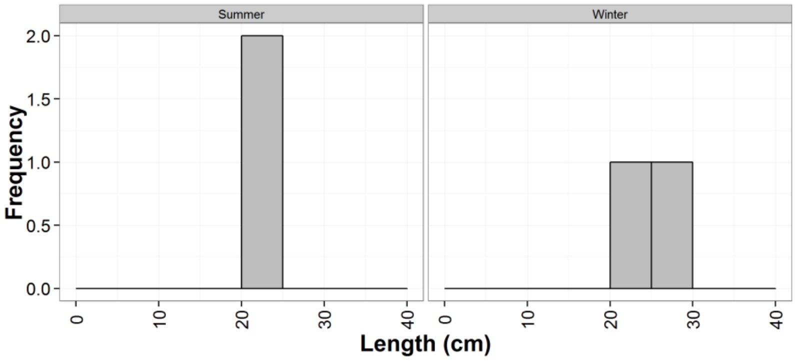
A) England



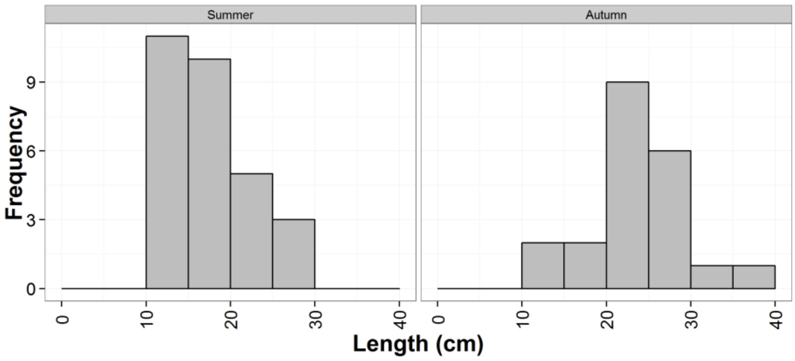
B) SE Scotland



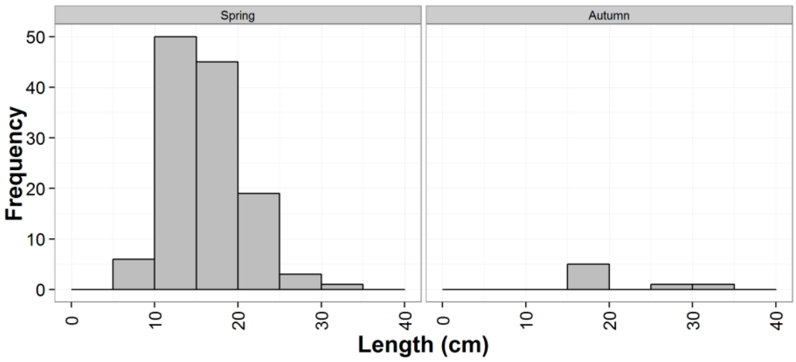
C) Moray Firth



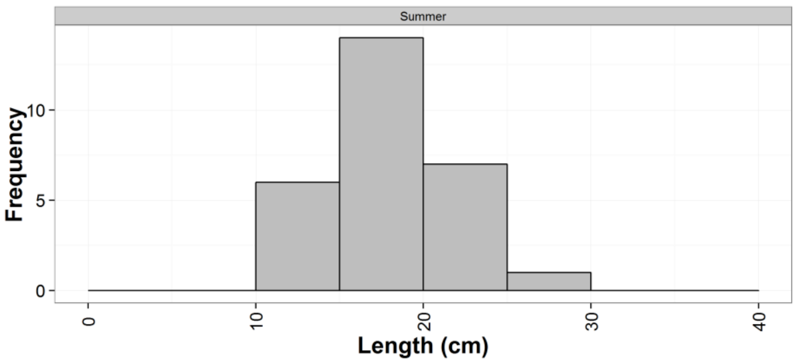
D) Orkney



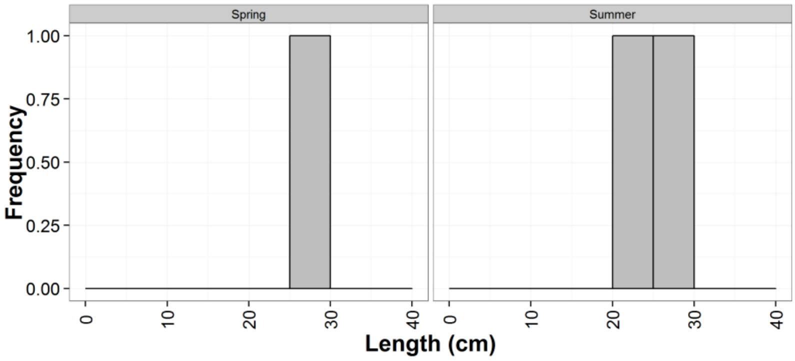
E) Shetland



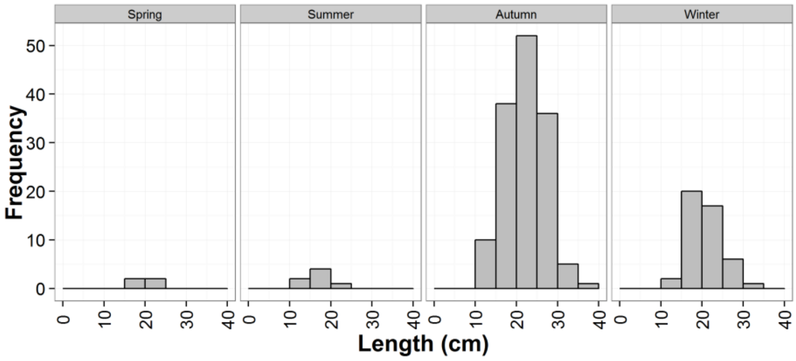
F) Outer Hebrides



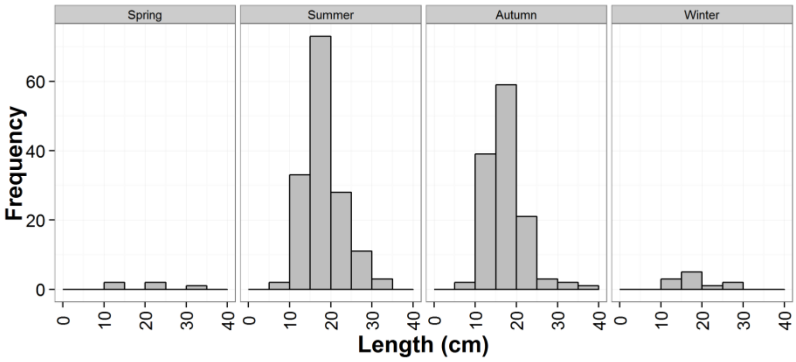
G) West coast – north



H) West coast – central



I) West coast – south



Chapter 4

SEX-SPECIFIC VARIATION IN THE DIET OF HARBOUR SEALS

4.1 Introduction

Knowledge of diet is an important factor contributing towards the conservation and management of wildlife populations. Individual activities such as resting, foraging and provisioning young influence an animal's activity/energy budget and can be influenced by intrinsic (*e.g.*, sex, age and size) and extrinsic factors (*e.g.*, food availability and predator density, Mooring and Rominger, 2004). Where resources are limiting, to maximise success there should be selective pressure and this can involve either intra-specific or inter-specific interaction. Intra-specific variation in diet including differences in; taxonomies, feeding rates, quality, quantity and size has been described across a number of taxa *e.g.*: mammals (Beier, 1987), reptiles (Perry, 1996), birds (Stauss *et al.*, 2012) and fish (Simpfendorfer *et al.*, 2001). Studies to date have tended to focus on animals which display strong sexual body-size dimorphism. However, species which are monomorphic with respect to body size have been suggested as model species for investigating sexual segregation because body-size effects are absent (Ruckstuhl and Neuhaus, 2000; Wearmouth and Sims, 2008).

4.1.1 Sexual segregation hypotheses

Both social and ecological factors are believed to influence sexual segregation. Based largely on studies of terrestrial ungulates (*e.g.*, Main *et al.*, 1996; Ruckstuhl and Neuhaus, 2000), five hypotheses (reviewed in; Wearmouth and Sims, 2008) have been proposed to account for observed differences: (i) predation risk, (ii) resource availability (forage selection), (iii) activity budget, (iv) thermal niche-fecundity and (v) social factors (intra-sexual affinity or aversion).

The **predation-risk hypothesis** proposes that females and/or their offspring are more at risk, due to differences in body size or because gestation / parental care hinder predator evasion. The primary driver for female habitat choice would therefore be the compulsion to reduce predation risk at the cost of sub-optimal foraging conditions (Wearmouth and Sims, 2008). For example, lactating spotted dolphins (*Stenella attenuata*) remain at the surface close to their calf rather than foraging for squid at depth (Bernard and Hohn, 1989) and bottlenose dolphins (*Tursiops truncatus*) have been shown to forage in less productive deeper waters in Shark Bay, Western Australia during months of high tiger shark (*Galeocerdo cuvier*) density (Heithaus and Dill, 2002).

The **forage selection hypothesis** proposes that different nutritional requirements are needed by animals of different body size. Despite larger metabolic requirements, large bodied animals are able to retain food longer and digest more efficiently (Gross, 1998). The less efficient digestion of smaller bodied individuals therefore constrains them to sites where they can prioritise high-quality food and in extreme cases smaller animals may competitively exclude larger animals (Wearmouth and Sims, 2008). However, this form of competitive exclusion is rare in marine vertebrates and competitive exclusion by the larger sex may be more usual (Wearmouth and Sims, 2008). Exclusion may also be driven by the reproductive condition of animals, for example the higher nutritional requirements of lactating females is different from that of other females in both common (*Delphinus delphis*) and spotted dolphins (Bernard and Hohn, 1989; Young and Cockcroft, 1994).

The **activity budget hypothesis** proposes that species which exhibit body size sexual dimorphism will also display sex differences in digestive efficiency, energetic requirements and possibly movement. Sex related differences in activity budgets therefore make group synchrony costly in mixed sex groups resulting in the formation of single-sex groups. For example in the blue-footed booby (*Sula nebouxii*), females are larger and due to a positive relationship between body size and diving ability, females dive significantly longer and deeper than males resulting in separation of vertical feeding niche (Zavalaga *et al.*, 2007).

However, for monomorphic species the different sexes will have similar energetic requirements and single-sex groups are unlikely to form except at times of high energetic demand *e.g.,* during lactation.

The **thermal niche-fecundity hypothesis** predicts that the sexes occupy different thermal habitats in an effort to maximise lifetime reproductive success (Wearmouth and Sims, 2008). This hypothesis emerged from studies of sexual segregation in ectotherms, for example; pregnant female grey reef sharks (*Carcharhinus amblyrhynchos*) aggregate in shallow lagoons of Johnston Atoll in the Central Pacific Ocean. Waters there are 1-2 °C warmer than in the open ocean and Economakis and Lobel (1998) hypothesised that by raising their body temperature female sharks were increasing the rate of embryonic development. Marked sexual segregation with males and females occupying different thermal habitats is also seen in sperm whales (*Physeter macrocephalus*). Females are typically found in tropical waters (Gaskin, 1982) while mature males are found in colder waters (Gaskin, 1982). Whitehead and Weilgart (2000) proposed that the restriction of females to low latitudes is possibly due to the thermal tolerances of offspring.

The **social factors hypothesis**, including both social preference and social avoidance behaviour, is relevant when social mechanisms determine sexual segregation. In cetacean societies stable groups offer communal care of offspring and co-ordinated foraging (*e.g.*, sperm whales, Whitehead *et al.*, 1991). In bottlenose dolphins sexual segregation has been attributed male (social) avoidance; females become sexually receptive after the death of a dependent calf (Dunn *et al.*, 2002) and dead calves often show signs of attacks from conspecifics (Patterson *et al.*, 1998; Dunn *et al.*, 2002). Furthermore, in some areas males appear to co-operate in pairs or triplets to appropriate and control the movements of females in mating condition (Connor *et al.*, 1992). In Galapagos sea lions (*Zalophus wollebaeki*) sexual segregation is presumed to arise as females also avoid unsolicited mating attempts. Females with pups which aggregate within the territory of a dominant male mostly avoid harassment from other males and this positively influences pup survival and growth (Wolf *et al.*, 2005).

4.1.2 Sex differences in pinniped foraging behaviour, diet and haul-out site use

Sex differences in seasonal foraging behaviour have been shown in a number of pinniped species. Using quantitative fatty acid signature analysis Beck *et al.*, (2007) showed male grey seal (*Halichoerus grypus*) diet to be more diverse across all seasons and less energy dense in spring than the diet of females. Habitat and space use differences in other species have also been linked to breeding systems. New Zealand fur seals (*Arctocephalus forsteri*), Galapagos sea lions and Antarctic fur seals (*Arctocephalus gazella*) with offspring have shorter foraging trips and remain closer to breeding colonies and in some instances dive shallower than unconstrained animals (Boyd *et al.*, 1998; Page *et al.*, 2005b; Wolf and Trillmich, 2007).

Sex differences have also been documented in non-breeding animals and in mature individuals outside of the breeding season. Differences in body lipid stores have been documented in female Australian fur seals (*Arctocephalus pusillus doriferus*) and Antarctic fur seal pups which have greater body lipid stores than males (Arnould *et al.*, 1996; Arnould and Hindell, 2002), juvenile male southern elephant seals (*Mirounga leonina*) spend less time at sea than females (Field *et al.*, 2005) and male juvenile Antarctic fur seals forage further away from land than females (Warren *et al.*, 2006).

Satellite tracking of grey seals has revealed sex-related differences in spatial and temporal foraging patterns (Breed *et al.*, 2006; Breed *et al.*, 2009). On Sable Island mature male grey seals make long distance foraging trips only returning just prior to the breeding season (Austin *et al.*, 2004) at which time the number of male feeding events was more than double that of females and the time between meals was shorter (Austin *et al.*, 2006). Male dive depths are also deeper than females and females spend more time diving and more time at depth in longer bouts (Beck *et al.*, 2003c; Beck *et al.*, 2003b). Northern (*Mirounga angustirostris*) and southern elephant seals show extreme sexual dimorphism and exhibit differences in diving behaviour with southern males attaining deeper maximum and targeted dive depths (McIntyre *et al.*, 2010) than females and northern males foraging in different locations and utilising different foraging-type dives (Le Boeuf *et al.*, 2000).

Sex differences in diet have been reported in mature grey seals with males eating larger and older prey (Hauksson and Bogason, 1997) and more benthic species (Tucker *et al.*, 2007) than females. Male harp seal (*Phoca groenlandica*) diet is more nitrogen enriched than the diet of female seals (Lesage *et al.*, 2001) and during breeding, the diet of male and female Steller sea lions (*Eumetopias jubatus*) was different with males consuming significantly fewer salmon (*Oncorhynchus* species) and more pollock (*Theragra chalcogramma*, Trites and Calkins, 2009).

Terrestrial habitat use differences have also been reported for pinnipeds, with females occupying optimal habitat. For example, adult female ringed seals (*Pusa hispida*) inhabit inner ice areas away from more unstable outer parts of fast-ice (Krafft *et al.*, 2007) and Galapagos sea lion females predominate in flat, shady habitats adjacent to the sea (Wolf *et al.*, 2005). During pupping, female harbour seals (*Phoca vitulina*) haul out more frequently than males but at the start of the moult males haul out more frequently than females (Thompson *et al.*, 1998).

Pinnipeds species that exhibit strong sexual dimorphism (such as grey seal and elephant seal) can minimise intra-specific competition through differences in movement and space use (*e.g.*, Le Boeuf *et al.*, 1993; Le Boeuf *et al.*, 2000; Breed *et al.*, 2006). For species in which individuals are roughly similar in size such as the harbour seal the potential for intraspecific competition is increased, either exploitatively through sharing a common limiting resource or by direct interference.

4.1.3 Evidence for sexual segregation in harbour seals

As a marine predator, harbour seals spend a large proportion of their time at sea foraging, but return to land for rest, to give birth and feed offspring. Both sexes aggregate throughout the year at haul-out sites and it is not easy to distinguish by behaviour if sexual segregation occurs on land (Thompson *et al.*, 1998). However, changes in the terrestrial distribution of females during pupping and lactation in the Moray Firth have been described (Thompson *et al.*, 1989; Thompson *et al.*, 1994). Furthermore, a study in Orkney showed that the sexes are sometimes segregated during the breeding season, *e.g.*, some haul-out groups are male dominated while others comprise mostly females with pups (Thompson *et al.*, 1998).

Seasonal changes in haul-out sites used by female harbour seals in Orkney have been proposed to result from the females need for safe pupping and lactation sites (Thompson *et al.*, 1989). Additionally, females with pups have been shown to markedly restrict their foraging range during early lactation (Thompson *et al.*, 1994) with longer trips being carried out during late lactation (Bowen *et al.*, 1992; Boness *et al.*, 1994; Thompson *et al.*, 1994).

There are no clear sex-related differences in foraging trip range and duration for harbour seals in Britain. In the Moray Firth, female seals were shown to have significantly shorter trip range and duration than males (Thompson *et al.*, 1998), however, on the west coast of Scotland no differences in foraging duration were detected between male and female harbour seals, although females did have a greater trip range (Cunningham *et al.*, 2009). Furthermore, in a much larger study that analysed harbour seal foraging trips from seven regions around Britain no individual level factors (sex, size or body condition) were found to be good predictors of foraging trip duration or distance (Sharples *et al.*, 2012). Variation in diving bouts between male and female harbour seals in the Salish Sea has been reported, however habitat or prey specialization by seals from different haul-out sites, or individual variability between seals was proposed to describe this variability (Wilson *et al.*, 2014). In a land based study by Härkönen *et al.*, (1999) clear differences between the sexes in summer haul-out patterns were identified.

Though adult male harbour seals do tend to be larger than adult females the species overall shows limited sexual dimorphism. However, male and female seals do have some different behavioural and physiological demands. Females cater to the nutritional requirements of their young, with no male assistance or extended social assistance. In mammals, provisioning of offspring (principally the production of milk) is considered to be energetically the costliest component of reproduction and parental care (*e.g.*, Clutton-Brock, 1991). In cases where males provide no parental care, female reproductive success is largely limited to access to resources (Emlen and Oring, 1977). Contrastingly, access to females is the limiting factor to male reproductive success (Davies, 1991). Mating behaviour in harbour seals has been associated with male underwater vocalisations and shallow diving during the breeding season (Coltman *et al.*, 1997; Van Parijs *et al.*, 1997).

Following lactation, female harbour seals are expected to need to recover condition quickly. A study by Thompson *et al.*, (1989) noted that females spent more time at sea after lactation doubtless feeding intensively at the cost of a slower moult; in contrast males hauled out every day during moult. As a consequence of the different maternal/ paternal strategies, male and female harbour seals may have different energetic requirements throughout the year which may be reflected in their diet.

4.1.4 The aims of this study

This study describes the diet of male and female harbour seals across three regions in Scotland; the Moray Firth, West coast – central and West coast - south and one in England: The Wash. Population surveys indicate that harbour seal numbers in the three regions in Scotland are stable and increasing in England (SCOS, 2013). I examined: diversity in species richness and evenness, percentage diet composition and diet quality between male and female diet within these regions and where possible included seasonal comparisons. I explored if any of the diet metrics provided evidence for or against the five standard sexual selection hypotheses.

Given the limited sexual dimorphism, I did not expect to find large differences in the diet between male and female harbour seals. However, I did anticipate some variation in diet metrics in response to the female life cycle. Loss of condition during the breeding season is greater for females (mean female mass decline 1.6 kg/d, Bowen *et al.*, 1992) than males (mean male mass loss 0.46 kg/d, Coltman *et al.*, 1997) and, in response to this, I expected some increase in diet quality, possibly detectable in changes in the proportions of prey with higher calorific density (*e.g,.* pelagic prey) in the diet. Any differences in dietary preference were anticipated to be reflected in lower levels of species richness and evenness, indicating specialisation in the diet.

4.2 Methods

4.2.1 Scat collection, molecular analysis and extraction, identification and measurement of prey remains

All scat collections were carried out as specified in Chapter 3; in addition collections in The Wash, England continued on a roughly monthly basis through to winter 2013. Techniques for laboratory processing of faecal samples and conducting molecular analysis were also the same as those described in detail in Chapter 3. Regions: The Wash, Moray Firth, West coast – central and West coast –south were selected *post-hoc* for inclusion in the sex analysis study based on the number of scats collected per region/season across the collection period (see Table 3.5, Chapter 3).

The method of Matejusová *et al.*, (2013) was used to ascertain the sex of the seals. Two Taqman assays targeting homologs of the ZFP on the X and Y chromosomes (ZFX and ZFY, respectively) and an additional assay amplifying the male-specific SRY gene were applied. Sex identification was determined in two ways after satisfactory amplification and no PCR inhibition. Initial determination was based on the outcome of each assay following the decision tree produced in (Matejusová *et al.*, 2013). Male seals are clearly distinguished based on the detection of either male-specific target (ZFY or SRY); female seals were identified if ZFX assay was positive and both ZFY and SRY assays were negative. Following, this initial identification, some scats were recorded as possibly being produced by females: in these cases, neither of the Y chromosome markers was amplified and ZFX also failed to amplify but species was successfully determined. The decision was made to include all possible female seals as females based on the size of the amplicon being detected. The assumption here is that the failure of both SRY and ZFY to amplify indicates a female seal but that the X chromosome assay failed due its relatively poor amplification efficiency. The amplicon size (SRY = 53 base pairs and ZFY 69 base pairs) of both male assays is smaller than that of the female (x chromosome) assay (ZFX = 71 base pairs). This approach was suggested by Dr. Tom Ashton (Xelect Ltd.) who conducted a large proportion of the genomics analysis for the chapter, due to the highly degraded nature and relatively low abundance of DNA from scat samples and consequently the ease of detecting smaller amplicons.

Molecular analysis was conducted on scats before they were checked for prey remains, results for scats with no prey remains were not used in the analysis. In total, for the four regions, for sex comparison DNA was extracted from 1,623 scats of which 1,432 were confirmed male or female. The remainder were unconfirmed sex most likely a result of low quantity and/or quality of DNA (Table 4.1 A). A total of 1,048 (73.2%) sex confirmed scats contained otoliths and/or beaks (Table 4.1 B). The highest proportions of scats that did not contain otoliths and/or beaks were from The Moray Firth, West coast – central and south regions all had similar proportions of The Wash (32.3%). Scats that did not contain prey remains (22.9, 23.0 and 22.0% respectively) and the regional proportion of scats that did not contain prey remains for male and female scats was similar (Table 4.1 B). Seasonal differences between the proportion of male and female scats containing otoliths were generally <10% in The Wash and Moray Firth, however, larger differences were observed in spring in both regions (Table 4.1 B). More female scats contained otoliths in The Wash (21.0%) and more male scats contained otoliths in the Moray Firth (13.5%).

4.2.2 Diversity of prey

Diet diversity was examined using rarefied estimates of species richness and species evenness (as described in Chapter 3). A high level analysis of diet diversity was conducted by examining diet across all seasons for males and for females. Where possible, diet diversity was also examined at a seasonal level.

4.2.3 Estimation of diet composition

Following the methods used in previous assessments of seal diet by SMRU; otolith/beaks recovered from scats were corrected for digestion and used to estimate the weight of prey ingested, values were summed over species and expressed as percentages in the diet by weight (Prime and Hammond, 1987; 1990; Hammond *et al.*, 1994a; Hammond *et al.*, 1994b; Hammond and Rothery, 1996; Hall *et al.*, 1998; Hammond and Grellier, 2006; Hammond and Harris, 2006). This method is described in detail in Chapter 3.

4.2.4 Estimation of variability

Variances of estimates of diet composition were estimated using the method described by Hammond & Rothery (1996) and implemented in Hammond & Grellier (2006) and Hammond & Harris (2006).

Further to this method described in more detail in Chapter 3, to estimate confidence limits of diet composition summed across seasons, bootstrapped estimates of consumption from each replicate were averaged and the percentiles taken from the distribution of averaged values.

4.2.5 Diet quality

The average energy density represented in male and female scats across regions and seasons was estimated following the method described in Chapter 3.

Table 4.1: Summary of the number of scats tested and confirmed sex (M=male and F=female) in each region/season (A) and the number of male/female scats containing otoliths and the percentage of sex confirmed scats that contained otoliths (B).

A)

	Number of scats DNA tested				
	M	**F**	**Unconfirmed**	**Total**	**M/F confirmed**
The Wash					
Summer	99	92	12	203	191
Autumn	128	66	23	217	194
Winter	85	40	6	131	125
Spring	39	70	26	135	109
TOTAL	351	268	67	686	619
Moray Firth					
Summer	38	49	7	94	87
Autumn/ Winter	25	46	2	73	71
Spring	43	57	7	107	100
TOTAL	106	152	16	274	258
West coast – central					

Summer	26	12	10	48	38
Autumn	139	14	12	165	153
Winter	44	6	10	60	50
Spring	51	4	9	64	55
TOTAL	260	36	41	337	296
West coast - south					
Summer	36	10	22	68	46
Autumn	79	17	16	112	96
Winter	27	7	18	52	34
Spring	72	11	11	94	83
TOTAL	214	45	67	326	259

B)

	Scats containing otoliths/beaks					
	Total			**Percentage**		
	M	**F**	**TOTAL**	**M**	**F**	**TOTAL**
The Wash						
Summer	81	67	148	81.8	72.8	77.5
Autumn	96	48	144	75.0	72.7	74.2
Winter	43	19	62	50.6	47.5	49.6
Spring	18	47	65	46.2	67.1	59.6
TOTAL	238	181	419	67.8	67.5	67.7
Moray Firth						
Summer	31	40	71	81.6	81.6	81.6
Autum/ Winter	19	33	52	76.0	71.7	73.2
Spring	36	40	76	83.7	70.2	76.0
TOTAL	86	113	199	81.1	74.3	77.1
West coast - central						
Summer	22	10	32	84.6	83.3	84.2
Autumn	102	10	112	73.4	71.4	73.2
Winter	35	5	40	79.5	83.3	80.0
Spring	42	2	44	82.4	50.0	80.0
TOTAL	201	27	228	77.3	75.0	77.0

West coast - south						
Summer	34	7	41	94.4	70.0	89.1
Autumn	66	13	79	83.5	76.5	82.3
Winter	8	7	15	29.6	100.0	44.1
Spring	59	8	67	81.9	72.7	80.7
TOTAL	167	35	202	78.0	77.8	78.0

4.3 Results

4.3.1 Diet sampling

The number of scats containing prey remains that were positively identified as either male or female was not even across regions, seasons and years (Table 4.2 A(i) and B(i)). To provide the best estimate of diet diversity some scats were grouped across years and/or seasons to improve sample size (Table 4.2 A(ii) and B(ii)). Grouping was conducted where previous results suggest that there are no marked differences between seasons/years or where sample size was very small (Chapter 3).

Following comparisons in Chapter 3 between current diet estimates for The Wash and West coast – south regions and those presented by Hall *et al.*, (1998) and Pierce and Santos (2003); scats collected from the same season were grouped over years for The Wash (spring, summer, autumn and winter 2011 and 2012, both sexes) and West coast – south (spring 2010 and 2011, males only). In the Moray Firth, where the diet was dominated in all seasons by sandeel (Chapter 3), scats were grouped across autumn and winter for both males and females. Due to the small number of female scats identified in all seasons/years in the West coast – central and south regions scats were combined across seasons (West coast - central, spring, summer, autumn, winter) and seasons/years (West coast – south, spring 2010 and 2011 and summer, autumn, winter 2010), creating a new season category “all seasons”.

To make high level comparisons of diet diversity, composition and quality, estimates for “all seasons” were generated by taking a simple average of each metric for each sex across each season. Where seasons had been combined (autumn and winter) the estimate was given double weight.

4.3.2 Diet diversity

The total number of otoliths and beaks of the main prey recovered from both male and female scats for each of the four regions is detailed in Appendix 4.1 (A – D; males and E – H; females). From 692 scats identified as being produced by male harbour seals, greater than 1,000 otoliths were recovered for seven prey species across all regions and seasons. Sandeel otoliths were most commonly recovered (22,708 otoliths) followed by whiting (3,214), poor cod (1,778), Norway pout (1,513), dragonet (1,362), plaice (1,175) and blue whiting *Micromesistius poutassou* (1,022). From 356 scats identified as being produced by female harbour seals, greater than 1,000 otoliths were recovered for only three prey species across all regions/seasons. Sandeel otoliths were most frequently recovered (9,913), followed by; gobies *Gobiidae* (3,712) and plaice (1,125).

Male-female variation in the species richness and evenness of prey in the diets of harbour seals was examined on a seasonal basis for each region (Table 4.3). As expected the rarefied (standardised) species richness was smaller than the observed species richness (Table 4.3). Rarefied species richness is hereafter referred to simply as species richness.

Table 4.2: Summary of seasonal and regional variation in the number of confirmed male A(i) and female B(i) scats which contained otoliths. To improve sample size in some regions/seasons, scats were grouped across years/season for males A(ii) and females B(ii).

A) Male (i)

Region	Season	Year	No. scats	Otoliths Total	Otoliths Measured
The Wash	Summer	2011	36	860	699
The Wash	Summer	2012	45	1529	863
The Wash	Autumn	2011	47	971	811
The Wash	Autumn	2012	49	980	802
The Wash	Winter	2011	21	86	80
The Wash	Winter	2012	22	674	307

The Wash	Winter	2013	8	115	114
The Wash	Spring	2011	3	13	13
The Wash	Spring	2012	15	177	157
SE Scotland	Summer	2010	8	742	290
SE Scotland	Autumn	2010	11	1086	568
SE Scotland	Winter	2011	1	61	29
SE Scotland	Spring	2011	3	9	9
Moray Firth	Summer	2010	31	3260	1299
Moray Firth	Autumn	2010	8	1132	371
Moray Firth	Winter	2011	11	156	140
Moray Firth	Spring	2011	36	2234	952
Orkney	Spring	2011	1	10	10
WC - central	Summer	2010	22	674	534
WC - central	Autumn	2010	102	2053	1357
WC - central	Winter	2011	35	1841	1001
WC - central	Spring	2011	42	484	431
WC - south	Summer	2010	34	1854	1493
WC - south	Autumn	2010	66	746	740
WC - south	Winter	2010	8	43	43
WC - south	Winter	2011	1	4	3
WC - south	Spring	2010	31	286	284
WC - south	Spring	2011	28	290	289

Male (ii)

Region	**Season**	**Year**	**No. scats**	**Otoliths Total**	**Otoliths Measured**
The Wash	Summer	2011/2012	81	2389	1562
The Wash	Autumn	2011/2012	96	1951	1613
The Wash	Winter	2011/2012	43	760	387
The Wash	Spring	2011/2012	18	190	170
Moray Firth	Summer	2010	31	3260	1299
Moray Firth	Autumn/ Winter	2010	19	1288	511
Moray Firth	Spring	2011	36	2234	952

WC - central	Summer	2010	22	674	534
WC - central	Autumn	2010	102	2053	1357
WC - central	Winter	2011	35	1841	1001
WC - central	Spring	2011	42	484	431
WC - south	Summer	2010	34	1854	1493
WC - south	Autumn	2010	66	746	740
WC - south	Winter	2010	8	43	43
WC - south	Spring	2010/ 2011	59	576	573

B) Female (i)

Region	**Season**	**Year**	**No. scats**	**Otoliths Total**	**Otoliths Measured**
The Wash	Summer	2011	51	1771	1054
The Wash	Summer	2012	16	714	431
The Wash	Autumn	2011	34	816	664
The Wash	Autumn	2012	14	270	240
The Wash	Winter	2012	19	940	430
The Wash	Winter	2013	2	25	24
The Wash	Spring	2011	29	787	412
The Wash	Spring	2012	18	1102	456
SE Scotland	Summer	2010	2	972	246
SE Scotland	Autumn	2010	1	21	21
SE Scotland	Spring	2011	1	125	34
Moray Firth	Summer	2010	40	5043	1734
Moray Firth	Autumn	2010	9	815	348
Moray Firth	Winter	2011	24	911	411
Moray Firth	Spring	2011	40	3797	1374
Shetland	Autumn	2011	1	2	2
WC - central	Summer	2010	10	124	123
WC - central	Autumn	2010	10	271	156
WC - central	Winter	2011	5	30	30
WC - central	Spring	2011	2	5	5

WC - south	Summer	2010	7	517	311
WC - south	Autumn	2010	13	544	362
WC - south	Winter	2010	7	170	144
WC - south	Spring	2010	4	187	112
WC - south	Spring	2011	4	79	78

Female (ii)

Region	**Season**	**Year**	**No. scats**	**Otoliths Total**	**Otoliths Measured**
The Wash	Summer	2011/2012	67	2485	1485
The Wash	Autumn	2011/2012	48	1086	904
The Wash	Winter	2011/2012	19	940	430
The Wash	Spring	2011/2012	47	1889	868
Moray Firth	Summer	2010	40	5043	1734
Moray Firth	Autumn/Winter	2010	33	1726	759
Moray Firth	Spring	2011	40	3797	1374
WC - central	All seasons	2010/2011	27	430	314
WC - south	All seasons	2010/2011	35	1497	1007

4.3.2.1 The Wash

The greatest difference in the observed number of species ingested by male and female harbour seals from sampled scats in The Wash occurred in autumn, when females ate more prey species than males (22 vs 17; Table 4.3 A). However, differences between male and female diet species richness (S) were generally small (Table 4.3 A), as reflected in the all seasons comparison (S = 28 male; S = 31 female). Species evenness was more variable. Females had more uneven diets in winter (PIE = 0.45) and spring (PIE = 0.41) than males (PIE = 0.70 and 0.72, respectively). These differences in evenness were moderated when comparing the evenness of the diets across all seasons (PIE = 0.72 females; PIE = 0.80 males).

4.3.2.2 Moray Firth

In autumn/winter and spring the species richness of female harbour seal diet in the Moray Firth was greater than that of males (Table 4.3 B). However, over all seasons species richness in the diet of female and male harbour seals was very similar (S = 19 females; S = 21 males). In the Moray Firth, where the diet was dominated by one prey species (sandeel), species abundance in the diet was very uneven across each individual season (Table 4.3 B). Across all seasons, species evenness was very low and very similar for both female and male harbour seals (PIE = 0.13 females; PIE = 0.11 males).

4.3.2.3 West coast – central

Species richness and evenness was only compared across all seasons for male and female harbour seals in the West coast – central region. Species richness was greater for male seals than female seals, although the difference was not large (S = 23 males; S = 18 females). Species evenness across all seasons was high for both male and female seals (PIE = 0.82 males; PIE = 0.81 females).

4.3.2.4 West coast – south

Species richness and evenness was only compared across all seasons for male and female harbour seals in the West coast – south region. Species richness was similar for both male and female harbour seals (S = 25 and 27, respectively). The species evenness was similarly high for both sexes (PIE = 0.88 males; PIE = 0.84 females).

Table 4.3: Variation in the number of scats collected with hard prey remains, observed number of prey species, rarefied species richness (S), and species evenness (PIE) across male and female diet within individual seasons and regions. Values should not be compared across seasons within a region or across regions because rarefaction was conducted on male and female diet within a region/season combination.

A) The Wash

	No. scats	**Observed No. prey species**	**Species richness (S)**	**Species evenness (PIE)**
Summer				
Male	82	28	23	0.68
Female	67	21	19	0.77
Autumn				
Male	96	22	17	0.80
Female	48	27	22	0.83
Winter				
Male	43	20	14	0.70
Female	19	16	14	0.45
Spring				
Male	18	16	13	0.72
Female	47	19	14	0.41
All seasons				
Male	239	31	28	0.80
Female	181	35	31	0.72

B) Moray Firth

	No. scats	Observed No. prey species	Species richness (S)	Species evenness (PIE)
Summer				
Male	31	19	16	0.20
Female	40	15	13	0.18
Autumn / Winter				
Male	19	12	10	0.06
Female	33	17	13	0.16
Spring				
Male	36	10	8	0.01
Female	40	15	12	0.05
All seasons				
Male	86	25	21	0.11
Female	113	22	19	0.13

C) West coast - central

	No. scats	Observed No. prey species	Species richness (S)	Species evenness (PIE)
All seasons				
Male	166	38	23	0.82
Female	27	21	18	0.81

D) West coast - south

	No. scats	Observed No. prey species	Species richness (S)	Species evenness (PIE)
All seasons				
Male	167	39	25	0.88
Female	35	31	27	0.84

4.3.3 Diet composition

The diet of male and female harbour seals in each region/season, expressed as percentage by weight of each prey species, is given in Table 4.4 and summarised by prey type (gadoids, flatfish etc.) in Appendix 4.2 and Figure 4.1 A-D. The 95% confidence limits are presented by prey type and species in Appendices 4.3 and 4.4 respectively.

4.3.3.1 The Wash

In The Wash, the diet of male harbour seals across all seasons was dominated by: scorpion fish (25.5%), flatfish (22.5%), sandy benthic prey (18.9%) and gadoids (17.1%) with important contributions of sandeel (11.8%; Figure 4.1 A and Appendix 4.2 A). The diet of female harbour seals was dominated by: sandy benthic prey (33.2%) and flatfish (20.1%) with important contributions of scorpion fish (15.0%), sandeel (11.3%) and pelagic species (11.1%; Figure 4.1 A and Appendix 4.2 A). The dominant prey species in the male diet was bullrout (24.4%, compared to 7.1% females) and the dominant prey in the female diet was dragonet (22.5%, compared to 8.4% males; Table 4.4 A). Gobies were important overall in the female diet (10.5% all seasons) but made very little contribution to the male diet (0.5% all seasons).

Seasonal variation in prey composition was observed in both male and female diets. Whiting peaked in male and female diet in autumn (28.7% and 18.1% respectively) and was high for males in winter (25.1%) but not for females (7.5%; Table 4.4 A). Sandeel peaked in the diet of both sexes in summer (>25%) and flatfish were more important in summer and autumn (> 20% both sexes) than in winter and spring (< 20%). Pelagic prey peaked in the female diet in winter (29.1%) and was also high in spring (12.1%) but reached a maximum of only 4.7% for males in winter (Figure 4.1 A and Appendix 4.2 A). Dragonet was important in male diet in summer and autumn (34.7% and 20.5%, respectively) and peaked in the female diet in spring and summer (30.8% and 33.0%, respectively).

4.3.3.2 Moray Firth

The diet of both male and female harbour seals was dominated by sandeel in the Moray Firth (Table 4.4 B, Figure 4.1 B and Appendix 4.2 B). Across all seasons, sandeel made up 76.7% of male diet and 70.6% of female diet. Flatfish prey were the only other major contributor to the diet (16.7% males and 18.4% females, Figure 4.1 B and Appendix 4.2 B). The major flatfish prey for males and females were similar but made up small proportions of their diet: dab (males 6.9% and females 4.7%), flounder (males 0.7% and females 5.0%) and plaice (males 3.6% and females 4.1%).

Sandeel contributed the least to male and female diet in summer (45.5% and 60.3%, respectively). In summer, both males and females consumed more dab (21.4% males and 15.3% females) and plaice (11.8% males; 12.7% females). Sprat peaked in the autumn/winter diet of both sexes (4.4% males; 5.1% females). Unidentified salmonid prey peaked in the diet of females in autumn/winter (5.1%) and in male diet in summer (1.9%).

4.3.3.3 West coast – central

The diet of female harbour seals could not be assessed seasonally in the West coast – central region due to small sample size. Across all seasons the diet of male harbour seals in the West coast – central region was dominated by gadoids (41.6%) and pelagic prey (22.3%) and the diet of females by pelagic prey (46.1%) and gadoids (25.8%; Figure 4.1 C and Appendix 4.2 C). Other important prey types for both sexes were sandy benthic species (11.1% males; 11.6% females) and *Trisopterus* species (8.9% males; 7.3% females).

The largest single prey contributor to the diet of male harbour seals was blue whiting (18.8%; Table 4.4 C) with supporting contributions of dragonet (11.1%) and mackerel (13.7%). Female diet was dominated by mackerel (34.8%) with important contributions of dragonet (11.6%), herring (10.1%) and cod (10.0%).

4.3.3.4 West coast - south

The diet of female harbour seals could not be assessed seasonally in the West coast – south region due to small sample size. Across all seasons male diet was dominated by gadoid prey (64.1%; Figure 4.1 D and Appendix 4.2 D). The main gadoid prey were: haddock (20.6%), whiting (12.6%), ling (11.9%) and cod (10.5%). Pelagic prey were also important (herring 8.4%, mackerel 6.7%; Table 4.4 D).

Gadoid prey (42.6%; Figure 4.1 D and Appendix 4.2 D) were also the main prey type consumed by female harbour seals in the West coast – south region. *Trisopterus* species and pelagic prey were supporting prey groups (17.7% and 16.7%, respectively). Whiting was the dominant prey species consumed by females (22.9%) followed by herring (14.0%) and poor cod (12.0%).

Table 4.4: Comparison of male (M) and female (F) harbour seal diet (expressed as the percentage of each species in the diet by weight). Prey species listed are those contributing >2% for either sex in any season across each region (A) The Wash, (B) Moray Firth, (C) West coast – central and (D) West coast south. Species which contributed >10% are in bold.

A) The Wash

	Summer		**Autumn**		**Winter**		**Spring**		**All seasons**	
Species	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**
Cod	0.4	0.0	0.4	0.0	5.2	0.0	1.4	0.0	1.8	0.0
Whiting	5.4	0.9	**28.7**	**18.1**	**25.1**	7.5	1.7	6.0	**15.2**	8.1
Sandeel	**33.1**	**25.2**	6.4	**11.9**	5.3	4.7	2.6	3.4	**11.8**	**11.3**
Plaice	8.3	7.3	**13.8**	2.9	2.6	0.1	1.4	0.5	6.5	2.7
Lemon sole	2.7	0.7	4.6	5.8	8.0	8.7	0.6	2.7	4.0	4.5
UnID flatfish	1.3	1.7	5.1	2.3	0.4	0.1	0.1	0.4	1.7	1.1
Dover sole	3.5	7.8	8.9	0.5	1.7	1.6	**11.8**	**13.9**	6.5	5.9
Flounder	0.2	7.8	0.6	1.9	0.0	0.0	0.0	0.0	0.2	2.4
Dab	3.6	5.8	5.9	5.2	0.9	0.0	0.0	0.6	2.6	2.9
Brill	2.5	0.1	1.2	1.6	0.0	0.0	0.0	0.0	0.9	0.4
Dragonet	**34.7**	**33.0**	**20.5**	**13.0**	**10.4**	**13.0**	7.8	**30.8**	**18.4**	**22.5**
Goby	0.2	8.2	0.2	2.3	1.8	**11.4**	0.0	**20.2**	0.5	**10.5**
Hooknose	0.0	0.0	0.0	6.7	0.0	0.3	0.1	0.6	0.0	1.9
Bullrout	0.5	0.0	1.7	**13.3**	**27.4**	8.6	**67.9**	6.4	**24.4**	7.1
Sea Scorpion	0.6	0.0	0.5	6.8	0.0	**14.8**	3.2	1.3	1.1	5.7
Mackerel	0.0	0.0	0.0	2.7	0.0	0.0	0.0	0.0	0.0	0.7
Herring	0.2	0.0	0.3	0.0	1.0	**15.6**	1.3	**10.7**	0.7	6.6
Sprat	0.0	0.0	0.0	0.0	3.0	**13.5**	0.0	1.4	0.7	3.7
Eledone	0.0	0.0	0.0	3.6	0.0	0.0	0.0	0.0	0.0	0.9
Loligo	0.8	0.0	0.9	0.0	4.8	0.0	0.0	0.0	1.6	0.0

B) Moray Firth

	Summer		Autumn/Winter		Spring		All seasons	
Species	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**
Saithe	0.4	0.2	3.0	1.4	1.8	0.8	2.1	1.0
Sandeel	**45.5**	**60.3**	**83.9**	**69.5**	**93.5**	**83.1**	**76.7**	**70.6**
Plaice	**11.8**	**12.7**	1.2	1.5	0.2	0.6	3.6	4.1
UnID flatfish	5.6	3.2	1.4	1.0	1.2	2.0	2.4	1.8
Flounder	0.9	1.5	0.0	4.3	1.8	9.9	0.7	5.0
Dab	**21.4**	**15.3**	3.0	1.4	0.0	0.7	6.9	4.7
Bullrout	0.0	4.7	0.0	5.7	0.0	0.2	0.0	4.1
Sprat	0.0	0.0	4.4	5.1	0.3	1.3	2.3	2.9
UnID Salmonid	1.9	0.0	0.0	5.1	0.0	0.0	0.5	2.5
Loligo	6.8	0.1	0.0	0.6	0.0	0.0	1.7	0.3

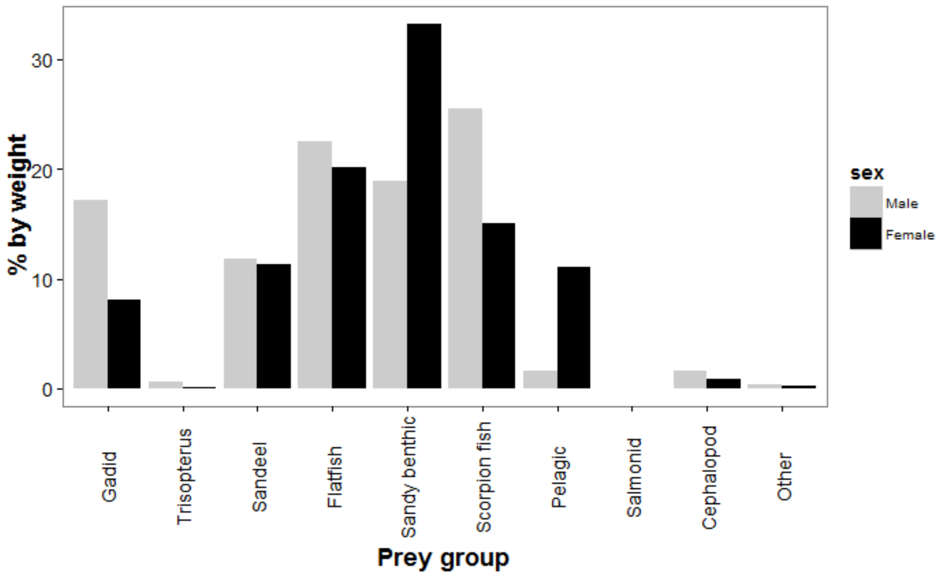
C) West coast - central

	Summer	**Autumn**	**Winter**	**Spring**	**All seasons**	
Species	**M**	**M**	**M**	**M**	**M**	**F**
Cod	0.0	3.0	0.0	2.8	1.5	**10.0**
Whiting	**14.4**	1.7	**10.4**	0.5	6.7	4.6
Haddock	0.7	2.0	0.3	9.7	3.2	0.9
Saithe	0.0	2.4	4.8	8.0	3.8	1.1
Ling	2.2	1.8	5.5	4.4	3.5	4.1
Unidentified gadid	4.9	0.5	2.4	1.0	2.2	1.1
Saithe or Pollock	0.0	0.4	4.7	0.0	1.3	0.0
Blue whiting	**35.3**	0.6	**16.2**	**23.0**	**18.8**	4.0
Poor cod	3.0	3.6	**14.3**	2.7	5.9	4.8
Norway pout	2.5	1.2	5.1	2.2	2.7	2.0
Sandeel	2.7	8.1	2.5	3.4	4.2	3.7
Plaice	0.0	2.4	0.0	0.0	0.6	0.0
Lemon sole	0.4	0.2	0.0	2.9	0.9	0.0
Dragonet	0.0	**23.1**	**20.3**	0.8	**11.1**	**11.6**
Unidentified *Cottidae*	**19.9**	1.8	0.0	0.0	5.4	1.7
Gurnard	0.0	0.0	0.5	0.0	0.1	2.0
Mackerel	7.3	**20.8**	0.0	**26.6**	**13.7**	**34.8**
Herring	2.7	**15.6**	5.9	3.7	7.0	**10.1**
Horse mackerel (Scad)	0.0	5.5	1.0	0.1	1.6	1.2
Eledone	2.3	0.7	0.0	3.0	1.5	0.0
Loligo	0.0	0.4	0.0	2.6	0.7	1.8

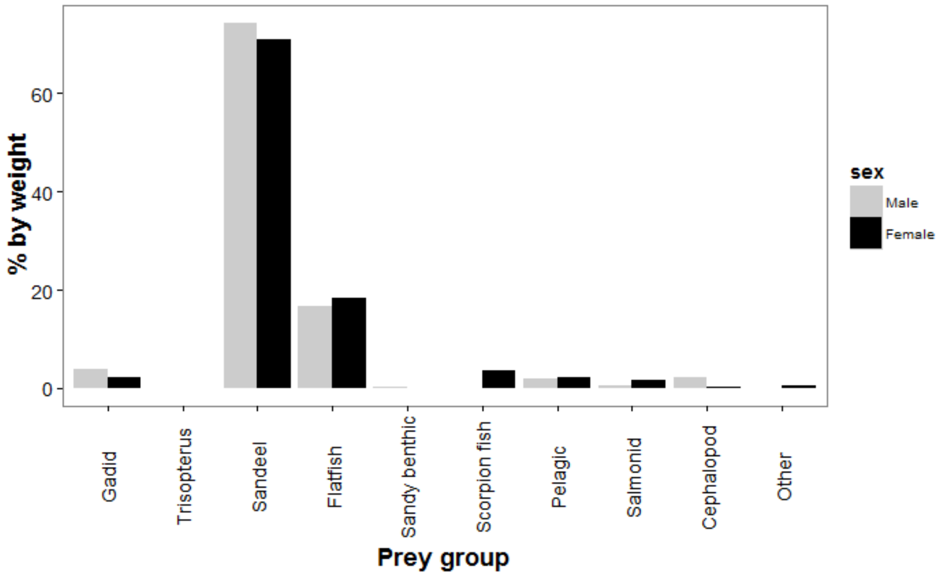
D) West coast - south

	Summer	Autumn	Winter	Spring	All seasons	
Species	**M**	**M**	**M**	**M**	**M**	**F**
Cod	7.8	7.7	0.0	**26.6**	**10.5**	1.7
Whiting	**22.0**	8.7	9.3	**10.6**	**12.6**	**22.9**
Haddock	**15.6**	**27.6**	**15.9**	**23.4**	**20.6**	5.9
Saithe	0.3	0.9	0.0	0.0	0.3	2.0
Ling	1.5	2.2	**38.8**	5.1	**11.9**	0.0
Rockling	0.3	3.7	0.0	0.3	1.1	0.6
Unidentified gadid	7.2	0.7	2.5	3.2	3.4	7.4
Blue whiting	6.0	0.0	0.5	5.4	3.0	2.0
Poor cod	3.0	1.1	4.6	1.4	2.5	**12.0**
Norway pout	3.7	0.0	0.8	2.6	1.8	5.2
Sandeel	0.5	1.7	0.4	2.1	1.2	0.9
Lemon sole	0.2	1.2	4.8	0.2	1.6	0.0
Witch	0.9	0.3	0.0	2.7	1.0	1.6
Dragonet	**16.0**	5.7	0.0	4.2	6.5	6.5
Bullrout	0.0	0.0	0.0	0.0	0.0	3.1
Gurnard	0.0	0.2	**10.9**	0.0	2.8	1.4
Mackerel	8.3	5.7	**11.3**	1.7	6.7	2.3
Herring	0.8	**27.2**	0.0	5.7	8.4	**14.0**
Eledone	3.3	0.2	0.0	0.0	0.9	3.2
Eelpout	0.0	0.0	0.0	0.0	0.0	2.0

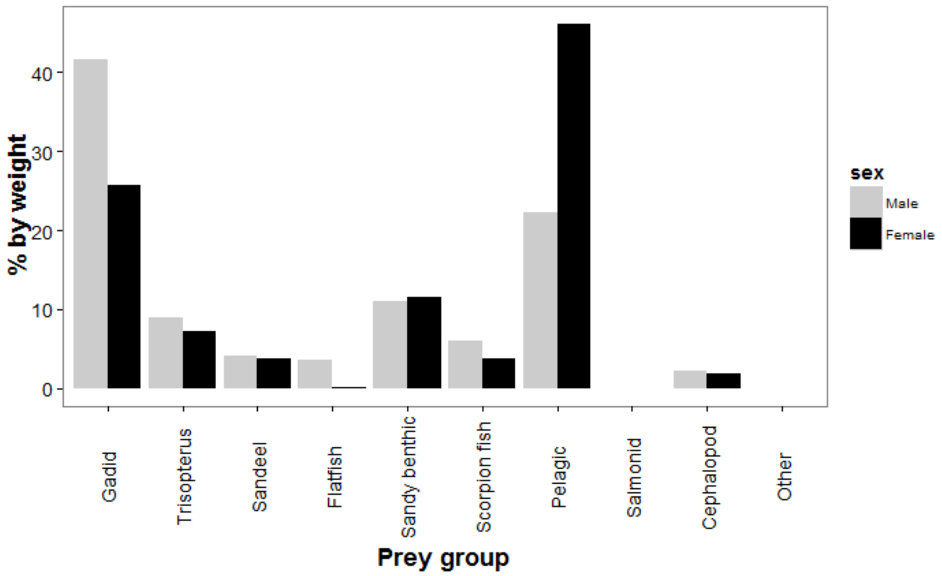
A) The Wash



B) Moray Firth



C) West coast – central



D) West coast – south

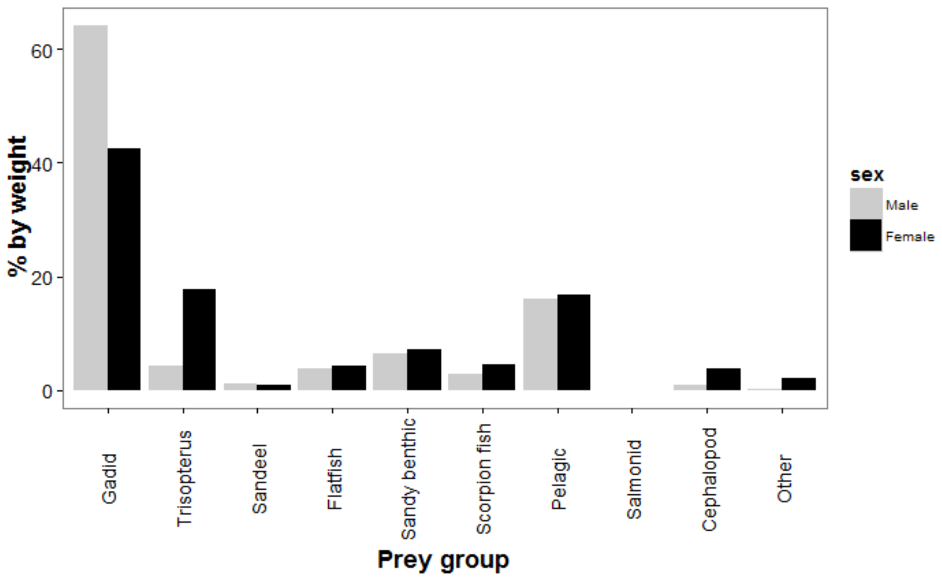


Figure 4.1: Variation in the diet of male and female harbour seals, averaged across all seasons. Diet is expressed as the percentage of each group in the diet, by weight.

4.3.4 Diet quality

Variation in the quality of the diet in male and female harbour seals was small, except in The Wash (Table 4.5, Figure 4.2).

4.3.4.1 The Wash

Overall, across all seasons, female harbour seals in The Wash had a higher quality diet than males (1112 cal.g^{-1} SE = 19 and 996 cal.g^{-1} SE = 15, respectively). In summer, autumn and spring the 95% confidence intervals of diet quality estimates for each sex overlapped. However, in winter, despite large standard errors, the quality of male and female diet was different (1049 cal.g-1 males; 1313 cal.g-1 females), with females consuming a higher quality diet than males (Table 4.5, Figure 4.2 A).

4.3.4.2 Moray Firth

Across all seasons, mean diet quality for male and female seals was very similar (1185 cal.g^{-1} SE = 27 males and 1198 cal.g^{-1} SE = 21 females). The diet quality overlapped for both sexes in all seasons and the standard errors around the seasonal (summer, autumn/winter and spring) quality estimates were fairly large (Table 4.5, Figure 4.2 B).

4.3.4.3 West coast - central

Comparison across all seasons revealed no difference in diet quality for male and female harbour seals in the West coast – central region (1052 cal.g^{-1} SE = 21 males and 1024 cal.g^{-1} SE = 44 females). Seasonal variation in the diet quality of males was evident (Table 4.5, Figure 4.2 C); however, it was not possible to make comparisons with females due to the small number of female scats identified.

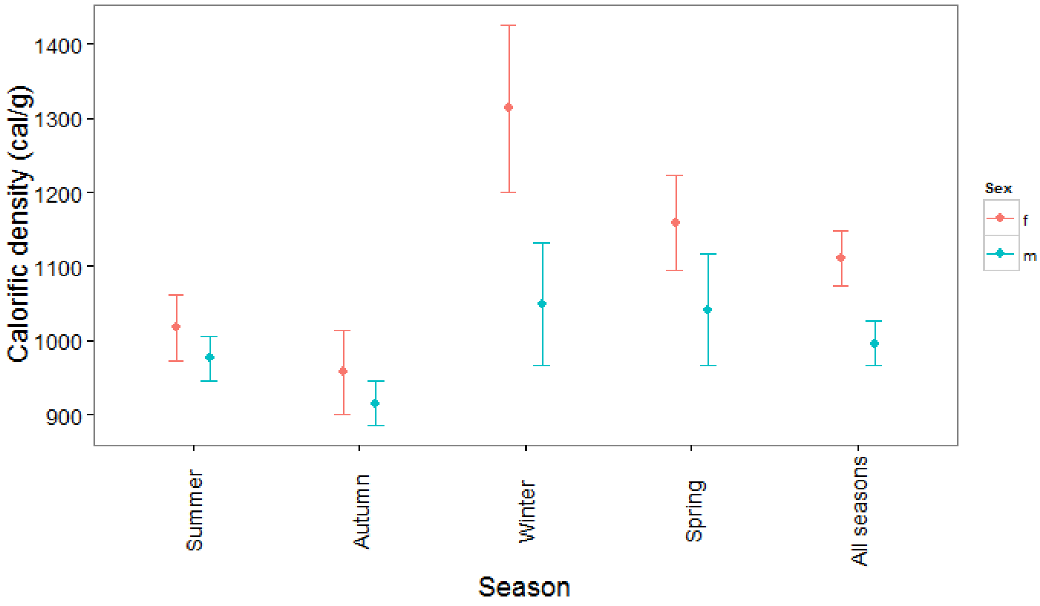
4.3.4.4 West coast - south

There was no difference in diet quality between the sexes, when compared across all seasons (948 cal.g^{-1} SE = 31 males and 994 cal.g^{-1} SE = 40 females) in the West coast – south region, nor was there any seasonal pattern in the quality of diet consumed by males in this region (Table 4.5, Figure 4.2 D).

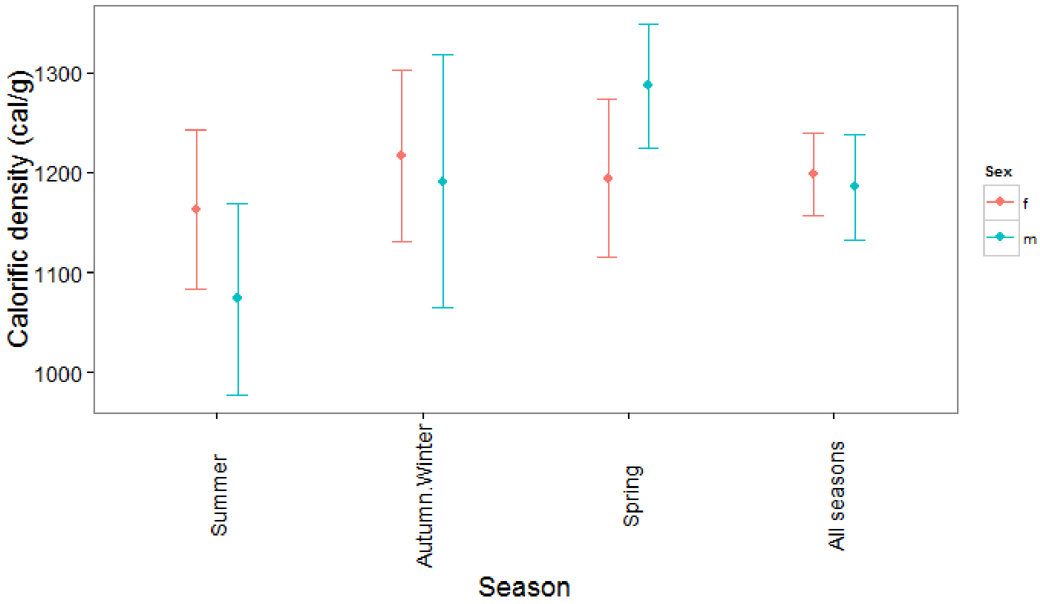
Table 4.5: Summary of male and female diet quality across each region and season.

		Calorific density (cal.g-1)			
Region	**Season**	**Male**	**(SE)**	**Female**	**(SE)**
The Wash	Summer	976	(16)	1018	(23)
The Wash	Autumn	916	(15)	958	(29)
The Wash	Winter	1049	(42)	1313	(58)
The Wash	Spring	1042	(38)	1159	(33)
The Wash	All seasons	996	(15)	1112	(19)
Moray Firth	Summer	1074	(49)	1163	(40)
Moray Firth	Autumn/Winter	1191	(64)	1217	(44)
Moray Firth	Spring	1286	(32)	1194	(40)
Moray Firth	All seasons	1185	(27)	1198	(21)
WC – central	Summer	989	(54)		
WC – central	Autumn	1176	(30)		
WC – central	Winter	954	(26)		
WC – central	Spring	1090	(47)		
WC – central	All seasons	1052	(21)	1024	(44)
WC – south	Summer	867	(25)		
WC – south	Autumn	972	(37)		
WC – south	Winter	1027	(110)		
WC – south	Spring	927	(31)		
WC – south	All seasons	948	(31)	994	(40)

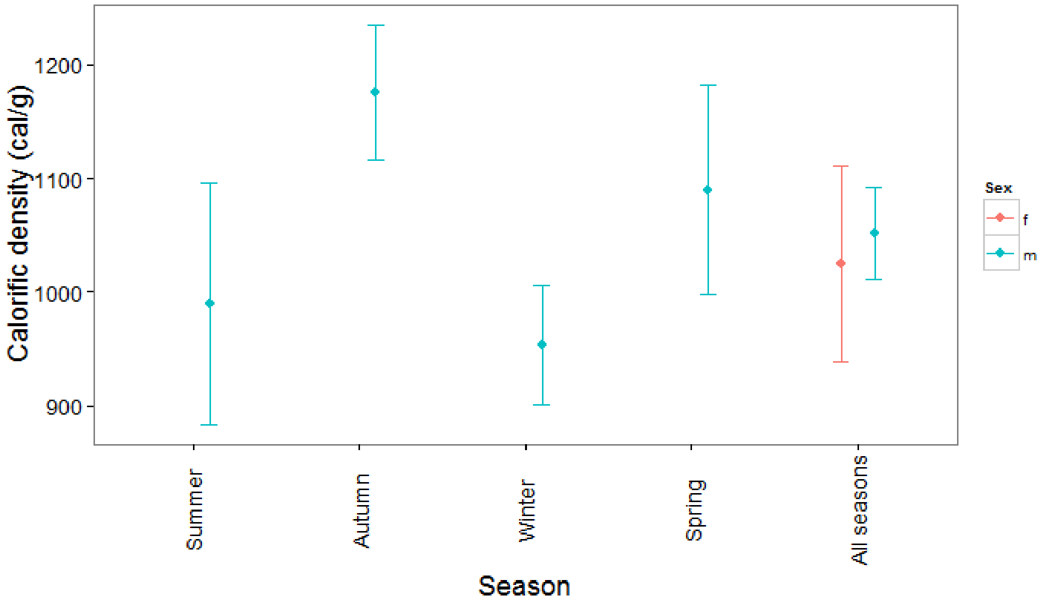
A) The Wash



B) Moray Firth



C) West coast - central



D) West coast – south

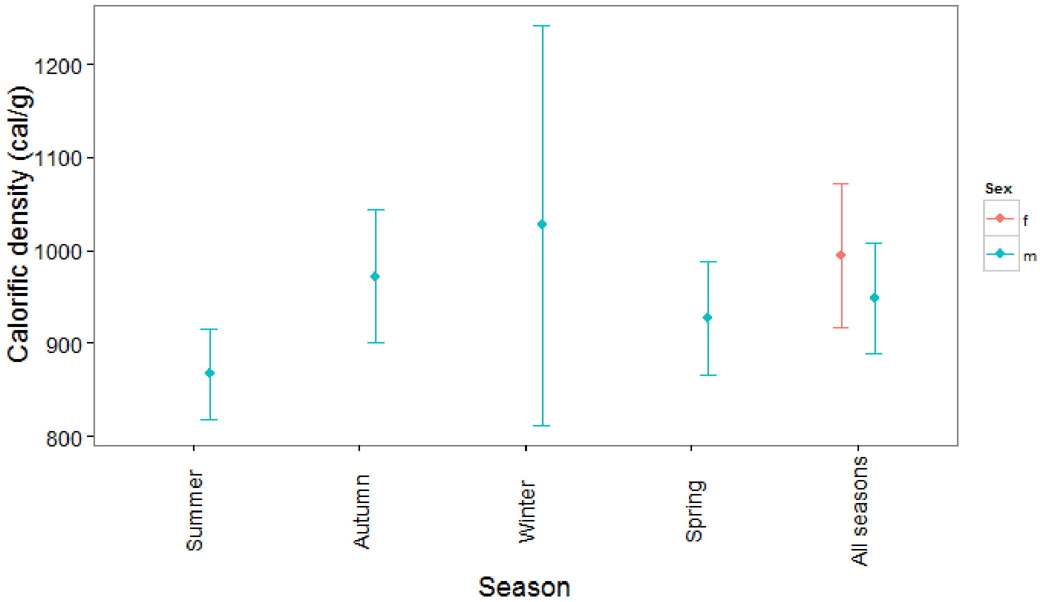


Figure 4.2: Diet quality estimates ± 95% confidence intervals for male and female harbour seals in each season.

4.4 Discussion

Determining the sex of harbour seals hauled-out on land is not easy as both sexes aggregate together throughout the year (Thompson *et al.*, 1998). In this thesis I have assumed that the scats collected from haul-out sites are representative of the regional population structure and diet. It was not possible to assess from the boat or from land the possible sex structure of any of the haul-out sites visited, however, by visiting a range of haul-out sites within each region and season I hoped to mitigate against any population differences (*e.g.*, sex, age class) in haul-out structure; *e.g.*, in summer haul-out sites were visited which did and did not contain pups and therefore the scats collected in this quarter are expected to be representative overall.

There were differences across the regions/seasons in the numbers of male and female scats collected (Table 4.1 A). In The Wash, in summer the number of male and female scats collected was similar, yet in autumn and winter more male scats were collected than female scats and in spring more female scats were collected. In the Moray Firth more female than male scats were collected in every season. In the West coast – central and south regions more male scats were collected in every season (Table 4.1 A). The overall percentage of scats that did not contain otoliths was however, small between males and females in all regions (Table 4.1 B). At a seasonal level the majority of differences were also small <10%. However, in The Wash in spring, more female than male scats contained otoliths (67.1% and 46.2%, respectively) and in the Moray Firth in spring more male than female scats contained otoliths (83.7% and 70.2%, respectively, Table 4.1 B).

For a species with limited sexual dimorphism neither sex should need to spend longer foraging to be satiated or to attain the diet quality required for basal metabolism. However, differences in foraging activity and time spent resting at haul-out sites might be expected to occur after energetically costly undertakings such as lactation (*e.g.,* Bowen *et al.*, 1992) and moult (Paterson *et al.*, 2012), when animals need to replenish diminished energy reserves. It is possible that such differences in at-sea movements might be reflected in the abundance of male or female scats at haul-out sites.

Telemetry studies of UK harbour seals have revealed inconsistent patterns in male and female movement's at-sea. In the Moray Firth female trip duration and range was reported to be significantly shorter than male trips (Thompson *et al.*, 1989). However, in the Inner Hebrides there was no male-female difference in trip duration but females did travel further from haul-out sites (Cunningham *et al.*, 2009). However, a much larger study of harbour seals around Britain did not find sex to be a good predictor of trip duration and distance travelled (Sharples *et al.*, 2012).

Across the regions in summer I had expected to recover more female than male scats as visual observations confirmed female presence (based on close association with a pup) at haul-out sites in all regions. Moreover, harbour seal males have been shown to spend more time in the water, conducting mating displays and defending territories July – August (Van Parijs *et al.*, 1997). However, Reder, *et al.*, (2003) showed that the haul-out behaviour of adult male harbour seals followed female distribution and movement patterns during the breeding period. If male seals continue to forage during the breeding season at a time when female seals spend less time foraging (Thompson *et al.*, 1994), it would be expected that more male scats will be collected during this time.

Scats collected in late summer and early autumn during the moult were more likely to be male dominated as female seals do not spend the same extended periods hauled-out out that adult males do (Reder *et al.*, 2003), presumably due to their need to replace energy reserves following lactation (Thompson *et al.*, 1989; Reder *et al.*, 2003).

The at-sea range of harbour seals has been shown to increase in winter months (Cunningham *et al.*, 2009). This period is expected to be a time when seals replenish their energy stores following the energetically costly breeding (*e.g.,* Bowen *et al.*, 1992) and moult (Paterson *et al.*, 2012) activities. The energetic costs of the summer/autumn are expected to be greater for females than males which receive no help in provisioning of young and if potentially pregnant need to regain energy stores quickly to support gestation as reduced body size and condition of pinnipeds has been linked to reduced numbers of births (Trillmich and Limberger, 1985; Lunn *et al.*, 1994).

Spring was the only time that more female than male harbour seal scats were collected in The Wash (Table 4.1 A). In the Moray Firth, it has been observed that, prior to pupping in June-July, female seals ceased to make trips out to foraging areas instead remaining within 2 km of haul-out sites each day and hauling out at every low tide (Thompson *et al.*, 1994). Despite not making extended trips out to known foraging locations, this does not mean that female seals are not eating, but indicates that they are foraging closer to the haul-out sites in late gestation. As females spend more time resting on land prior to pupping it is predictable that more female scats would be collected in this season.

The proportions of male and female scats collected from haul-out sites in The Wash appear to reflect the annual life cycle of harbour seals, matching the requirements of each sex to spend more time on land or at-sea in relation to pupping, breeding, moult and replenishment of energy stores. In the Moray Firth, the high prevalence of female scats at haul-out sites may be a consequence of female seals spending less time at-sea foraging (Thompson *et al.*, 1989) and more time hauled-out compared to males. The very low recovery of female scats from haul-out sites in the West coast regions may also reflect differences in the at-sea movement of the sexes. As females travel significantly further from haul-out sites than males (Cunningham *et al.*, 2009) it is possible that as a consequence of the increased activity level, females voided their bowel contents before arriving at the haul-out site and so less female scats were available for collection.

Without detailed information on sex specific differences in: the length of gastrointestinal tracts, metabolic rates, activity levels and energetic content of the previous meal it is difficult to draw firm conclusions about observed differences in the numbers of male and female scats at haul-out sites and inferences about population sex ratios should be made with caution.

4.4.1 Sex-specific variation in diet diversity

Building on the study of species richness and evenness to examine the diversity of the diet of harbour seals around Britain presented in Chapter 3, I present a study of the diversity of diet in male and female harbour seals in four regions of Britain: The Wash in southeast England, the Moray Firth in northeast Scotland and the West coast – central and south regions (part of the Inner Hebrides in Scotland). In this study the seal is the sampling unit and faecal prey remains provide an insight into what prey species were available to the seal and what the seal chose to eat. Rarefied estimates of species richness and evenness were used to standardise the data and allow for meaningful comparison (Gotelli and Colwell, 2001).

Differences in species richness of male and female diets were generally small across the different regions and seasons. The largest differences were seen across all seasons in the West coast – central region and in the summer in The Wash where males consumed more prey species than females.

Across all seasons, differences in the evenness of the diet of male and female harbour seals were also small. In The Wash the diet of both sexes was fairly even (Table 4.3), in the Moray Firth diet was very uneven for both sexes and in the West coast central and south the diet was quite even and similar between the sexes (Table 4.3).

Seasonal comparison showed that in The Wash, female diets were more uneven in winter and spring than males (Table 4.3). In winter and spring in The Wash, gobies constituted 11.4% and 20.2% of the diet of female harbour seals (Table 4.4). Goby's are small fish (typically <10 cm in length and weighing a few grams. The number of otoliths recorded in scats for these seasons was large to constitute such biomass in the diet. In this study, species evenness is a metric based on the count of otoliths and does not take into account the weight of prey and the unevenness in the diet is directly related to the higher incidence of goby in female diet in winter and spring than in the diet of male seals.

Overall, across all seasons, species richness and evenness did not vary greatly between the diet of male and female harbour seals and only a small degree of seasonal variation was observed across the diet of both sexes in The Wash in winter and spring.

4.4.2 Sex-specific variation in diet composition

Some sex-specific variation, by region, was observed in diet composition for results combined across all seasons.

The Wash. Flatfish were important in the diet of both male and female harbour seals in The Wash across all seasons. Other important prey were sandy benthic and pelagic species (more prevalent in female diet), scorpion fish and gadoids (more prevalent in male diet) and sandeels (equally important to both sexes, Appendix 4.2 A).

Moray Firth. The diet of both male and female harbour seals was dominated by sandeel in the Moray Firth (Table 4.4 B and Appendix 4.2 B). Flatfish was the only other important prey type.

West coast – central. The diet of both male and female harbour seals in the West coast – central region across all seasons was dominated by gadoids (more important in male diet) and pelagic prey (more important in female diet, Appendix 4.2 C).

West coast – south. Across all seasons the diet of both sexes was dominated by large gadoid prey and pelagic fish were equally important to both (Appendix 4.2 D). Female seals consumed more *Trisopterus* species than males.

In summary, in all regions except the Moray Firth, there were some differences in male and female diet across all seasons. In The Wash and West coast regions females ate fewer large gadoids and made up the difference in percentage contribution with; sandy benthic and pelagic fish in The Wash, pelagic fish in West coast – central region and *Trisopterus* species in the West coast – south region. Those prey groups for which the percentage weight was higher in the female diet all had higher calorific densities (*e.g.*, poor cod = 1102 and herring = 1587 cal.g-1, Murray and Burt, 1977) than the larger gadoid prey (*e.g.*, whiting = 772 cal.g-1, Murray and Burt, 1977).

In The Wash, there were also some seasonal differences. Whiting peaked in the diet of both sexes in autumn and was high for males in winter. Sandeel peaked for both sexes in summer and flatfish in summer and autumn. Dragonet was important for both sexes peaking in male diet in summer and autumn and in female diet in spring and summer.

The diet of male and female harbour seals was most closely matched during the summer. The similarity in prey composition of the diet may reflect male seals mirroring the distribution of female seals at this time (Reder *et al.*, 2003).

4.4.3 Diet quality

There was limited variation in diet quality between male and female harbour seals in any region. In The Wash, across all seasons, female diet overall was a higher quality than male diet (difference in quality 82 – 150 cal.g^{-1}). No differences were observed in the diet of male and females in the Moray Firth, West coast – central or West coast - south regions across all seasons.

The difference observed in the diet of male and female harbour seals in The Wash across all seasons was driven by the difference in diet quality in winter. Despite large standard errors the diet quality of male and female harbour seals in The Wash was markedly different in winter (difference in quality 164 – 364 cal.g^{-1}). During all other seasons there was no difference in the diet of either sex in The Wash.

In winter, male seals ate 22.7% more large gadoid prey and females ate 24.4% more pelagic and 12.3% more sandy benthic prey (Appendix 4.2 A). The gadoid prey consumed by male seals constituted roughly half the calorific density of the pelagic prey consumed by females; mean energy density herring and sprat = 1587 cal.g^{-1} and mean energy density cod and whiting = 755.5 cal.g^{-1} (Murray and Burt, 1977).

Fine scale fish distribution information is not available for The Wash; however, there is no evidence to date that male and female harbour seals in The Wash forage in different areas (Sharples *et al.*, 2012; Russell *et al.*, In Prep.). Body condition in late gestation is crucial in pinnipeds because females have significantly larger energetic costs as they support rapidly growing foetuses (Trillmich and Limberger, 1985; Pitcher *et al.*, 1998). By eating a high energy diet in The Wash in winter, female harbour seals increase the likelihood that they will have good body condition by spring/summer (late gestation/lactation), thus reducing the likelihood that foetuses may be aborted in the late stages of pregnancy and increasing the probability of survival of dependent pups.

In summary overall, variation in diet quality between the sexes was minimal, which is perhaps to be expected given the limited sexual dimorphism in harbour seals. Where a difference did occur in The Wash, the variation in diet between males and females, with females eating a higher quality diet in winter, was large enough to influence the difference in diet quality across all seasons. Female predation on pelagic prey is likely driving this difference in conjunction with greater consumption of gadoid prey by male seals. The recovery of body condition following breeding in females is likely driving this difference in prey consumption, consistent with the principles of the forage selection and activity budget sexual selection hypotheses (see below); differences are only expected in species with limited sexual dimorphism at times of high energetic demand.

In the Moray Firth, the diet of males and females was very similar with both sexes eating high proportions of sandeel. This prey species has a relatively high calorific density (Murray and Burt, 1977), which can presumably provide females with enough energy to replenish lost body condition post-breeding. In the West coast – central and south regions, where the diet was heavily dominated by gadoids, I would have expected higher proportions of high calorific density prey in female diet in winter/spring. However the sample sizes did not support season-specific analysis and inferences about diet fluctuations in response to the female life cycle could not be made.

4.4.4 Evidence for sexual segregation hypotheses

Behavioural patterns which cause sexual segregation are likely influenced by both social and ecological factors, *e.g.,* mating opportunities, population density and resource availability. Information on diet does not provide evidence for all sexual segregation hypotheses; however each one is discussed below to place the dietary evidence in a broader context.

4.4.4.1 Predation risk

This hypothesis proposes that females and/or their offspring are more at risk, due to differences in body size or because gestation /parental care hinder predator evasion.

Killer whale (*Orcinus orca*) predation on harbour seals has been reported around both Shetland and Orkney (Weir, 2002; Bolt *et al.*, 2009; Foote *et al.*, 2010; Deecke *et al.*, 2011), two areas which have seen recent large scale declines in population size (Lonergan *et al.*, 2007). Furthermore, in Shetland sightings peak during June – July coincident with harbour seal pupping (Bolt *et al.*, 2009). In the North Pacific, killer whale predation has been postulated as being largely responsible for large-scale declines in pinnipeds (Springer *et al.*, 2003; Williams *et al.*, 2004).

In Orkney where killer whales are frequently sighted (Bolt *et al.*, 2009) harbour seals which are heavily pregnant or lactating have been observed to alter their haul-out and foraging behaviour (Thompson *et al.*, 1998). These changes in distribution and behaviour were proposed to result from the females need for safe pupping and lactation sites (Thompson *et al.*, 1989) and may be driven by current or historical predator evasion strategies. Due to limited sample sizes, Orkney and Shetland were not selected for inclusion in this chapter and differences in diet particularly at the time when predation risk might influence segregation of the sexes was not possible.

4.4.4.2 Forage selection

This hypothesis proposes that different nutritional requirements are needed by animals of different body size or are driven by reproductive condition.

Harbour seals do not show pronounced sexual dimorphism, though males do tend to be larger than females. However, they follow a fairly typical mammalian reproductive cycle of mating, gestation, parturition, lactation, and maternal recovery (Gittleman and Thompson, 1988). In this study, scats were collected on a quarterly basis designed to match the harbour seal annual life cycle. Seasonal differences in diet composition have been reported for harbour seals around Britain (Thompson *et al.*, 1996b; Tollit and Thompson, 1996; Brown *et al.*, 2001; Pierce and Santos, 2003 and Chapter 3). However, links to harbour seal nutritional requirements and reproductive condition have not been made.

Following lactation, female harbour seals have been observed to spend more time at sea (presumably foraging) at the cost of a slower moult and Thompson *et al.*, (1989) proposed that this behaviour, which was different from male seals, was driven by the female requirement to recover body condition following lactation. Declines in female body mass of up to 33% have been recorded in harbour seals during lactation (Bowen *et al.*, 1992) and reduced body size and condition of pinnipeds has been linked to reduced numbers of births (Trillmich and Limberger, 1985; Lunn *et al.*, 1994). Consequently, for female seals to achieve their reproductive potential each year, they need to improve their body condition following the breeding season.

The diet of female harbour seals in The Wash in winter and spring appears to fit with the prediction that nutritional requirements are driven by reproductive condition. In these seasons (covering mid-late gestation), female diet was more uneven than that of male seals. Females ate greater proportions of pelagic prey (herring and sprat) and sandy benthic prey (dragonet and gobies) compared to males, which ate more large gadoids and scorpion fish (Table 4.4 A). As a consequence of the proportions of prey types consumed, the quality of the female diet in winter was higher than that of male seals (Figure 4.2 A). In spring mean diet quality of females was also higher than males but the 95% confidence intervals did overlap slightly (Figure 4.2 A).

4.4.4.3 Activity budget

This hypothesis proposes that species that exhibit body size sexual dimorphism will also display sex differences in digestive efficiency, energetic requirements and possibly movement.

Although harbour seals do not show distinct sexual dimorphism, sex-specific differences in activity budgets have recently been investigated for harbour seals. Using telemetry data within a state-space modelling framework, Russell *et al.*, (In Review) allocated the proportion of time resting (split between land and sea) and diving (split between foraging and travelling) on a six hour resolution. They found sex-specific seasonal trends in the proportion of time resting versus diving; females rested more during very late gestation, parturition and lactation. Thompson *et al.*, (1998) also reported sex differences in the behaviour of harbour seals with female seals hauling-out more frequently than males during pupping, and females with pups markedly restricting their foraging range during early lactation (Thompson *et al.*, 1994).

Late gestation and provisioning of young is considered the critical period for reproductive success in pinnipeds (Trillmich and Limberger, 1985) because females supporting rapidly growing foetuses and neonates incur large energetic costs in addition to their own metabolic requirements (Bowen *et al.*, 1992). For example, during lactation, female harbour seals experience fat and energy depletion equating to 16.3 kg loss of stored fat and 3.1 kg loss of stored protein (Bowen *et al.*, 1992).

The higher calorific density of female diet in The Wash in winter may indicate the motivation of female seals to replenish energy reserves prior to late gestation and lactation, the energetic costs of which are supported primarily by mobilisation of stored fat.

4.4.4.4 Thermal niche-fecundity

This hypothesis predicts that the sexes occupy different thermal habitats in an effort to maximise lifetime reproductive success.

Harbour seals as endotherms; maintain consistent body temperature through metabolism of energy. However, during the annual moult, a period characterised by loss and regrowth of hair over a 4-6 week period, seals minimise the energetic cost of the moult by hauling out so that they can maintain optimal high skin surface temperature for hair growth (Paterson *et al.*, 2012).

Thompson *et al.,* (1989) reported that, during the moult, male harbour seals hauled out every day but female seals spent more time at sea. The strategy employed by females increases their metabolic costs (Paterson *et al.*, 2012) during a period when they are likely already compromised energetically following a 4-6 week period of lactation (considered to be energetically the costliest component of reproduction, Clutton-Brock, 1991) and reduced foraging effort (Thompson *et al.*, 1994).

The preference for females to spend more time at sea at this time when their metabolic costs will be further increased indicates the necessity for females to recover body condition quickly following lactation. However, there was no difference in the quality of the diet of male and female harbour seals in autumn in either The Wash or Moray Firth and only limited evidence that females has a more diverse diet than males in autumn in The Wash as the species richness of female diet was higher than males.

4.4.4.5 Social factors

This hypothesis includes both social preference and social avoidance behaviours that exist when social mechanisms determine sexual segregation.

In harbour seals no communal care is offered for offspring and there is no evidence of co-ordinated foraging. Harbour seals do not remain ashore during the mating period and it is not expected that females form sex-specific groups on haul-out sites as there are no reports of dominance or territory holding by male seals on land.

4.5 Final Remarks

Though adult male harbour seals do tend to be larger than adult females, the species is interesting for investigating sexual segregation as overall there is very little size difference between males and females. Furthermore, there are no clear sex-related differences in activity budget or foraging trip range and duration for harbour seals around Britain. I have explored the diet of male and female harbour seals looking for sex specific variation in diet diversity, composition and quality in two regions on the west coast of Scotland, one in northeast Scotland and in The Wash in England. Due to limited sample sizes seasonal variation could only be explored in the North Sea regions; The Wash and Moray Firth. Overall differences in the diet metrics between male and female seals tended to be small, however, some patterns did emerge. In the Moray Firth, both sexes ate mainly sandeels in all season with other prey making only minor contributions to the diet. In The Wash the diet quality of female seals was significantly higher than male seals in winter and this difference was large enough to influence the difference in diet quality in the all seasons combined comparison. The difference appeared to be driven by greater consumption of higher calorific pelagic prey by female seals and lower calorific gadoid prey by male seals. In The Wash I attempted to associate this difference with the seasonal energetic requirements of females during the annual life cycle; improved diet quality being driven by the need of females to recover body condition; following lactation and moult and preceding their support of rapidly growing foetuses and neonates. This proposition is consistent with the principles of the forage selection and activity budget sexual selection hypotheses where sex related differences are predicted to develop based on the reproductive condition and energetic requirements of animals. However, sample sizes were relatively small in this study and no strong conclusions linking diet and sexual selection hypotheses can be made. Diet results from the Inner Hebrides did not support seasonal analysis due to small sample sizes however, the dominance of low calorific gadoids in the diet and the seasonal pulses of higher calorific prey seen in the diet of harbour seals overall in the region (Chapter 3) indicate that differences could exist in those regions if greater sample sizes were available for analysis.

Appendix 4.1: Seasonal and regional variation in the number of otoliths recovered for up to the 20 most abundant species or higher taxon prey in the diet of male (A – D) and female (E – H) harbour seals.

A) The Wash (male)

Species	**Summer**	**Autumn**	**Winter**	**Spring**	**Total**
Sandeel	928	181	72	46	1227
Whiting	138	683	64	15	900
Plaice	514	329	9	6	858
Dragonet	460	304	28	14	806
Goby	40	50	488	2	580
Unidentified flatfish	92	182	3	1	278
Dab	105	92	5	0	202
Dover sole	22	56	4	20	102
Bullrout	1	5	20	63	89
Lemon sole	12	29	4	3	48
Pout whiting (Bib)	27	0	10	1	38
Unidentified roundfish	3	6	2	6	17
Garfish	14	2	0	0	16
Brill	4	10	0	0	14
Sea Scorpion	3	4	0	7	14
Cod	2	3	6	2	13
Flounder (Butt)	4	5	0	0	9
Herring	1	2	4	1	8
Loligo	3	3	2	0	8
Unidentified gadid	3	2	0	0	5

B) Moray Firth (male)

Species	**Summer**	**Autumn**	**Winter**	**Spring**	**Total**
Sandeel	2622	1118	110	2207	6057
Plaice	264	6	1	3	274
Unidentified flatfish	141	3	1	12	157
Dab	142	1	5	0	148
Cod	16	3	2	0	21
Whiting	16	0	4	1	21

Loligo	20	0	0	0	20
Haddock	11	0	0	0	11
Saithe	3	0	5	2	10
Flounder (Butt)	6	0	0	3	9
Long rough dab	5	0	0	0	5
Unidentified gadid	3	0	1	1	5
Dragonet	2	0	0	0	2
Lemon sole	2	0	0	0	2
Scaldfish	2	0	0	0	2
Unidentified Salmonid	2	0	0	0	2
Brill	1	0	0	0	1
Herring	1	0	0	0	1
Mackerel	1	0	0	0	1

C) West coast - central (male)

Species	**Summer**	**Autumn**	**Winter**	**Spring**	**Total**
Poor cod	82	609	574	57	1322
Norway pout	83	139	396	56	674
Blue whiting	207	25	207	170	609
Whiting	189	68	297	5	559
Sandeel	16	413	21	32	482
Dragonet	1	195	98	4	298
Unidentified *Trisopterus*	14	40	90	14	158
Unidentified gadid	41	26	69	10	146
Herring	3	102	25	8	138
Mackerel	5	85	0	22	112
Haddock	5	27	2	40	74
Cod	1	21	2	5	29
Unidentified *Cottidae*	13	9	0	0	22
Silvery pout	3	2	14	2	21
Ling	1	3	3	5	12
Unidentified flatfish	1	9	0	2	12
Lemon sole	1	2	0	7	10
Eledone	1	3	0	3	7

Long rough dab	1	2	1	2	6
Hake	3	0	1	0	4

C) West coast - south (male)

Species	**Summer**	**Autumn**	**Winter**	**Spring**	**Total**
Whiting	665	125	835	109	1734
Haddock	165	198	384	113	860
Norway pout	323	5	405	106	839
Unidentified gadid	178	21	220	42	461
Poor cod	148	60	218	26	452
Blue whiting	154	1	204	54	413
Herring	4	120	132	21	277
Dragonet	88	34	128	6	256
Sandeel	24	28	62	17	131
Unidentified *Trisopterus*	31	25	56	7	119
Cod	18	19	42	20	99
Rockling	2	34	41	6	83
Witch	11	6	25	18	60
Plaice	3	16	19	5	43
Mackerel	12	7	20	3	42
Argentine	5	1	15	9	30
Ling	2	3	8	3	16
Long rough dab	2	5	7	0	14
Lemon sole	1	5	6	1	13
Saithe	2	3	5	0	10

E) The Wash (female)

Species	**Summer**	**Autumn**	**Winter**	**Spring**	**Total**
Goby	1071	298	770	1568	3707
Plaice	533	65	7	26	631
Sandeel	334	191	22	21	568
Dragonet	243	67	11	53	374
Whiting	10	215	15	84	324
Dab	124	29	3	29	185
Unidentified flatfish	64	93	1	13	171

Dover sole	42	3	2	31	78
Flounder (Butt)	23	14	0	0	37
Lemon sole	3	5	2	16	26
Unidentified roundfish	3	10	5	2	20
Lesser weever	8	11	0	0	19
Sepiolids	8	1	0	0	9
Smelt	6	1	0	0	7
Flounder or Plaice	6	0	0	0	6
Brill	1	2	0	0	3
Alloteuthis spp	2	0	0	0	2
Butterfish	1	1	0	0	2
Unidentified *Cottidae*	1	0	0	1	2
Bass	1	0	0	0	1

F) Moray Firth (female)

Species	**Summer**	**Autumn**	**Winter**	**Spring**	**Total**
Sandeel	4159	723	791	3624	9297
Plaice	456	10	6	13	485
Unidentified flatfish	157	1	15	56	229
Dab	177	3	1	18	199
Cod	27	21	4	1	53
Flounder (Butt)	12	1	4	33	50
Whiting	13	12	6	2	33
Saithe	5	8	1	11	25
Unidentified gadid	6	15	0	1	22
Bullrout	12	3	0	1	16
Eelpout	1	1	2	5	9
Flounder or Plaice	9	0	0	0	9
Haddock	6	0	0	0	6
Loligo	1	2	0	0	3
Long rough dab	2	0	0	0	2

G) West coast - central (female)

Species	**Summer**	**Autumn**	**Winter**	**Spring**	**Total**
Poor cod	4	180	8	1	193

Norway pout	42	9	0	0	51
Whiting	33	5	0	0	38
Sandeel	18	0	9	1	28
Blue whiting	19	0	0	0	19
Dragonet	1	7	5	0	13
Herring	1	6	0	0	7
Unidentified gadid	3	0	0	3	6
Gurnard	1	0	1	0	2
Norwegian topknot	1	0	0	0	1
Silvery pout	1	0	0	0	1

H) West coast - south (female)

Species	**Summer**	**Autumn**	**Winter**	**Spring**	**Total**
Poor cod	79	283	75	34	471
Whiting	184	22	58	54	318
Norway pout	97	0	10	132	239
Unidentified gadid	50	67	16	5	138
Dragonet	18	31	2	1	52
Haddock	20	21	0	2	43
Herring	3	21	0	4	28
Blue whiting	12	9	1	4	26
Unidentified *Trisopterus*	19	2	4	0	25
Sandeel	18	2	0	0	20
Cod	1	11	3	2	17
Plaice	4	5	0	0	9
Dab	3	1	0	2	6
Bullrout	1	4	0	0	5
Goby	2	0	0	3	5
Saithe	2	0	1	2	5
Unidentified flatfish	1	2	0	1	4
Argentine	1	0	0	2	3
Mackerel	2	1	0	0	3

Appendix 4.2: Male (M) and female (F) harbour seal diet (expressed as the percentage of each prey type in the diet by weight) listed according to prey type for each region and season combination.

A) The Wash

	Summer		Autumn		Winter		Spring		All seasons	
Prey type	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**
Gadid	5.9	0.9	29.1	18.1	30.3	7.5	3.1	6.0	17.1	8.1
Trisopterus	0.4	0.0	0.0	0.4	1.8	0.0	0.1	0.2	0.6	0.1
Sandeel	33.1	25.2	6.4	11.9	5.3	4.7	2.6	3.4	11.8	11.3
Flatfish	22.2	31.3	40.1	20.3	13.6	10.5	14.0	18.1	22.5	20.1
Sandy benthic	35.0	41.6	20.7	16.0	12.1	24.4	7.8	51.0	18.9	33.2
Scorpion fish	1.3	0.2	2.2	26.8	27.4	23.7	71.2	9.1	25.5	15.0
Pelagic	0.2	0.2	0.3	2.8	4.7	29.1	1.3	12.1	1.6	11.1
Salmonid	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cephalopod	0.8	0.1	0.9	3.6	4.8	0.0	0.0	0.0	1.6	0.9
Other	1.0	0.5	0.2	0.1	0.0	0.0	0.0	0.0	0.3	0.2

B) Moray Firth

Prey type	Summer		Autumn/Winter		Spring		All seasons	
	M	**F**	**M**	**F**	**M**	**F**	**M**	**F**
Gadid	3.6	1.9	5.8	4.1	2.7	1.1	4.0	2.3
Trisopterus	0	0	0.1	0.3	0	0	0	0.1
Sandeel	45.5	60.3	83.9	69.5	93.5	83.1	74.3	71
Flatfish	40.9	33.0	5.6	8.2	3.5	14.1	16.7	18.4
Sandy benthic	0.6	0	0.1	0.3	0	0	0.2	0.1
Scorpion fish	0	4.7	0	5.7	0	0.2	0	3.5
Pelagic	0.7	0	4.4	5.3	0.3	1.3	1.8	2.2
Salmonid	1.9	0	0	5.1	0	0	0.6	1.7
Cephalopod	6.8	0.1	0	0.6	0	0	2.3	0.2
Other	0	0.1	0	0.9	0	0.2	0	0.4

C) West coast - central

Prey type	Summer	Autumn	Winter	Spring	All seasons	
	M	M	M	M	M	F
Gadid	58.6	12.8	45.1	49.9	41.6	25.8
Trisopterus	5.6	5.3	19.8	5.1	8.9	7.3
Sandeel	2.7	8.1	2.5	3.4	4.2	3.7
Flatfish	0.6	6.0	2.9	4.8	3.6	0.1
Sandy benthic	0.1	23.1	20.3	0.8	11.1	11.6
Scorpion fish	20.1	1.8	2.4	0	6.1	3.7
Pelagic	10.0	41.9	7.0	30.5	22.3	46.1
Salmonid	0	0	0	0	0	0
Cephalopod	2.3	1.1	0	5.6	2.3	1.8
Other	0.1	0	0	0	0	0

D) West coast - south

Prey type	Summer	Autumn	Winter	Spring	All seasons	
	M	M	M	M	M	F
Gadid	60.7	52.7	67.0	75.8	64.1	42.6
Trisopterus	6.8	1.2	5.7	4.1	4.4	17.7
Sandeel	0.5	1.7	0.4	2.1	1.2	0.9
Flatfish	2.4	4.0	4.8	4.2	3.8	4.4
Sandy benthic	16.0	5.7	0	4.2	6.5	7.1
Scorpion fish	0	0.2	10.9	0	2.8	4.5
Pelagic	9.9	33.1	11.3	9.6	16.0	16.7
Salmonid	0	0	0	0	0	0
Cephalopod	3.3	0.8	0	0	1.0	3.9
Other	0.4	0.6	0	0	0.3	2.2

Appendix 4.3: 95% Confidence Limits (CL) for male (M) and female (F) harbour seal diet composition expressed as the percentage of each prey type in the diet by weight (Table 4.4). Prey species listed are those that contributed >2% in any season across each region (A) The Wash, (B) Moray Firth, (C) West coast – central and (D) West coast – south.

A) The Wash

	95% CL									
Prey type	**Summer**		**Autumn**		**Winter**		**Spring**		**All seasons**	
	M	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**
Gadid	1.5-12.4	0.1-2.5	14.5-44.1	5.7-34.7	14.4-50.1	1.0-13.4	1.3-7.4	1.0-13.6	11.0-23.3	3.9-12.9
Trisopterus	0-1		0-0.2	0-1.6	0-6.7		0-0.6	0-0.5	0.1-1.8	0-0.5
Sandeel	10.8-53.7	4.3-48.9	1.5-16	2.6-30.3	0.4-16.2	0.4-15.2	0.3-13	0.9-8	5.8-18.6	5.0-18.2
Flatfish	11.5-33.2	17.4-46.9	24.4-54.4	10.1-35.8	3.8-30.9	0-26.0	3-66.2	7.5-30.2	15.9-36.1	13.1-27.1
Sandy benthic	20.9-58.8	23.5-64.8	13.5-35.1	8.3-32.8	3.9-26.1	5.8-41.8	2.3-41.5	29.5-71.4	14.7-30.7	26.3-43.6
Scorpion fish	0.2-4.3	0-1.0	0.3-5.7	1.1-53.9	0.9-51.3	4.3-50.4	1.7-89.5	0.7-26.9	6.2-32.8	4.9-25.7
Pelagic	0-0.8	0-0.5	0-0.9	0-10.0	0.9-13.4	5.9-70.8	0-6.2	2.2-28.0	0.5-4.0	3.9-21.6
Salmonid										
Cephalopod	0-1.9	0-0.1	0-2.5	0-14.1	0-15.6				0.2-4.2	0-3.5
Other	0.1-3.1	0-2.0	0-0.9	0-0.2	0-0.1	0-0.1	0-0.1	0-0	0.1-0.9	0-0.5

B) Moray Firth

Prey type	95% CL Summer M	F	Autumn/Winter M	F	Spring M	F	All seasons M	F
Gadid	0.9-8.7	0.6-4.4	0.7-30.9	1.3-12.2	0-19.2	0.2-5.5	1.4-17.4	1.3-7.0
Trisopterus	20.1-69.1		0-0.6	0-1.1		0-0.1	0-0.3	0-0.6
Sandeel	18.8-67.9	34.5-85.3	44-94.6	37.5-88.7	74.5-98.3	60.6-95.0	55.6-85	51.5-83.1
Flatfish	0-2.5	8.5-57.9	1.4-18.5	2.8-18.4	0.6-10.6	3.0-35.0	7.9-23.7	8.6-25.8
Sandy benthic			0-0.8	0-1.1			0-0.8	0-0.5
Scorpion fish	0-3.4	0-19.1		0-20.1		0-0.8		0.1-11.4
Pelagic	0-6.7		0.1-19.4	0.3-16.2	0-1.2	0.4-3.8	0.2-9.9	0.4-8.5
Salmonid	0-22.6			0-17.5			0-1.7	0-8.7
Cephalopod		0-0.2		0-2.5			0-5.7	0-1.3
Other		0-0.4		0-2.2	0-0	0-0.6	0-0	0.1-1.2

C) West coast - central

	95% CL					
Prey type	**Summer**	**Autumn**	**Winter**	**Spring**	**All Seasons**	
	M	**M**	**M**	**M**	**M**	**F**
Gadid	26.9-83.1	6.2-29.2	23-73.5	23.7-75.2	30.7-54.1	7.1-59.8
Trisopterus	2.2-12.2	2.2-9.8	5.7-36.1	1.3-12.1	4.9-13.4	1.5-22.6
Sandeel	0.5-8	0.7-22.1	0.3-7	0.8-9.3	1.6-7.9	0.1-14.2
Flatfish	0-2.2	1-13.3	0.8-8.3	1.1-10.6	1.7-6.3	0-0.4
Sandy benthic	0-0.2	3.2-49	1.1-49.6	0-2.8	2.8-21.0	0.6-41.7
Scorpion fish	0-54.2	0-5.9	0-5.2		0.6-14.9	0-14.2
Pelagic	0.2-32.8	20.4-63.5	0.1-24.9	9.4-62.1	13-32.7	1.5-79.9
Salmonid						
Cephalopod	0-7.8	0.1-2.8	0-0	0.8-13	0.6-4.5	0-7.9
Other	0-0.2	0-0		0-0	0-0	

D) West coast - south

	95% CL					
Prey type	**Summer**	**Autumn**	**Winter**	**Spring**	**All Seasons**	
	M	**M**	**M**	**M**	**M**	**F**
Gadid	42.7-79.3	36.4-66.5	24.9-88.1	59.1-85.1	51.3-71.7	24.8-59.4
Trisopterus	4.5-9.1	0.3-2.5	0.9-25.9	2.3-6.5	2.9-9.4	8.1-28.5
Sandeel	0.1-1	0.3-5.2	0-0.7	0.4-6	0.5-2.4	0-2.0
Flatfish	0.7-5.2	1.7-7	0-11.8	1.5-8.1	1.8-6.0	0.3-11.7
Sandy benthic	0.7-31.8	2.3-12.4		0-12.3	2.4-11.5	1.7-18.6
Scorpion fish		0-0.7	0-21.7		0-5.4	0-13.6
Pelagic	2-25.5	17.3-50.8	0-64.6	3.4-20.8	9.0-30.4	3.7-38.1
Salmonid						
Cephalopod	0-12.8	0-1.8		0-0	0.1-3.5	0-11.8
Other	0-0.8	0-2.1			0-0.6	0-7.4

Appendix 4. 4: 95% Confidence Limits (CL) for male (M) and female (F) harbour seal diet composition expressed as the percentage of each species in the diet by weight (Table 4.4). Prey species listed are those that contributed >2% in any season across each region (A) The Wash, (B) Moray Firth, (C) West coast – central and (D) West coast – south.

A) The Wash

	95% CL									
	Summer		**Autumn**		**Winter**		**Spring**		**All seasons**	
Species	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**
Cod	0-1.5		0-1.1		0-15.4		0-4.1		0-11.0	
Whiting	1.1-12.1	0.1-2.5	14-43.3	5.7-34.7	11.2-41.9	1.0-13.4	0.7-5.7	1.0-13.5	1.0-39.4	0.2-28.3
Sandeel	10.8-53.7	4.3-48.9	1.5-16.0	2.6-30.3	0.4-16.2	0.4-15.2	0.3-13	0.9-8	0.5-45.7	1.0-40.0
Plaice	2.0-19.7	3.2-12.8	4.6-27.6	0.9-6.4	0.1-7.6	0-0.4	0-10.5	0.2-1	0-22.2	0-10.4
Lemon sole	0.5-6.7	0-2.4	0.7-13.2	0.6-17.9	0-25.0	0-23.7	0-1.6	0-9.1	0-18.1	0-18.0
UnID flatfish	0.3-2.8	0.5-3.4	2.3-8.6	0.5-6.2	0-1.1	0-0.3	0-1.1	0.1-1	0-7.1	0-4.5
Dover sole	1.2-6.7	2.0-15.9	2.3-18.8	0-1.7	0-5.3	0-3.3	1.5-59.2	4.9-23.5	0.3-38.7	0-19.4
Flounder	0-0.7	1.9-16.8	0-2.1	0-6.0					0-1.5	0-12.9
Dab	1.3-7.3	2.0-9.9	2.6-10.3	1.6-10.8	0-3.5	0-0.2		0.1-1.2	0-8.5	0-9.4
Brill	0-5.9	0-0.4	0.2-2.8	0-5.8					0-4.4	0-3.9
Dragonet	20.6-58.7	16.5-56.4	13.4-34.8	5.9-29.4	2.6-23.9	0-29.4	2.2-41.5	11.7-54.6	2.8-51.6	0-52.6
Goby	0-0.4	3.3-14.1	0-0.4	0.7-5.3	0.1-4.8	1.9-36.2	0-0.2	8.7-34.3	0-3.4	1.0-31.0
Hooknose	0-0.2			0-19.8		0-1.8	0-1.2	0-2.3	0-0.6	0-13.2
Bullrout	0-2.0		0-5.0	0-32.3	0.9-51.3	0-21.3	1-86.5	0-23.7	0-81.7	0-25.6

Sea Scorpion	0-2.4		0-2.3	0-24.1		3.0-46.1	0-9.8	0-5.5	0-6.6	0-33.7
Mackerel				0-9.9						0-6.2
Herring	0-0.8		0-0.9		0-3.8	0-49.2	0-6.2	1.4-26.3	0-4.3	0-36.9
Sprat					0.1-9.8	2.3-46.5		0-4.6	0-6.4	0-30.7
Eledone				0-14.1						0-8.4
Loligo	0-1.9		0-2.5		0-15.6				0-10.7	

B) Moray Firth

	95% CL							
	Summer		**Autumn/Winter**		**Spring**		**All seasons**	
Species	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**
Saithe	0-3.3	0-1.5	0-25.9	0.1-9.2	0-17.5	0.1-5	0-21.2	0-7.1
Sandeel	20.1-69.1	34.5-85.3	44-94.6	37.5-88.7	74.5-98.3	60.6-95	27.5-97.3	37.6-91.8
Plaice	5-21.9	2.6-24.8	0.1-4.9	0.4-3.2	0-0.9	0.1-1.5	0-17.6	0.2-20.5
UnID flatfish	1.4-11.9	0.4-6.8	0-6.4	0.1-2.6	0.1-3.9	0.2-6.0	0-9.4	0.2-5.8
Flounder	0-3.6	0.1-4.6		0.6-12.0	0-6.6	0.7-28.1	0-4.6	0-13.1
Dab	6.6-40.2	2.5-31.8	0.5-11	0-3.6		0-2.9	0-32.5	0.2-20.4
Bullrout		0-19.1		0-20.1		0-0.8		0-24.7
Sprat			0.1-19.4	0.3-15.8	0-1.2	0.4-3.8	0-15.5	0-18.5
UnID Salmonid	0-6.7			0-17.5			0-4.5	0-14.5
Loligo	0-22.6	0-0.2		0-2.5			0-15.6	0-2.1

C) West coast - central

	95% CL					
	Summer	Autumn	Winter	Spring	All seasons	
Species	**M**	**M**	**M**	**M**	**M**	**F**
Cod		0.7-6.5		0-7.1	0-5.9	0-31.3
Whiting	4.4-30.5	0.7-3.1	2.1-19.3	0-1.2	0.2-24.2	0.8-14.5
Haddock	0.1-2	0.8-3.9	0-1.5	1.9-21.8	0-16.5	0-3.6
Saithe		0.2-17.8	0.1-42.9	0.8-41.6	0-32.9	0-9.2
Ling	0-7.5	0-4.7	0-20.4	0-11.9	0-13.0	0-18.1
UnID gadid	1.3-10.7	0.1-1.1	0.4-4.4	0.2-2.3	0.2-8.1	0-3.9
Saithe or Pollock		0-3.5	0-35.9		0-18.0	
Blue whiting	6.3-65	0-2.1	5.3-29.1	6.0-46.6	0-54.8	0.4-14.7
Poor cod	1.0-6.6	1.1-7.4	4.5-26.7	0.8-5.7	1.0-22.0	0.5-16.6
Norway pout	0.9-5.6	0.5-2.3	1.0-10.0	0.1-8.0	0.2-8.7	0.4-6.1
Sandeel	0.5-8.0	0.7-22.1	0.3-7.0	0.8-9.3	0.5-15.4	0.1-14.2
Plaice		0.4-5.5			0-4.1	
Lemon sole	0-2.0	0-0.9		0.3-8.1	0-5.7	
Dragonet	0-0.2	3.2-49	1.1-49.6	0-2.8	0-44.6	0.6-41.7
UnID *Cottidae*	0-54.2	0-5.9			0-41.3	0-8.9
Gurnard			0-1.9		0-1.1	0-8.3
Mackerel	0-29.2	6.3-45.7		6.4-58.8	0-48.5	0-69.4

Herring	0-11.7	6.1-28.9	0-23.3	0.3-10.8	0-24.1	0-21.8
Horse mackerel		2.1-10.2	0-2.6	0-0.4	0-8.1	0-4.2
Eledone	0-7.8	0-2.1		0-8.0	0-6.6	
Loligo		0-1.3		0-7.1	0-4.8	0-7.9

D) West coast - south

	95% CL					
	Summer	**Autumn**	**Winter**	**Spring**	**All seasons**	
Species	**M**	**M**	**M**	**M**	**M**	**F**
Cod	1.2-20.1	1.9-16.2		9.3-42.9	0-36.9	0.3-4.1
Whiting	14.1-31.2	4.1-14.1	0-36.3	6.1-16.6	1.0-30.5	6.7-37.8
Haddock	9.2-24.4	15.4-38.9	0-61.4	10.4-36.9	0-46.6	1.3-12.8
Saithe	0-1.8	0-7.3			0-3.7	0-14.0
Ling	0-5.8	0-6.1	0-64.6	0-15.5	0-55.1	
Rockling	0-1.2	0-9.7		0-0.7	0-7.0	0-1.8
UnID gadid	3.2-14.2	0.1-2.0	0-14.0	1.3-6.7	0-12.4	2.4-15.2
Blue whiting	2.3-12.2	0-0.1	0-3.7	2.1-11.6	0-10.6	0.6-4
Poor cod	1.6-4.6	0.2-2.4	0-21.7	0.5-2.6	0.3-14.0	4.5-21.9
Norway pout	2.3-5.3	0-0.1	0-5.0	1.2-4.4	0-4.8	0.7-11.6
Sandeel	0.1-1.0	0.3-5.2	0-0.7	0.4-6.0	0-4.5	0-2
Lemon sole	0-0.6	0.2-3.5	0-11.8	0-1.1	0-8.4	

Witch	0-2.9	0-1.1		0.8-5.6	0-4.5	0-5.7
Dragonet	0.7-31.8	2.3-12.4		0-12.3	0-26.7	1.3-18.1
Bullrout						0-11.3
Gurnard		0-0.7	0-21.7		0-17.2	0-5.5
Mackerel	1.2-23.8	0-20.2	0-64.6	0-9.1	0-42.4	0-11.1
Herring	0-1.8	11.9-42.9		1.2-14.0	0-36.6	2.0-34.7
Eledone	0-12.8	0-0.6			0-7.9	0-11.1
Eelpout					0-0.1	0-6.9

Chapter 5

COMPARING THE DIET OF HARBOUR AND GREY SEALS AROUND BRITAIN

5.1 Introduction

5.1.1 Resource partitioning in response to interspecific competition

It is widely accepted that interspecific competition can play an important role in community structure (Connell, 1983; Schoener, 1983; Begon *et al.*, 2006). From a dietary perspective, competition can influence an individual's energy budget by affecting the quality and/ or quantity of prey consumed and this can have negative consequences for individual growth, reproduction and survival (Cody and Diamond, 1975; Eccard and Ylönen, 2003). Population level consequences can include declines in abundance of the less competitive species as seen, for example, in red squirrel (*Sciurus vulgaris*) populations in Britain (Wauters *et al.*, 2000). However, the existence of competition between species is extremely difficult to assess, and is often determined by overlap or partitioning in resource use by species.

A common response to interspecific competition is that individuals of a species modify the way they use resources, altering the niche exploited and thereby reducing the intensity of competition (Loveridge and Macdonald, 2003). Species that consume similar prey may do so in different proportions (Whitehead *et al.*, 2003), change their dominant prey type (Clarke *et al.*, 1998) or partition habitats (Schoener, 1968). Competition can also have more extreme consequences, such as a species being excluded from contested habitat (Kruuk *et al.*, 1994).

The strong dependency of several species on a single prey item, Antarctic krill (*Euphausia superba*), makes the Southern Ocean a potentially good place to look for evidence of resource overlap or partitioning. Studies of sympatric penguin species have revealed differences in both diet and breeding chronology (Trivelpiece *et al.*, 1987; Hindell *et al.*, 1995; Hull, 1999). Disparity in foraging locations of Adélie

(*Pygoscelis adeliae*) and chinstrap penguins (*P. antarctica*) has been identified in years of low krill abundance leading Lynnes *et al.*, (2002) to propose that chinstrap penguins may be able to competitively exclude Adélie penguins from potential inshore foraging sites during times of limited prey availability. Both species have a similar diet and breeding chronology and no segregation in foraging locations in years where prey availability is not low. However, in years of low krill abundance Adélie penguins foraged significantly further from the colony (mean 100 km) than chinstrap penguins (mean 58 km) and this affected breeding success which was 51% lower in Adélie penguins compared to 15% lower in chinstrap penguins (Lynnes *et al.*, 2002).

Around South Georgia, the Antarctic fur seal (*Arctocephalus gazella*) and macaroni penguin (*Eudyptes chrysolophus*) are sympatric higher predators. They consume similar sized prey (Antarctic krill, Croxall and Prince, 1980; Reid and Arnould, 1996; Croxall *et al.*, 1999), dive to similar depths (Croxall *et al.*, 1988; Boyd and Croxall, 1992) and restrict their foraging while provisioning offspring (Gentry and Kooyman, 1986; Williams and Croxall, 1991). Differences in the population trajectories of macaroni penguins (declining, Trathan *et al.*, 1998) and fur seals (expanding, Payne, 1977) was linked to increased competition for resources between the two species (Barlow *et al.*, 2002). Satellite tracking revealed significant spatial segregation of foraging activity between the two species, leading Barlow *et al.* (2002) to infer that the species were not exploiting the same krill population during the breeding season. Though the size of the krill eaten by both species remained similar, the contribution of krill to the diet of fur seals remained fairly constant at around 77%, whereas the amount of krill in macaroni penguin diets declined between 60 and 90% since the 1970s (Reid and Arnould, 1996; Croxall *et al.*, 1999; Barlow *et al.*, 2002).

Evidence of resource partitioning and overlap also exists in areas where diet is not dominated by one species. Comparing the diet of sympatric adult male New Zealand (*Arctocephalus forsteri*) and Australian fur seals (*A. pusillus*), Page *et al*., (2005a) found little overlap in diet. Australian fur seal diet was dominated by fish species but important prey in New Zealand fur seal diet included little penguins (*Eudyptula minor)* and squid. Any overlap in diet occurred in fish consumption but the proportions consumed were different (Page *et al.*, 2005a).

Jeglinski *et al.,* (2013) studied foraging niche overlap between similar-sized sympatric juvenile Galapagos sea lions (*Zalophus wollebaeki*) and adult Galapagos fur seals (*Arctocephalus galapagoensis*). The two species exploited spatially and bathymetrically distinct foraging habitats despite similarities in diving depth and activity period. Stable isotope analysis revealed that the juveniles fed at a lower trophic level (Jeglinski *et al.*, 2013).

For two similar and relatively closely related carnivores to co-exist, ecological theory predicts that they must partition resources to reduce interspecific competition (Rosenzweig, 1966). Furthermore, body size and prey size are often correlated and differences in size between sympatric predators may indicate that resource partitioning is occurring (Rosenzweig, 1968).

A leading question about the cause of the decline of harbour seal (*Phoca vitulina*) populations in some areas around Scotland (Lonergan *et al.*, 2007; SCOS, 2013) is: do grey (*Halichoerus grypus*) and harbour seals compete for food? (SCOS, 2012). In this Chapter, I examine resource partitioning, as indicated by diet, in grey and harbour seals around Britain to investigate evidence for inter-specific competition. However, diet forms only part of the wider picture of inter-specific interactions and a multidisciplinary approach is underway including investigations into foraging area overlap to make a full assessment of competition.

5.1.2 Pinnipeds as sympatric higher predators around Britain

Grey and harbour seals around Britain are sympatric along much of the coastline. These species differ in body size, annual life cycle (Bonner, 1972), at-sea movements and haul-out behaviour (Figure 5.1). There is also a large difference in population abundance. The estimated population size of grey seals based on annually monitored colonies in 2010 was 111,300 (95 % CI 90,100 - 137,700, SCOS, 2012) and the estimated total population of harbour seals in the UK in 2010 was 36,500 (95 % CI 29,900 - 48,650, SCOS, 2012).

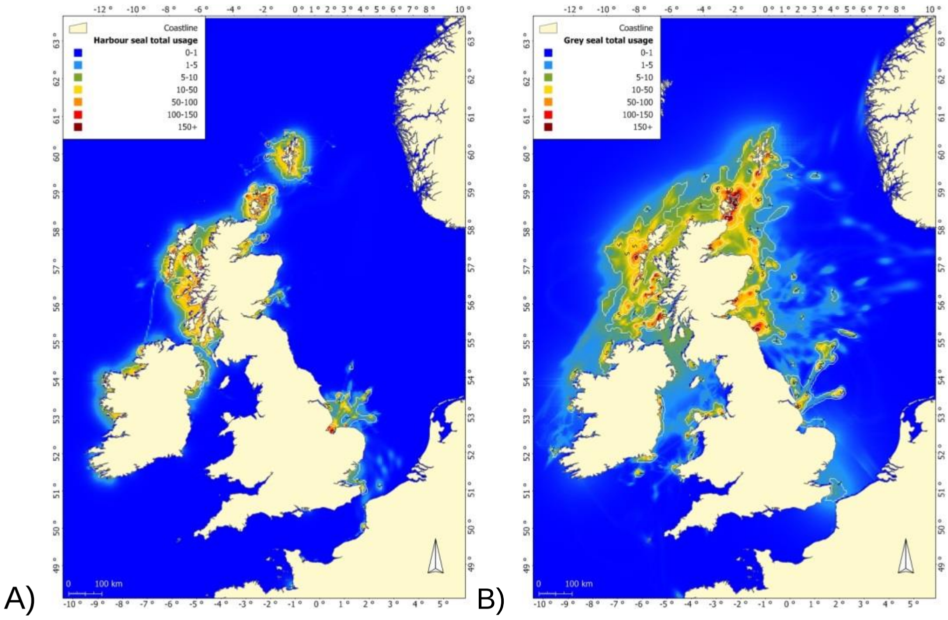


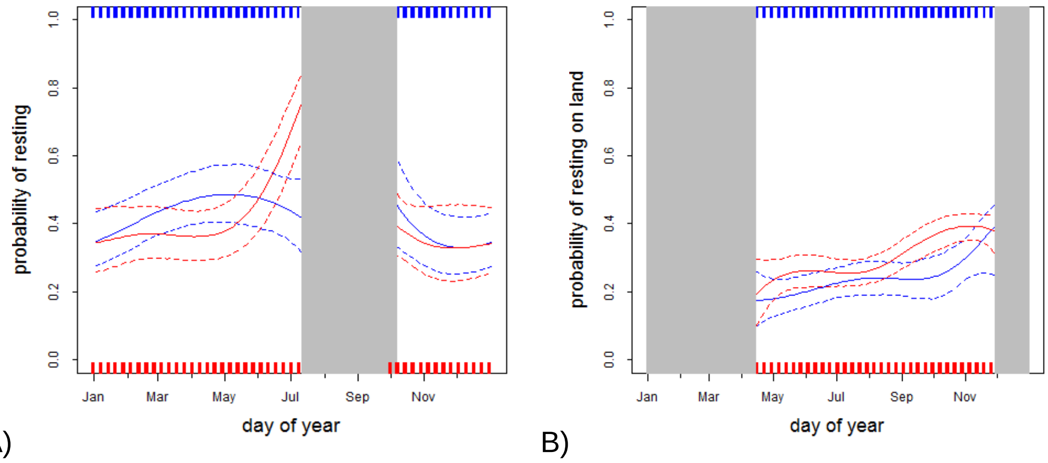
Figure 5.1: Estimated harbour seal (A) and grey seal (B) total (at-sea and hauled-out) usage around Britain (Jones *et al.*, 2013).

Male and female harbour seals are roughly similar in size (80 - 100 kg), though males are generally larger than females. The annual life cycle of the species comprises: aquatic mating (courtship and oestrous) in July; gestation, parturition and lactation in June-July and moult in August-September. Harbour seals spend more time on land during parturition, lactation and moult (Thompson *et al.*, 1994; Thompson *et al.*, 1998) and, as income breeders, they adjust food intake concurrently with breeding. This is seen in a marked restriction in foraging range during early lactation (Thompson *et al.*, 1994) and longer trips during late lactation (Bowen *et al.*, 1992; Boness *et al.*, 1994; Thompson *et al.*, 1994). Outside these times they return to land regularly to rest following periods of foraging at sea. Large scale electronic tagging studies around Britain have revealed regional differences in the foraging behaviour of harbour seals (Cunningham *et al.*, 2009; Sharples *et al.*, 2012). Harbour seals in the west and north of Scotland made short distance and duration trips (<25 km and 1-2 days) while North Sea harbour seals made much longer distance and duration foraging trips (<100 km and 1 – 6 days, Sharples *et al.*, 2012).

Grey seals are larger than harbour seals and show strong sexual size dimorphism; males can weigh over 300 kg and females typically weigh 150-200 kg. Grey seals return regularly to land to rest and spend more time on land during the breeding season August-December and the moult December-April. There is a clockwise cline in mean birth date and therefore breeding seasons around the UK, pups in southwest Britain are born August-September, in north and west Scotland in September-December and eastern England November to mid-December (SCOS, 2013). As capital breeders, grey seal females acquire the resources needed to support parturition and lactation in advance of their return to the breeding colony as poor maternal condition cannot be offset by foraging during the breeding season (Boyd, 2000). Grey seal movements at sea can be considered at two geographical scales: long and distant travel, and shorter repeated trips to local discrete offshore areas (McConnell *et al.*, 1999). These shorter (<2.5 days) foraging trips made up 88% of the trips to sea with seals returning to the same haul-out site from which they departed (McConnell *et al.*, 1999).

Body size differences have previously been used as an indicator of resource partitioning because of their associated foraging traits such as effective handling of prey in Darwin's finches, *Geospiza* spp, and coyotes, *Canis latrans* (Boag and Grant, 1984; La Croix *et al.*, 2011). Furthermore, physiological limits can also be determined by body size, for example diving depth and duration is usually linked to body size (*e.g.*, Weise *et al.*, 2010). For seals around Britain, adult grey seals are larger than adult harbour seals but juveniles of both species and sub-adult grey seals and adult harbour seals overlap in body size.

Differences in breeding and main foraging times are apparent in harbour and grey seal annual cycles; during autumn and winter grey seals spend more time on land and harbour seals spend more time away from haul-out sites, a pattern which is apparent throughout their range (Thompson *et al.*, 1989; Boyd and Croxall, 1996; Lowry *et al.*, 2001; Reder *et al.*, 2003; Simpkins *et al.*, 2003). The reverse is true in spring and summer when harbour seals spend more time on land (*e.g.*, Thompson *et al.*, 1994; Thompson *et al.*, 1998) and grey seals more time at-sea (Figure 5.2, Russell *et al.*, In Review). This difference in breeding and foraging chronology may reflect how these sympatric high level predators partition their niches on an annual basis.



A) B)

Figure 5.2: Probability of resting for male (blue lines) and female (red lines) harbour seals (A) and grey seals (B) throughout the year. The grey area denotes no telemetry data due to tags falling off during the moult. Figure provided by (Russell *et al.*, In Review).

Major seasonal changes in body mass, composition and energy reserves prior to reproduction have been reported in pinnipeds including Californian sea lions, *Zalophus californianus* (Schusterman and Gentry, 1971), grey seals (Sparling *et al.*, 2006) and harp seals, *Phoca groenlandica* (Chabot and Stenson, 2002). Seasonal changes in metabolic rates have also been reported in grey seals (Boily and Lavigne, 1997; Sparling *et al.*, 2006), harbour seals (Rosen and Renouf, 1998) and harp seals (Renouf and Gales, 1994). Furthermore, in grey seals, seasonal and sex-related changes have been reported in energy storage (Beck *et al.*, 2003a) as well as foraging behaviour (Beck *et al.*, 2003c) and increased foraging effort nearing the breeding season is considered a strategy to maximise energy accumulation prior to reproduction.

Adult female grey seals have seasonal patterns in energy storage (total body mass and fat content) and foraging behaviour that appear to maximize the allocation of energy to reproduction, a period of both high energy demand and low food availability (Sparling *et al.*, 2006). However, in harbour seals, seasonal changes in metabolism were found not to be linked to the annual life cycle but were in response to the energy used/ activity of the seals (Rosen and Renouf, 1998).

5.1.3 Diet composition of pinnipeds around Britain

Essential information for assessing competition between harbour and grey seals for prey includes which species of fish are taken. Direct observations of prey consumption is rare in pinnipeds, consequently analysis of hard prey remains recovered from scats collected at haul-out is has become an established technique for estimating pinniped diet (reviewed in Tollit *et al.*, 2010).

5.1.3.1 Diet of harbour seals

Regional and seasonal differences in the diet of harbour seals around Britain were described in Chapter 3. On the east coast of Scotland sandeel (*Ammodytidae*) and flatfish were the most important prey, with sandeel dominating in the north and flatfish in the south. In the southern North Sea, sandy benthic species, flatfish, gadoids and sandeel were important seasonal prey. In the Northern Isles; sandeel or scorpion fishes dominated the diet depending on the season with large gadoids important as additional prey. In Orkney and Shetland, sandeel peaked in autumn and pelagic prey in summer and spring; large gadoid prey were also consistently important in the diet. In the Outer Hebrides in summer, *Trisopterus* spp, pelagic, gadoid and scorpion fishes and sandeel were all important prey. In the Inner Hebrides, large gadoids dominated the diet throughout most of the year with important seasonal contributions of pelagic species. Large changes in the diet of harbour seals from earlier studies were not observed when compared to this most recent study of diet (Chapter 3).

5.1.3.2 Diet of grey seals

The most recent estimates of grey seal diet around Britain are from studies conducted in 2002 (Hammond and Grellier, 2006; Hammond and Harris, 2006). In the North Sea, sandeel, cod (*Gadus morhua*), other gadoids and plaice (*Pleuronectes platessa*) were the most important prey. Marked changes were found in diet composition between 2002 and a 1985 study (Hammond *et al.*, 1994a); although the core species remained similar the proportions they contributed were different both regionally and seasonally (Hammond and Grellier, 2006). In the southern North Sea, benthic prey (dragonet, *Callionnymus lyra* and sea scorpions, *Taurulus bubalis*) were more important and sandeel less important in 2002 than in 1985 and considerably less cod and much more whiting (*Merlangius merlangus*) were consumed in 2002 compared to 1985. Changes were generally less pronounced in the central North Sea; the percentage of gadoids in the diet was lower and the percentage of sandeel was higher in 2002. Within the gadoids, the percentage of cod in the diet overall declined almost 5-fold, and the percentage of haddock (*Melanogrammus aeglefinus*) increased by an order of magnitude. In Orkney, the change in diet was dominated by an increase in the percentage of gadoids and a decrease in the percentage of sandeel.

In a concurrent study on the west coast of Scotland in 2002, the main prey of grey seals in the Hebrides were sandeel, large gadoids and herring, *Clupea harengus* (Hammond and Harris, 2006). The diet in the Inner Hebrides consisted of: dragonet, sandeel, cod and haddock in the northern Inner Hebrides, sandeel early in the year in the Minch and cod, haddock, ling (*Molva molva*) and sprat (*Sprattus sprattus*) in the rest of the year and sandeel and cod in the southern Inner Hebrides. Sandeel dominated the diet of grey seals in the northern Outer Hebrides with herring and cod seasonally important. At the Monach Isles, sandeel dominated in autumn/winter and herring in spring/summer with gadoids making up the rest of the diet. In the southern Outer Hebrides sandeel and gadoids were dominant and plaice was important in spring and summer. Compared to a previous study of grey seal diet on the west of Scotland in 1985 (Hammond *et al.*, 1994b) there were limited changes in grey seal diet composition in the Hebrides. The main difference detected was a decrease in the proportion of sandeel and an increase in the proportion of herring in 2002 compared to 1985 (Hammond and Harris, 2006).

5.1.4 Aims of this study

Interspecific competition for food with grey seals has been suggested as a potential cause of the decline of harbour seals around Britain (SCOS, 2009). Major declines in several harbour seal populations around Scotland have been documented since 2000 including 75% in Orkney, 30% in Shetland and 85% in the Firth of Tay (Lonergan *et al.*, 2007; SCOS, 2013). Conversely, grey seal populations around Britain are either increasing or stable (SCOS, 2013). Based on pup production, colonies in the North Sea are growing rapidly, while colonies in the Northern Isles and west of Scotland have shown very little change over several years (SCOS, 2013).

Following the identification of major declines in harbour seals in some areas around Scotland (SCOS, 2006; Lonergan *et al.*, 2007) targeted research programmes were initiated to increase monitoring to confirm the magnitude and geographical extent of the declines. In 2009, the Special Committee on Seals (SCOS) recommended a further programme of work be developed to address the specific question; do grey and harbour seals compete for food, and is the decline of harbour seals in some areas linked to this competition for prey?

This study compares the diet of harbour and grey seals around Britain. I explore whether food may be limiting to harbour seal populations by comparing diversity in species richness and evenness, percentage diet composition and diet quality between harbour and grey seal diet seasonally and regionally around Britain.

Differences in breeding and the main foraging times are apparent in harbour and grey seal annual cycles; during autumn and winter grey seals spend more time on land and harbour seals spend more time away from haul-out sites, a pattern which is apparent throughout their range (Thompson *et al.*, 1989; Boyd and Croxall, 1996; Lowry *et al.*, 2001; Reder *et al.*, 2003; Simpkins *et al.*, 2003). The reverse is true in spring and summer when harbour seals spend more time on land (*e.g.*, Thompson *et al.*, 1994; Thompson *et al.*, 1998) and grey seals more time at-sea (Figure 5.2, Russell *et al.*, In Review). This difference in breeding and foraging chronology may reflect how these sympatric high level predators partition their niches on an annual basis. The seals may exploit the same prey resources, but at different times of the year. For example, harbour seals which spend more time at sea in autumn/winter may have greater proportions of pelagic fish in their diet at this time of year as the majority of herring spawn around Britain between August and October (Marine Scotland, 2014a). Grey seals which spend more time at sea in spring/summer may have more sandeel in their diets as these fish emerge infrequently from the sea bed September – March except during spawning (December – January, Wright and Begg, 1997).

Differences in the at-sea distribution of harbour and grey seals may also be indicative of niche separation. Harbour seals have a more coastal distribution at-sea (Cunningham *et al.*, 2009; Sharples *et al.*, 2012; Jones *et al.*, 2013) than grey seals (McConnell *et al.*, 1992; McConnell *et al.*, 1999; Jones *et al.*, 2013) and diet may reveal differences in prey availability at a local level.

While dietary analysis does not take into account overlap or segregation in foraging behaviour or location, it can provide insights into inter-specific population dynamics. For example, I would expect that each species may have greater diet quality at critical life history times of the year *e.g.*, prior to pupping and lactation. Higher diet quality may be reflected in variation of the seasonal composition of the diet, with seals consuming prey with greater calorific density at times when improved body condition is required.

5.2 Methods

5.2.1 Scat collection, molecular analysis and extraction, identification and measurement of prey remains

All harbour seal scat collections were carried out as specified in Chapter 3. Grey seal haul-out sites were accessed using a helicopter during targeted surveys in December (breeding season) and February (moult). At other times of the year haul-out sites were accessed by boat *ad hoc* while conducing targeted harbour seal scat collection trips. Haul-out sites for both species were chosen based on annually updated maps showing the number and distribution of harbour and grey seals around the coast of Britain (Figure 5.3).

Techniques for laboratory processing of faecal samples and conducting molecular analysis were also the same as those described in detail in Chapter 3. For grey seal diet analysis, the degree by which each measured otolith was digested was graded using the traditional three grade system: grade 1 was pristine, grade 2 moderately digested and grade 3 considerably digested (Leopold *et al.*, 2001; Hammond and Grellier, 2006).

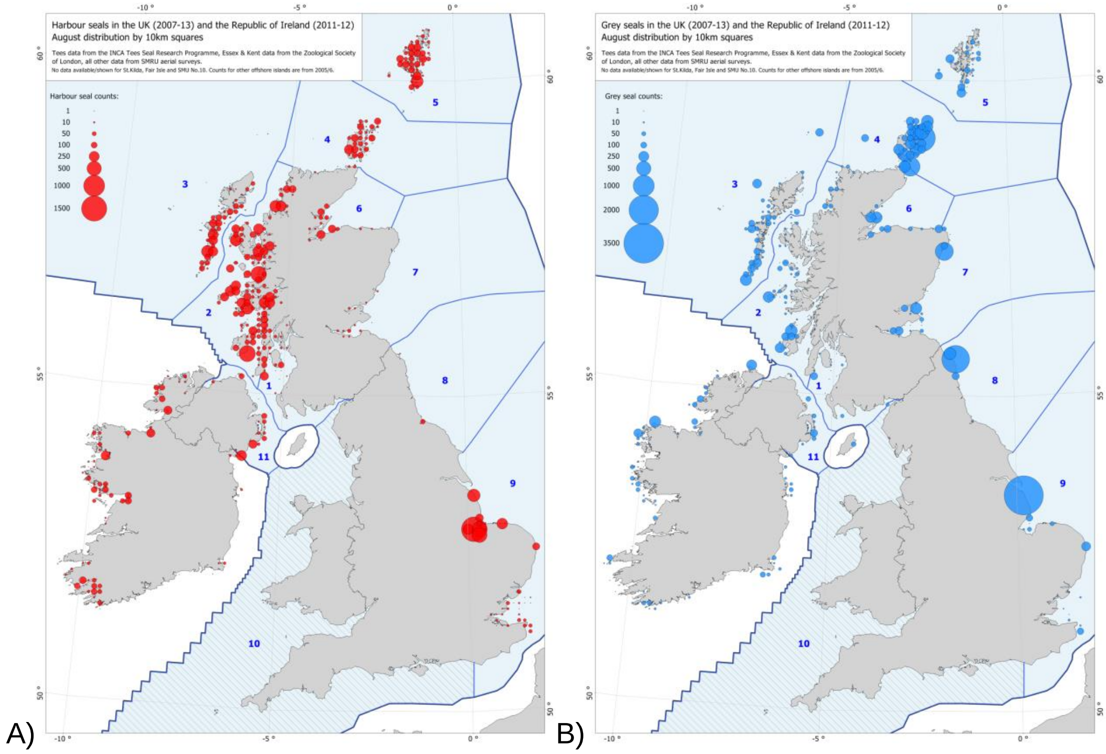


Figure 5.3: Number and distribution of (A) harbour seals and (B) grey seals around the British Isles, from surveys carried out in August between 2007 and 2013 (Duck and Morris, 2014). The geographic regions are: 1) SW Scotland, 2) W Scotland, 3) Western Isles, 4) N Coast & Orkney, 5) Shetland, 6) Moray Firth, 7) E Scotland, 8) NE England, 9) SE England, 10) W England & Wales, 11) Northern Ireland.

5.2.2 Diversity of prey, estimation of diet composition and diet quality

Diet diversity was examined using rarefied estimates of species richness and species evenness (as described in Chapter 3). Diet composition is presented as an estimate of the percentage contribution to the diet of both individual species and prey groups; this method and the method to estimate variability in composition is described in detail in Chapter 3.

The average energy density represented in harbour and grey seal scats across regions and seasons was estimated following the method described in Chapter 3. Differences in diet quality were investigated using generalised linear models (GLM) with a factorial analysis of variance (ANOVA) design for categorical variables, a Gaussian error distribution and identity link function. Seven models were tested: individual region, season and species models; region + season, region + species and species + season models; and a region + species + season model. The best model was selected using Akaike's Information Criterion (AIC, Akaike, 1973; Burnham and Anderson, 2002).

I further calculated the difference in the number of grams of fish that would need to be consumed for harbour and grey seals to have equivalent diet quality (measured as mean calorific density of the diet in kcal.g^{-1}).

For each region/season the mean weight of prey (g) that an average seal has to eat to attain the estimated mean calorific density of diet was calculated as:

$$Mean\ prey\ weight\ ingested(g) = \frac{Estimated\ daily\ energy\ requirement\ of\ an\ average\ seal}{Mean\ calorific\ density\ of\ diet}$$

where the estimated daily energy requirement of an average harbour seal is 4,680 kcal (Härkönen and Heide-Jørgensen, 1991) and an average grey seal is 5,497 kcal (Sparling and Smout, 2003).

I calculated whether the seals were eating more or less prey than the seasonal average by deducting the mean seasonal daily ingested prey weight from the region-specific estimated daily weight of prey ingested.

A comparison between harbour and grey seals was not attempted for this metric as grey seals have a larger body size than harbour seals (SCOS, 2013) and have greater estimated daily energy requirements (5,497 kcal, Sparling and Smout, 2003) than harbour seals (4,680 kcal, Härkönen and Heide-Jørgensen, 1991). In order to balance their energy budgets grey seals need to consume more prey than harbour seals and so comparison across seal species is restricted to the relative measure of diet quality; diet calorific density (cal.g^{-1}).

5.2.3 Diet sampling

To allow for a meaningful comparison of harbour and grey seal diet metrics, scats were grouped across some regions and seasons. This was necessary because harbour and grey seal diet around Britain is usually estimated based on different regional scales and seasonal timing, based on species distribution (*e.g.*, Thompson *et al.*, 1994; SCOS, 2013), movement (*e.g.*, Matthiopoulos *et al.*, 2004; Sharples *et al.*, 2012; Jones *et al.*, 2013) and annual life cycle (*e.g.*, Bonner, 1972; SCOS, 2013) of each species.

Seasonal variation in harbour seals is best examined according to the following seasons: spring (March – May), summer (June – August, pupping and moult), autumn (September – November) and winter (December - February, Sharples *et al.*, 2009 and Chapter 3). Grey seal diet has previously been examined according to quarters of the year, partly to match with fisheries statistics: quarter 1 (January – March, moult), quarter 2 (April – June), quarter 3 (July – September) and quarter 4 (October - December, breeding, Hammond and Grellier, 2006; Hammond and Harris, 2006).

Spatial distribution of harbour seals around Britain is described here based on the nine Scottish seal Management Regions and The Wash (see Chapter 3). Previous studies of grey seal diet analysis have focused on six regions: Inner and Outer Hebrides, subdivided into three areas each (Figure 5.4) and four regions in the North Sea: southern North Sea, central North Sea, Orkney and the northern North Sea (including the Moray Firth), and Shetland (Figure 5.5).

Care was taken to choose seasons which best reflected the annual life cycle (Bonner, 1972) and at-sea and haul-out behaviour of both harbour and grey seals around Britain (Matthiopoulos *et al.*, 2004; Sharples *et al.*, 2012; Jones *et al.*, 2013). It is more difficult to find and collect harbour seal scats during October-March and grey seal scats during April-September.

Seasons were therefore grouped into larger seasonal periods: “spring/summer” constituted the harbour seal seasons of spring and summer (March-August) and the grey seal quarters 2 and 3 (April-September). The “autumn/winter” season constituted the harbour seal seasons autumn and winter (September-May) and the grey seal quarters 4 and 1 (October-March).

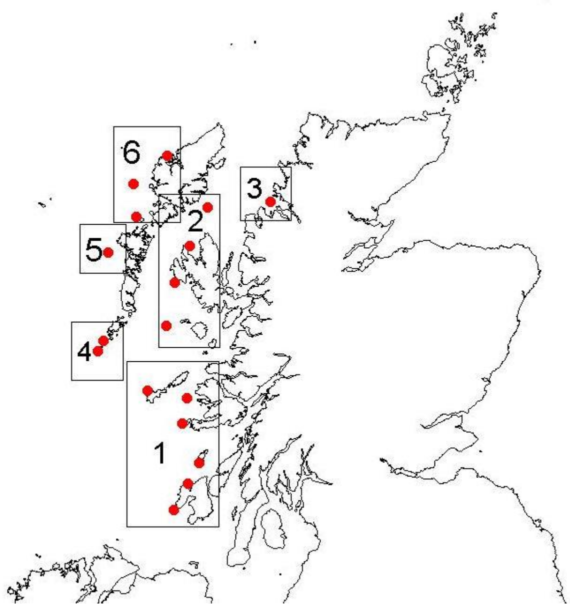


Figure 5.4: Sites where grey seal scats were collected in 2002 on the west coast of Scotland. The numbered regions are: 1. South Inner, 2. Minch, 3. North Inner, 4. South Outer, 5. Monach Isles and 6. North Outer. Map reproduced from Hammond and Harris (2006).

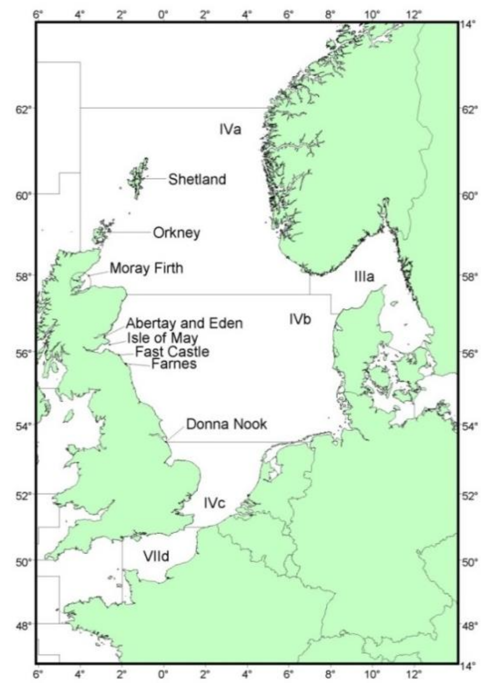


Figure 5.5: Locations of grey seal haul-out sites, within ICES Divisions, from which faecal samples were collected in the 2002 assessment of grey seal diet. Reproduced from Hammond and Grellier (2006).

Regions were either grouped or subdivided to best represent the comparison of both species. They included: southern North Sea (harbour seal region The Wash and grey seal haul-outs north (Donna Nook) and south (Blakeney Point) of The Wash), southeast Scotland (Firth of Forth, Isle of May, Rivers Tay and Eden and River Ythan), Moray Firth, Orkney, Shetland, Outer Hebrides and Inner Hebrides. Scat collections from the Farne Islands were not included in this dietary comparison.

5.3 Results

5.3.1 Diet sampling

There was variation in the number of harbour and grey seal scats containing hard prey remains across the regions and seasons (Table 5.1). The number of scats collected in spring/summer (SS) and autumn/winter (AW) in southeast Scotland (harbour seals) and SS in the Inner Hebrides (grey seals) was low and caution should be used interpreting these results. Due to the small sample size of scats and otoliths/beaks recovered in the Outer Hebrides in AW, harbour seal diet analysis was not conducted for this region/season.

5.3.2 Diet diversity

Standardised (rarefied) diversity metrics were calculated from the total numbers of otoliths/beaks recovered from individual scats (Appendix 5.1). Variation in species richness and evenness of prey in the diet of harbour and grey seals around Britain was examined within each region and season (Table 5.2 A-E). The rarefied species richness was smaller than the observed species richness as expected; standardised species richness is hereafter referred to simply as species richness. Both species richness and evenness were rarefied within each region/season combination and, as such, comparisons across regions or seasons within a region should not be made.

5.3.2.1 Southern North Sea

In the southern North Sea species richness was similar for harbour and grey seals within each season (S = 21 and 24 in SS and S = 23 and 22 in AW, respectively, Table 5.2 A). Species evenness, however, showed more variation between the two species. Grey seals had a very uneven diet (PIE= 0.14 and 0.30, SS and AW, respectively,

Table 5.2 A) compared to a much more even spread of prey in the diet of harbour seals (PIE = 0.77 and 0.81, SS and AW, respectively, Table 5.2 A).

Table 5.1: Number of harbour and grey seal scat samples containing hard prey remains (fish otoliths and cephalopod beaks), the total number of hard prey remains recovered and the number of otoliths/beaks measured for each season (SS = spring/ summer and AW = autumn/ winter) and region.

		Scats containing otoliths/beaks		Otoliths/ beaks recovered		Otoliths / beaks measured	
Region	**Season**	**Harbour**	**Grey**	**Harbour**	**Grey**	**Harbour**	**Grey**
Southern	SS	145	86	4148	4401	2790	1899
North Sea	AW	143	75	2790	3277	1919	1548
SE	SS	22	107	2018	4667	716	1998
Scotland	AW	17	162	4208	5105	1419	2516
	SS	192	29	17037	2740	6452	865
Moray Firth	AW	73	90	3484	7991	1506	2905
	SS	140	57	4932	1332	2813	767
Orkney	AW	117	563	1529	12292	986	7872
	SS	75	45	2145	492	1233	465
Shetland	AW	111	206	2622	3647	1642	2472
Outer	SS	99		1584		1180	
Hebrides	AW	13	274	799	5300	385	3419
Inner	SS	438	18	10627	104	8804	103
Hebrides	AW	391	314	7611	4904	5384	4056

5.3.2.2 Southeast Scotland

Harbour and grey seals consumed a similar number of prey species in SS (S = 10 and 8, respectively, Table 5.2 B). However, in AW there was a larger difference in species richness in the diet (S = 19 and 14, harbour and grey seals, respectively). Harbour seal diet was uneven in SS (PIE = 0.38) and more even in AW (PIE = 0.51). Grey seal diet showed greater unevenness than harbour seal diet in both SS and AW (Table 5.2 B).

5.3.2.3 *Moray Firth*

In the Moray Firth, harbour seals ate the greatest number of species in SS (S = 14, Table 5.2 C) and grey seals in AW (S = 27, Table 5.2 C). The diet of both species was very uneven in SS and AW (Table 5.2 C), although greater evenness was observed in harbour seal diet in both seasons (SS PIE = 0.10 and AW PIE = 0.12).

5.3.2.4 *Orkney*

In both SS (S = 31) and AW (S = 42) grey seals had greater species richness than harbour seals (Table 5.2 D). The consumption of prey species was more uneven in harbour seal diet than in grey seal diet in both seasons (Table 5.2 D). In SS, harbour seal PIE = 0.30 and grey seal PIE = 0.71 and in AW, harbour seal PIE = 0.41 and grey seal PIE = 0.57.

5.3.2.5 *Shetland*

The species richness of harbour and grey seals in Shetland in SS was similar (S = 17 and 20, respectively, Table 5.2 E). However, in AW, grey seal species richness was greater (S = 40 grey seals and S = 21 harbour seals). In both seasons, harbour seals had a more uneven diet than grey seals (Table 5.2 E) and this was most pronounced in SS (PIE = 0.54 and 0.77, respectively, Table 5.2 E).

5.3.2.6 *Outer Hebrides*

Species richness and evenness of the diet of harbour and grey seals could not be compared seasonally in this region. In SS, harbour seals species richness = 20 and prey were eaten in relatively even quantities (PIE = 0.73, Table 5.2 F). In AW, grey seals species richness = 41 (Table 5.2 F) and there was moderately even distribution of abundance amongst species (PIE = 0.46, Table 5.2 F).

5.3.2.7 *Inner Hebrides*

Harbour seals had greater species richness in SS in the Inner Hebrides (S = 19, Table 5.2 G) and in AW harbour and grey seal species richness was similar (S = 46 and 49, respectively). A high degree of evenness in the number of each prey species consumed was observed for both harbour and grey seals in both seasons (PIE = 0.82 SS and PIE = 0.87 AW, harbour seals and PIE = 0.82 SS and PIE = 0.77 AW, grey seals, Table 5.2 G).

Table 5.2: Variation in the number of scats collected with hard prey remains, observed and rarefied species richness and species evenness. Comparisons across regions or seasons within a region should not be made for either species richness or evenness as data were rarefied within each region/ season combination.

A) Southern North Sea

	No. scats	Observed No. prey species	Species richness (S)	Species Evenness (PIE)
Spring/Summer				
Harbour seal	145	26	21	0.77
Grey seal	86	28	24	0.14
Autumn/Winter				
Harbour seal	143	29	23	0.81
Grey seal	75	24	22	0.3

B) Southeast Scotland

	No. scats	Observed No. prey species	Species richness (S)	Species Evenness (PIE)
Spring/Summer				
Harbour seal	22	12	10	0.38
Grey seal	107	18	8	0.04
Autumn/Winter				
Harbour seal	17	22	19	0.51
Grey seal	162	31	14	0.24

C) Moray Firth

	No. scats	Observed No. prey species	Species richness (S)	Species Evenness (PIE)
Spring/Summer				
Harbour seal	192	28	14	0.1
Grey seal	29	10	9	0.01
Autumn/Winter				
Harbour seal	73	21	18	0.12
Grey seal	90	32	27	0.07

D) Orkney

	No. scats	Observed No. prey species	Species richness (S)	Species Evenness (PIE)
Spring/Summer				
Harbour seal	140	34	24	0.3
Grey seal	57	35	31	0.71
Autumn/Winter				
Harbour seal	117	25	23	0.41
Grey seal	563	61	42	0.57

E) Shetland

	No. scats	Observed No. prey species	Species richness (S)	Species Evenness (PIE)
Spring/Summer				
Harbour seal	75	25	17	0.54
Grey seal	45	24	20	0.77
Autumn/Winter				
Harbour seal	111	24	21	0.45
Grey seal	206	47	40	0.56

F) Outer Hebrides

	No. scats	Observed No. prey species	Species richness (S)	Species Evenness (PIE)
Spring/Summer				
Harbour seal	99	22	20	0.73
Autumn/Winter				
Grey seal	274	46	41	0.46

G) Inner Hebrides

	No. scats	Observed No. prey species	Species richness (S)	Species Evenness (PIE)
Spring/Summer				
Harbour seal	438	49	19	0.82
Grey seal	18	13	11	0.82
Autumn/Winter				
Harbour seal	391	52	46	0.87
Grey seal	314	53	49	0.77

5.3.3 Diet composition

The diet of harbour and grey seals around Britain is expressed as a percentage by weight for the seasons: spring/summer (SS) and autumn/winter (AW). Diet is summarised by prey type (gadoids, flatfish etc.) in Appendix 5. 2 A-G and Figure 5.6, and by species in Table 5.3. In Table 5.3 the major portion of the diet (> 75%) for each seal species in each season/region is highlighted in bold. The 95% confidence limits are presented by prey type and species in Appendices 5.3 and 5.4 respectively.

5.3.3.1 Southern North Sea

Harbour seal diet in the southern North Sea in SS was dominated by sandy benthic prey and supported by flatfish and sandeel, while grey seal diet was dominated by sandeel with lesser contributions of large gadoids (Appendix 5. 2 A and Figure 5.6 A). The AW diet of harbour seals consisted mostly of flatfish, large gadoids and sandy benthic prey and grey seal diet mostly: sandeel and scorpion fish (Appendix 5. 2 A and Figure 5.6 G).

The main prey species by percentage contribution to the diet in SS for harbour seals were: dragonet, sandeel, plaice and Dover sole (*Solea solea*) and grey seals: sandeel and whiting (Table 5.3 A). In AW the main prey for harbour seals were: whiting, dragonet, plaice, Dover sole, sandeel, lemon sole (*Microstomus kitt*) and bullrout (*Myoxocephalus scorpius*) and grey seals: sandeel, sea scorpion, dragonet, Dover sole and whiting (Table 5.3 A).

5.3.3.2 Southeast Scotland

In SS, the diet of harbour seals in southeast Scotland was dominated by sandeel and flatfish with lesser contributions of large gadoids (Appendix 5. 2 B and Figure 5.6 B). Grey seal diet was dominated by sandeel (Appendix 5. 2 B and Figure 5.6 B). In AW, flatfish dominated harbour seal diet supported by large gadoid, pelagic and cephalopod prey (Appendix 5. 2 B and Figure 5.6 H). Grey seal diet in AW was dominated by sandeel with lesser contributions of large gadoids and flatfish (Appendix 5. 2 B and Figure 5.6 H).

Overall, four harbour seal prey and one grey seal prey species made up greater than 75% of the diet in southeast Scotland in SS (Table 5.3 B). After sandeels, harbour seals ate mainly plaice, dab (*Limanda limanda*) and whiting while sandeel contributed > 80% to the diet of grey seals (Table 5.3 B). In AW, seven prey species made up greater than 75% of the diet of harbour seals and four prey species in grey seal diet. The main prey of harbour seals were: plaice, *Loligo* spp, whiting, sprat, mackerel (*Scomber scombrus*), dab and cod, and grey seals: sandeel, bullrout, plaice and cod.

5.3.3.3 Moray Firth

The diet of both seal species was strongly dominated by sandeel in both seasons (Appendix 5. 2 C and Figure 5.6 C and I). Other prey species played only a minor role in the diet (Table 5.3 C).

5.3.3.4 Orkney

Harbour seals in Orkney in SS ate mostly sandeel and large gadoids (Appendix 5. 2 D and Figure 5.6 D) and grey seals ate mostly large gadoids with lesser contributions of sandeel and pelagic prey (Appendix 5. 2 D and Figure 5.6 D). In AW, pelagic fish and large gadoids dominated the diet of harbour seals and large gadoids and sandeel the diet of grey seals (Appendix 5. 2Appendix 5. 2 D and Figure 5.6 J).

After sandeel, harbour seals in SS consumed mainly cod and saithe (*Pollachius virens*). Grey seal prey consumption was more catholic including: sandeel, saithe, herring, cod, bullrout, Norway pout and haddock (Table 5.3 D). In AW harbour seals consumed mostly: herring, cod, sandeel and sandeel while grey seals ate: sandeel, cod, herring, bullrout, saithe, and haddock (Table 5.3 D).

5.3.3.5 Shetland

In Shetland in both SS and AW, harbour seal diet was made up of mostly pelagic prey, large gadoids and sandeels (Appendix 5. 2 E and Figure 5.6 E). The SS diet of grey seals comprised mostly large gadoids, scorpion fish and sandeel and the AW diet mostly large gadoids and sandeel (Appendix 5. 2 E and Figure 5.6 K).

The main prey species in the SS diet of harbour seals were: herring, sandeel, saithe and dragonet and in grey seals: bullrout, saithe, sandeel and cod (Table 5.3 E). In AW the main prey species in the diet of harbour seals were: sandeel, saithe, herring and mackerel and in grey seal diet: sandeel, saithe, dragonet, cod, bullrout and ling (Table 5.3 E).

5.3.3.6 Outer Hebrides

Trisopterus species, pelagic species, large gadoids, scorpion fish and sandeel were the dominant prey groups ingested by harbour seals in SS (Appendix 5. 2 F and Figure 5.6 M). Grey seals in AW fed mostly on sandeel and large gadoids and to a lesser extent pelagic prey (Appendix 5. 2 F and Figure 5.6 M).

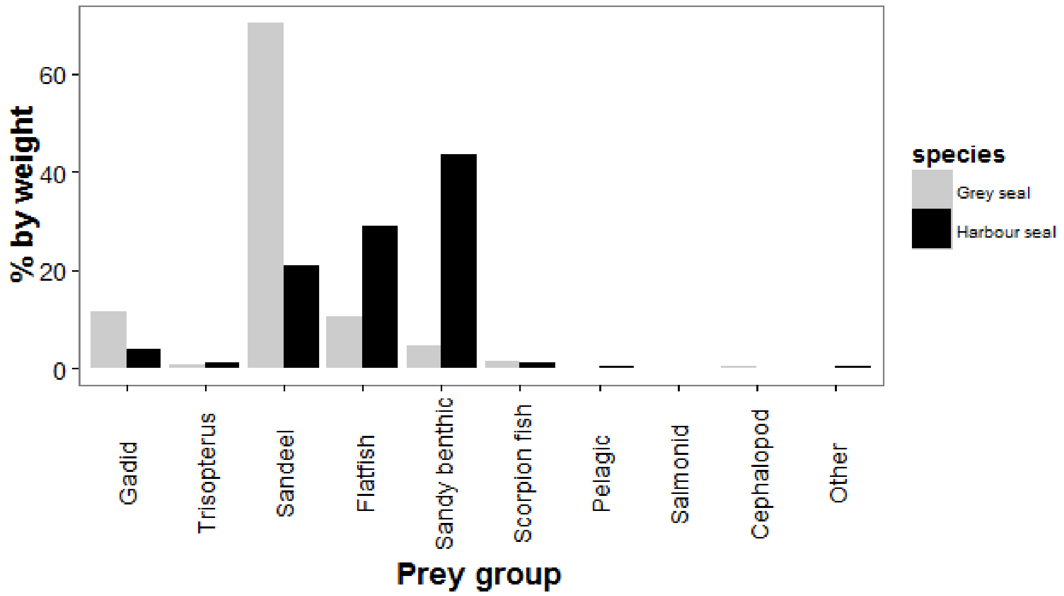
The main prey species of harbour seals in SS were: Norway pout, unidentified *Cottidae*, sandeel, mackerel, herring, cod and ling. The main prey species of grey seals in AW were: sandeel, herring, cod, ling, Norway pout and mackerel.

5.3.3.7 Inner Hebrides

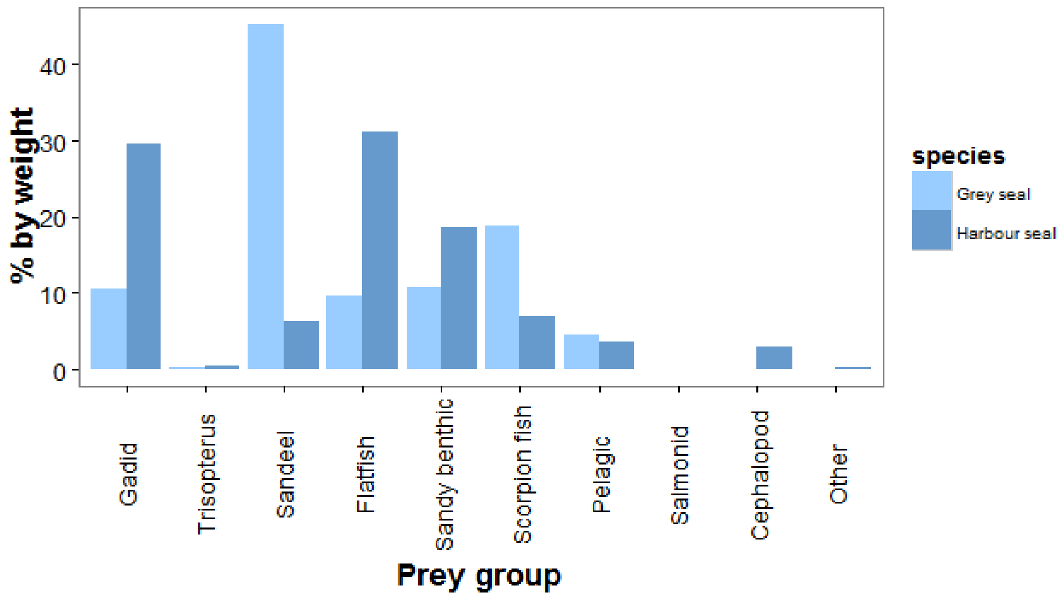
Large gadoids dominated the diet of harbour seals in SS in the Inner Hebrides (Appendix 5. 2 G and Figure 5.6 F). Lesser contributions were made by pelagic prey and *Trisopterus* species. Large gadoids also dominated the diet of grey seals in SS with the remainder of the diet made up of mostly sandy benthic prey and *Trisopterus* species Appendix 5. 2 G and Figure 5.6 F). In AW, harbour seals ate mostly large gadoids and pelagic prey and grey seals mostly large gadoids and sandeel (Appendix 5. 2 G and Figure 5.6 L).

Harbour seal diet in SS consisted mostly of: whiting, mackerel, haddock, cod, blue whiting, herring, Norway pout, poor cod, ling, and dragonet. The main prey species in the diet of grey seal diet in SS were: dragonet, ling, Norway pout and sandeel (Table 5.3 G). In AW, harbour seals ate mostly: dragonet, herring, mackerel, haddock, poor cod, whiting, cod, sandeel and blue whiting. Grey seal diet comprised: sandeel, cod, dragonet, ling, ballan wrasse (*Labrus bergylta*), Norway pout, herring, poor cod, blue whiting, haddock and whiting nge (Table 5.3 G).

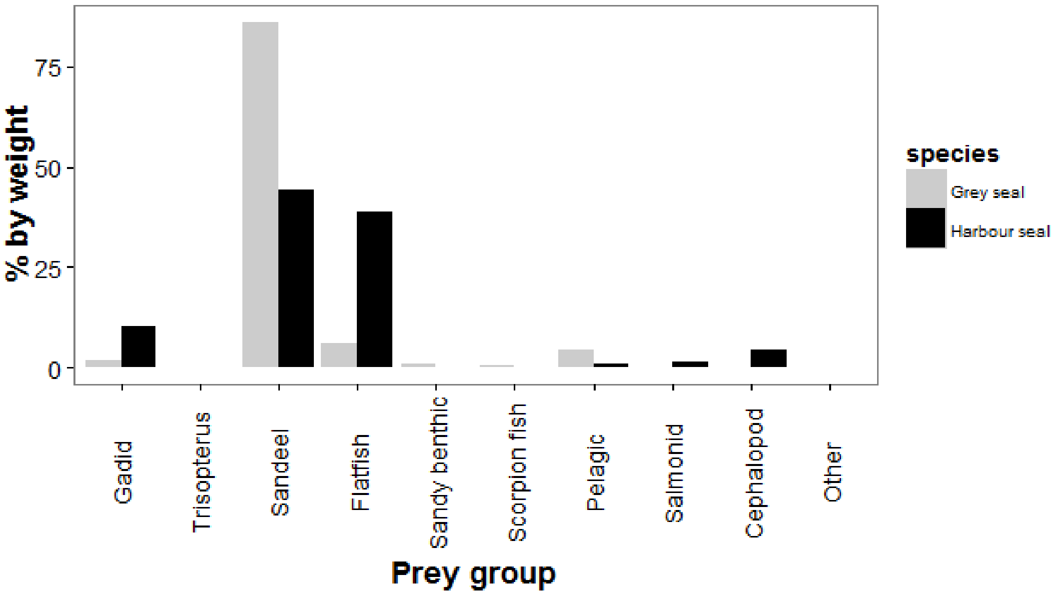
A) Spring/summer: southern North Sea



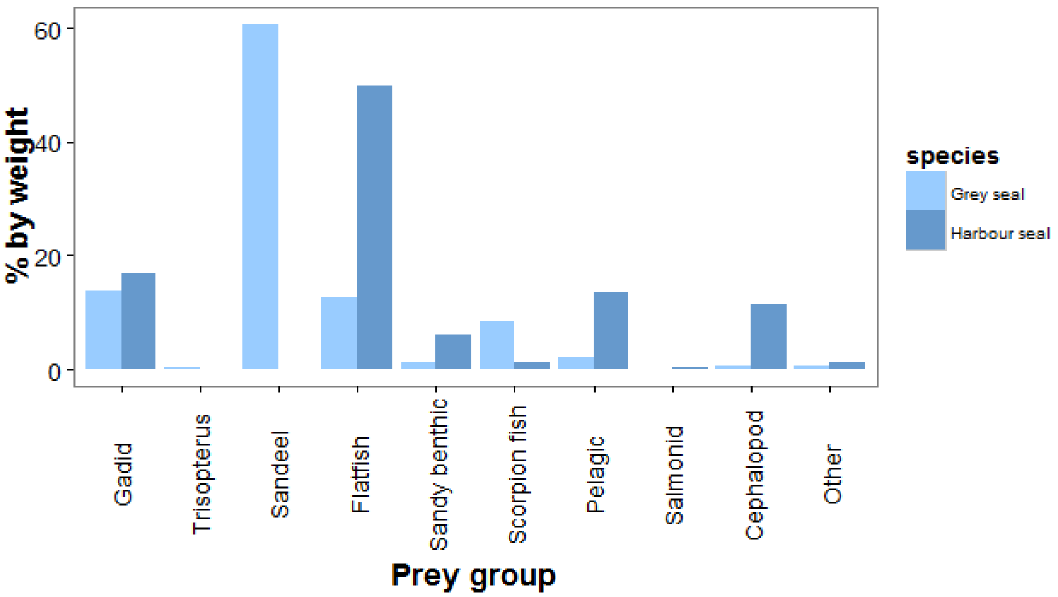
B) Autumn/winter: southern North Sea



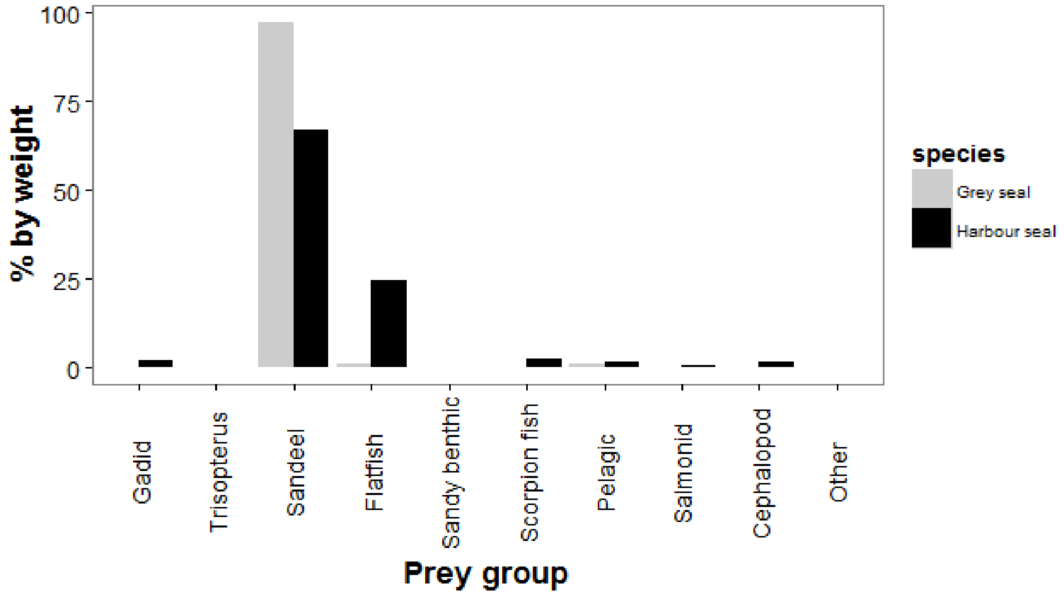
C) Spring/summer: southeast Scotland



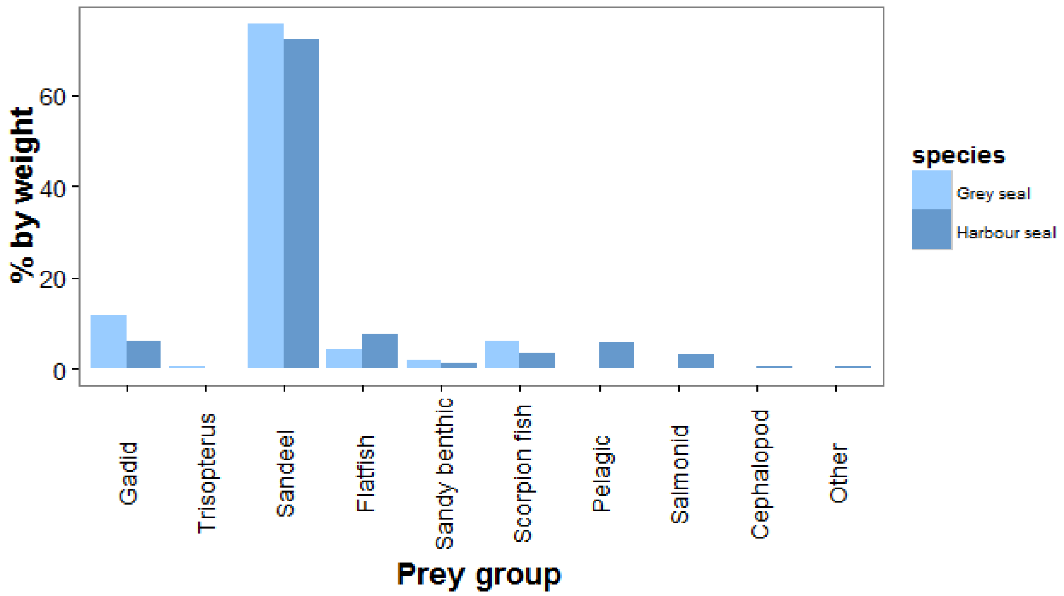
D) Autumn/winter: southeast Scotland



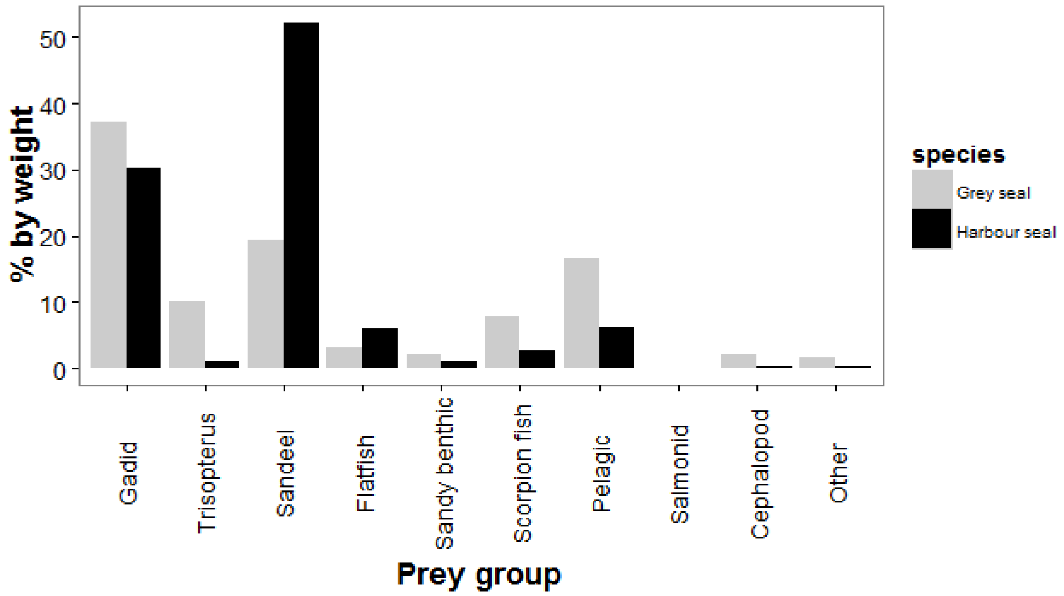
E) Spring/summer: Moray Firth



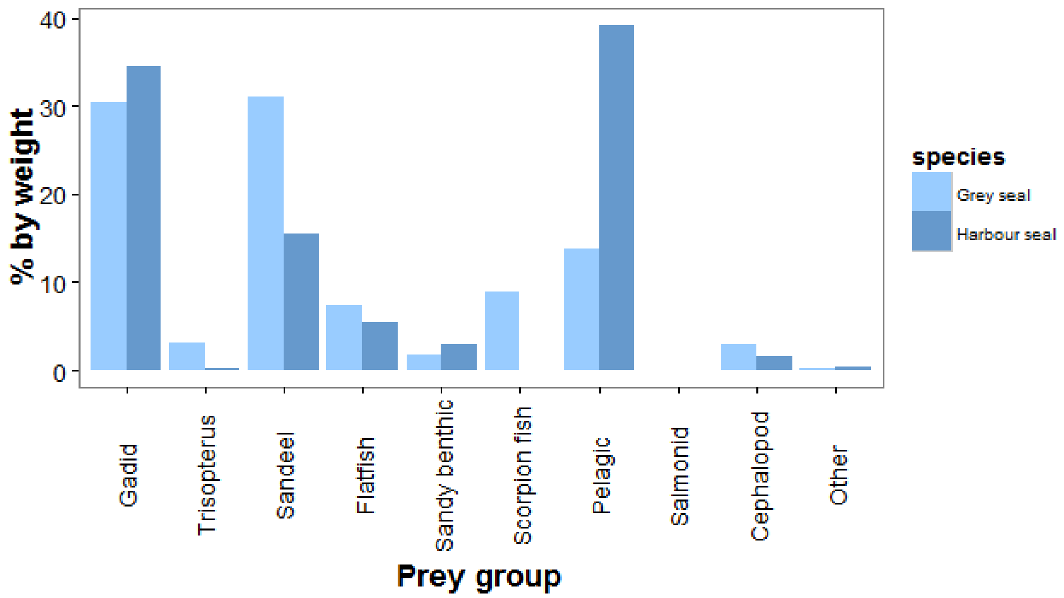
F) Autumn/winter: Moray Firth



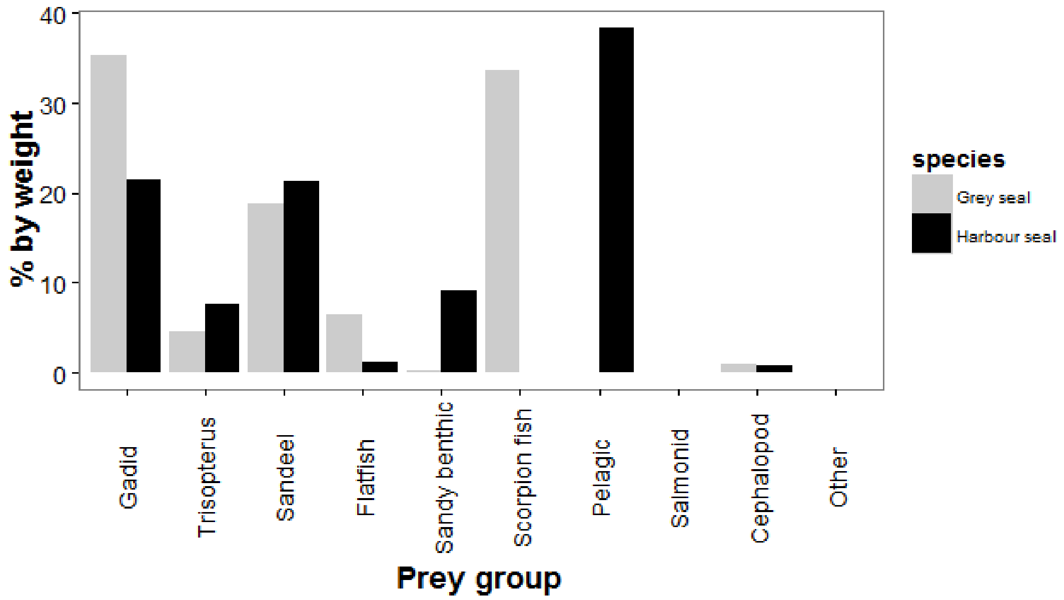
G) Spring/summer: Orkney



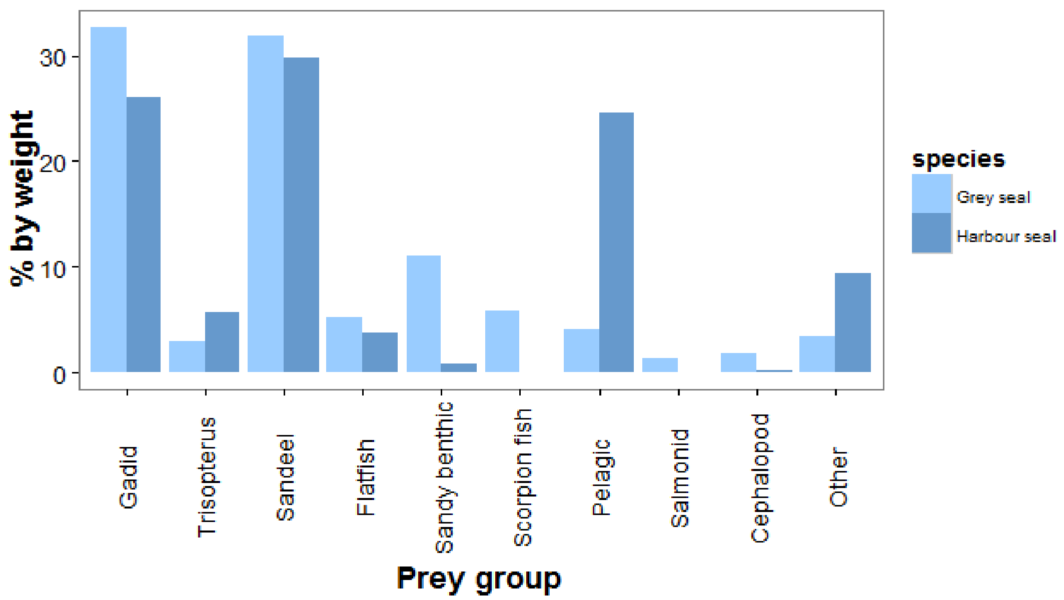
H) Autumn/winter: Orkney



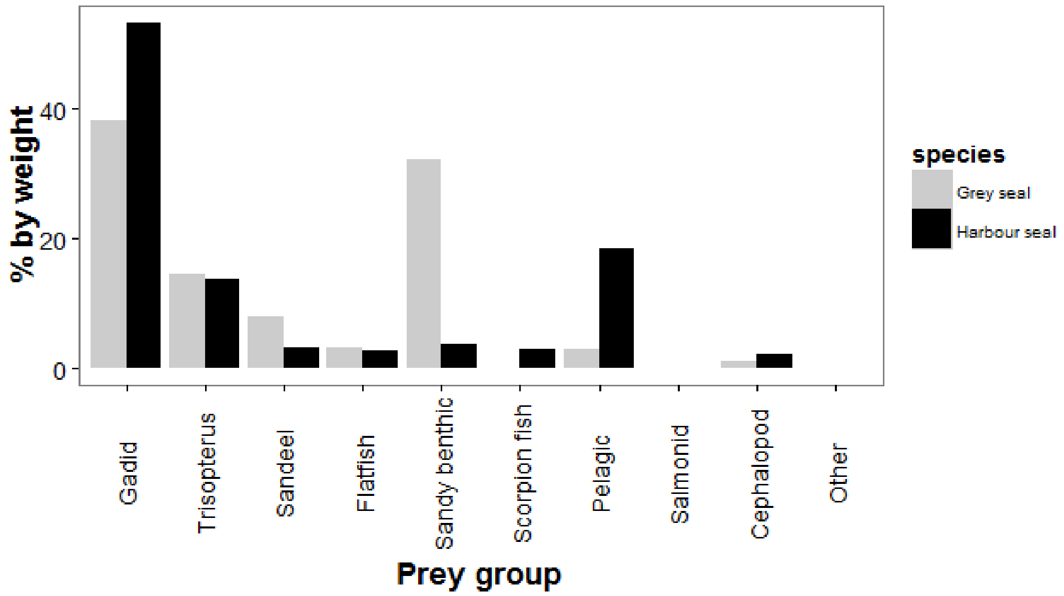
I) Spring/summer: Shetland



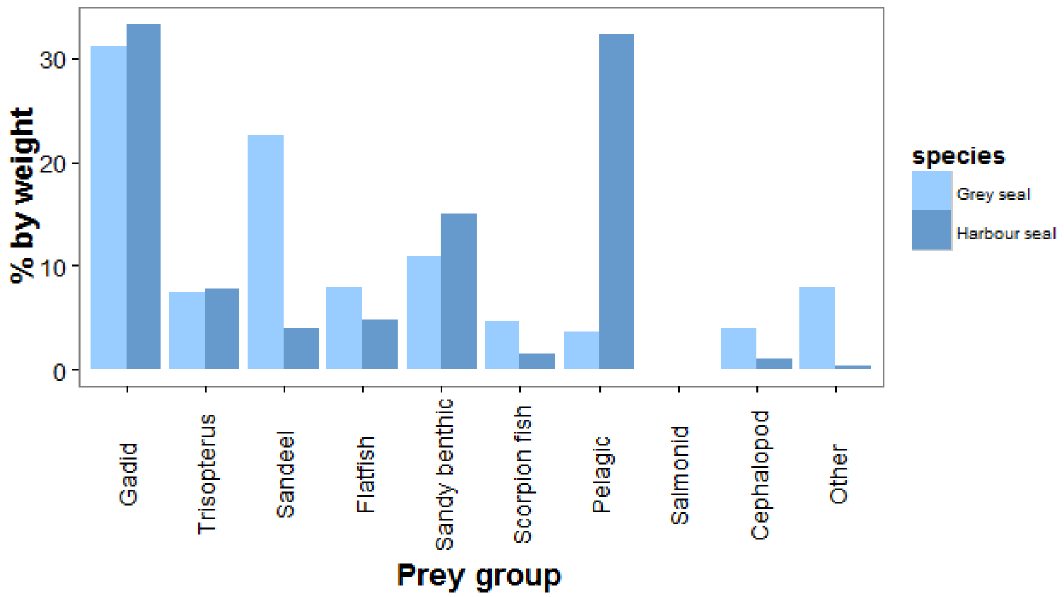
J) Autumn/winter: Shetland



K) Spring/summer: Inner Hebrides



L) Autumn/winter: Inner Hebrides



M) Spring/summer harbour seals and autumn/winter grey seals: Inner Hebrides

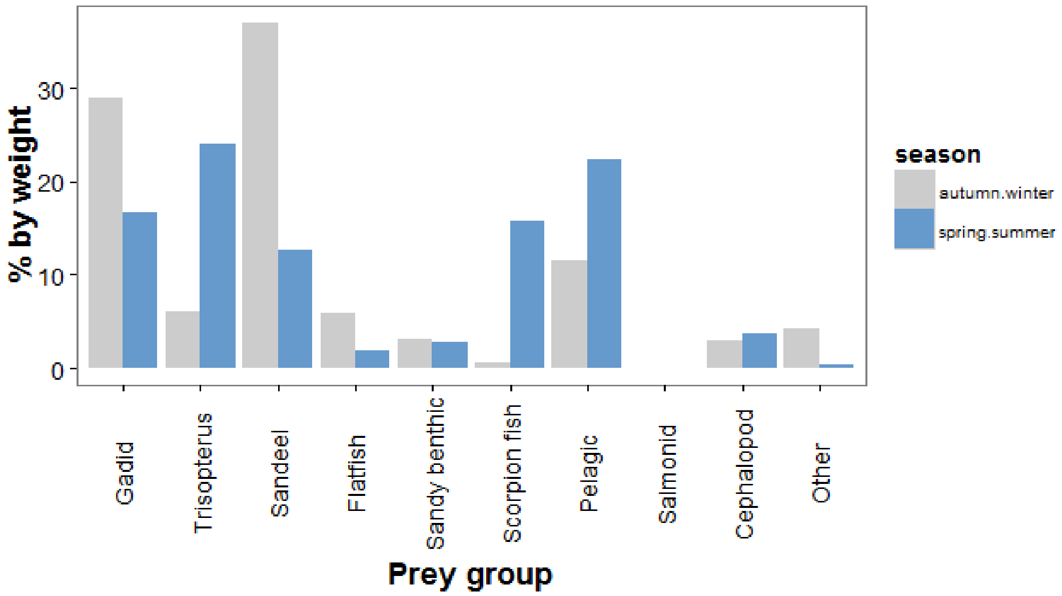


Figure 5.6: Variation in the diet of harbour and grey seals during spring/ summer (SS) and autumn/ winter (AW). Diet is expressed as the percentage of each prey group in the diet, by weight. (A) SS : southern North Sea, (B) AW : southern North Sea, (C) SS: southeast Scotland, (D) AW: southeast Scotland, (E) SS: Moray Firth, (F) AW: Moray Firth, (G) SS: Orkney, (H) AW: Orkney, (I) SS: Shetland, (J) AW: Shetland, (K) SS: Inner Hebrides, (L) AW: Inner Hebrides, (M) represents diet estimates for grey seals only in autumn/winter (grey bars) and harbour seals only in spring/ summer (blue bars): Outer Hebrides.

Table 5.3: Seasonal variation in the diet of harbour and grey seals expressed as the percentage of each species in the diet by weight. Prey species listed are those contributing > 5% in any season for either seal species. Numbers in bold represent those prey species required to reach 75% of the diet of each seal species in each season and region.

A) Southern North Sea

	Spring/ Summer		Autumn/ Winter	
Species	**harbour**	**grey**	**harbour**	**grey**
Cod	2.3	5.3	1.2	2.3
Whiting	1.5	**5.9**	**28.3**	**6.0**
Plaice	**8.3**	4.1	**8.2**	1.2
Lemon sole	1.8	0.4	**6.0**	1.5
Dover sole	**8.2**	3.8	**7.7**	**6.2**
Sandeel	**20.8**	**70.5**	**6.4**	**45.3**
Dragonet	**38.1**	4.2	**16.5**	**10.6**
Goby	5.1	0.0	2.0	0.0
Bullrout	0.8	1.0	**5.0**	5.6
Sea Scorpion	0.1	0.4	1.6	**12.2**

B) SE Scotland

	Spring/ Summer		Autumn/ Winter	
Species	**harbour**	**grey**	**harbour**	**grey**
Cod	2.4	0.5	**4.8**	**5.7**
Whiting	**7.9**	0.8	**8.6**	4.4
Plaice	**18.4**	1.9	**34.9**	**6.1**
Flounder (Butt)	7.4	0.0	3.9	0.1
Dab	**9.7**	0.0	**5.6**	2.8
Mackerel	0.0	0.1	**6.1**	0.0
Sprat	0.8	0.0	**7.3**	2.1
Sandeel	**44.4**	**86.1**	0.0	**60.7**
Bullrout	0.0	0.5	1.3	**6.3**
Loligo	4.2	0.2	**11.4**	0.5

C) Moray Firth

Species	Spring/ Summer harbour	Spring/ Summer grey	Autumn/ Winter harbour	Autumn/ Winter grey
Haddock	0.7	0.0	0.0	7.3
Plaice	7.6	0.6	**1.4**	0.9
Dab	**10.5**	0.3	**2.0**	0.6
Sandeel	**67.1**	**97.4**	**72.3**	**75.6**

D) Orkney

Species	Spring/ Summer harbour	Spring/ Summer grey	Autumn/ Winter harbour	Autumn/ Winter grey
Cod	**18.7**	**8.0**	**25.4**	**14.6**
Haddock	0.6	**5.0**	3.2	**5.1**
Saithe	**6.8**	**18.4**	2.0	**6.1**
Norway pout	0.0	**7.3**	0.0	1.4
Mackerel	1.1	0.6	**7.2**	0.3
Herring	5.0	**14.0**	**32.0**	**13.0**
Sandeel	**52.2**	**19.4**	**15.5**	**31.1**
Bullrout	0.8	**6.7**	0.0	**7.3**

E) Shetland

Species	Spring/ Summer harbour	Spring/ Summer grey	Autumn/ Winter harbour	Autumn/ Winter grey
Cod	0.1	**8.5**	1.6	**8.1**
Saithe	**7.9**	**19.9**	**21.9**	**16.7**
Ling	7.5	0.8	0.7	**3.7**
Poor cod	1.2	2.6	5.1	1.8
Norway pout	6.2	1.9	0.5	1.1
Mackerel	1.3	0.0	**10.3**	0.5
Herring	**37.0**	0.0	**14.3**	2.9
Sandeel	**21.3**	**18.8**	**29.7**	**31.9**
Dragonet	**9.1**	0.3	0.8	**10.9**
Bullrout	0.0	**28.5**	0.0	**5.0**
Sea Scorpion	0.0	5.2	0.0	0.6
Garfish	0.0	0.0	9.4	0.1

F) Outer Hebrides

Species	Spring/ Summer harbour	Spring/ Summer grey	Autumn/ Winter harbour	Autumn/ Winter grey
Cod	**3.5**			**9.5**
Ling	**2.6**			**7.2**
Norway pout	**19.3**			**3.8**
Mackerel	**12.3**			**0.8**
Herring	**7.3**			**10.5**
Sandeel	**12.7**			**37.0**
Unidentified Cottidae	**15.8**			0.0

G) Inner Hebrides

Species	Spring/ Summer harbour	Spring/ Summer grey	Autumn/ Winter harbour	Autumn/ Winter grey
Cod	**9.0**	0.0	**5.4**	**10.9**
Whiting	**12.0**	5.0	**5.5**	**1.2**
Haddock	**9.3**	3.4	**8.9**	**1.5**
Ling	**4.3**	**27.2**	3.0	**8.5**
Blue whiting	**8.9**	0.0	**3.5**	**1.5**
Poor cod	**5.8**	3.7	**5.6**	**2.3**
Norway pout	**7.0**	**10.7**	1.7	**4.8**
Mackerel	**10.4**	2.8	**14.7**	0.0
Herring	**7.1**	0.0	**14.9**	**3.5**
Sandeel	3.1	**8.0**	**4.0**	**22.6**
Dragonet	**3.6**	**32.0**	**14.9**	**10.8**
Ballan wrasse	0.0	0.0	0.1	**7.5**

5.3.4 Diet Quality

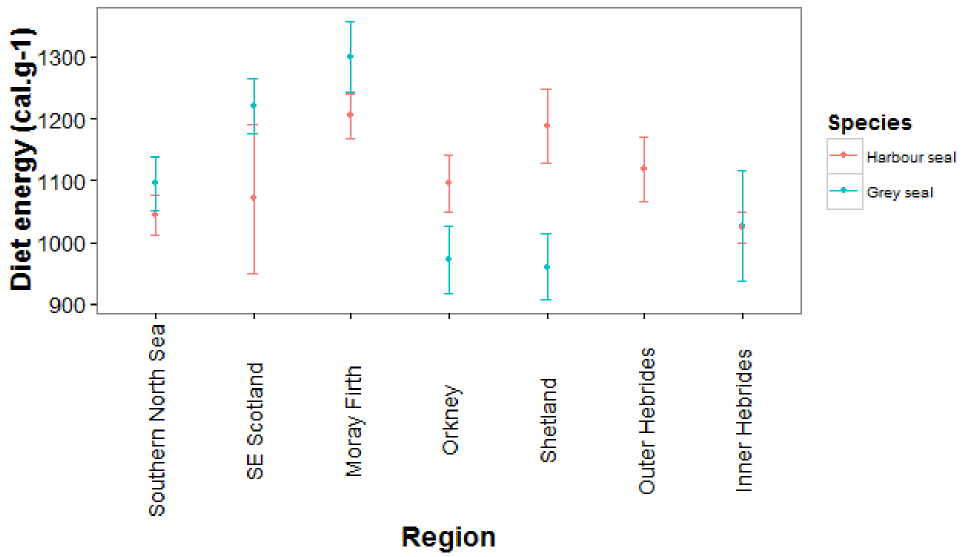
Where differences were observed in diet quality estimates, harbour seal diet quality was greater than that of grey seals (Table 5.4 and Figure 5.7). However, the range of mean energy densities for each region/season were similar: 989 – 1205 $cal.g^{-1}$ for harbour seals, and 960 – 1300 $cal.g^{-1}$ for grey seals (Table 5.4).

The GLM revealed differences in diet quality in each region, species and season (Table 5.5). The model with the lowest AIC included all covariates (model = region + species + season). The full model results indicate that overall; the diet of harbour seals was significantly higher than average and that diet in the Moray Firth was the highest quality. In the southern North Sea and Inner Hebrides diet quality was significantly lower than average (Table 5.5). The spring/summer diet was also significantly higher than average however, between the full model and model = region + species there was only a difference of 2 AIC units. This indicates that they both have similar support from the data and that there is only weak evidence for a seasonal effect.

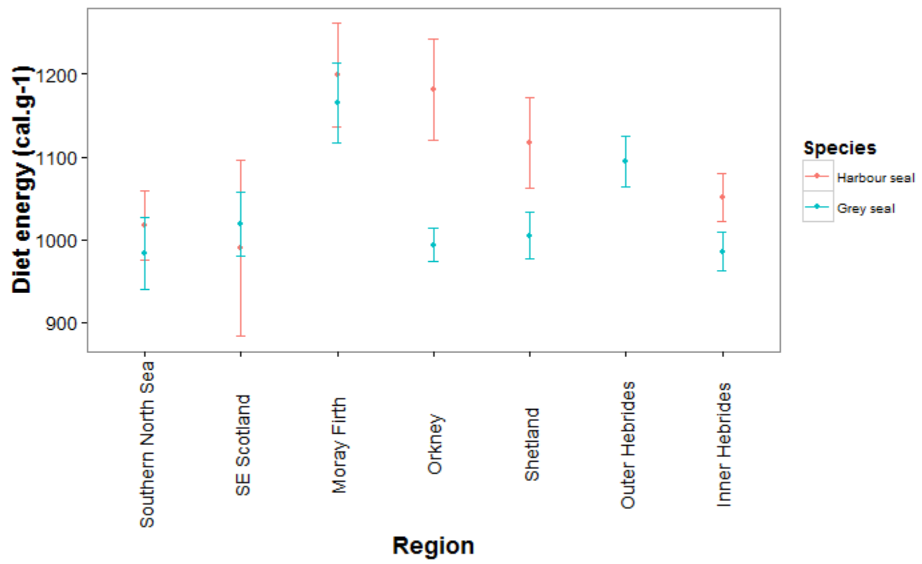
Table 5.4: Mean energy density (cal.g^{-1}) of the diet (SE) of harbour and grey seals

Spring/Summer	(i) Harbour seal			(ii) Grey seal		
Region	**Calorific density (cal.g-1)**	**(SE)**	**No. scats**	**Calorific density (cal.g-1)**	**(SE)**	**No. scats**
S. North Sea	1044	(16)	145	1095	(23)	86
SE Scotland	1070	(61)	22	1220	(23)	107
Moray Firth	1205	(18)	192	1300	(29)	29
Orkney	1095	(24)	140	971	(28)	57
Shetland	1188	(30)	75	960	(27)	45
Outer Hebrides	1118	(26)	99			
Inner Hebrides	1024	(13)	438	1026	(46)	18

Autumn/Winter	(i) Harbour seal			(ii) Grey seal		
Region	**Calorific density (cal.g-1)**	**(SE)**	**No. scats**	**Calorific density (cal.g-1)**	**(SE)**	**No. scats**
S. North Sea	1017	(22)	143	983	(22)	75
SE Scotland	989	(54)	17	1018	(20)	162
Moray Firth	1199	(32)	73	1165	(24)	90
Orkney	1181	(31)	117	994	(10)	563
Shetland	1117	(28)	111	1005	(15)	206
Outer Hebrides				1095	(15)	274
Inner Hebrides	1051	(15)	391	986	(12)	314



A)



B)

Figure 5.7: Diet quality estimates ± 95% confidence intervals for harbour (red) and grey seal (blue) in each region in (A) spring/summer and (B) autumn/winter.

Table 5.5: Summary results of the GLMs to investigate differences in diet quality across regions and species and seasons. A) Model diagnostics and AIC values. B) Parameter estimates for the region + species + season model.

A)

Model	**Null deviance**	**Null DF**	**Residual deviance**	**Residual DF**	**AIC**	
Species	270869128	4001	268346727	4000	55838	
Season	270869128	4001	268571194	4000	55842	
Region	270869128	4001	259636112	3995	55716	
Region+Species	270869128	4001	256231024	3994	55665	
Region+Season	270869128	4001	258179511	3994	55696	
Species+Season	270869128	4001	267445575	3999	55827	
Region+Species+Season	270869128	4001	255951698	3993	55663	*

* indicates the lowest AIC

B) Model = Region+Species+Season

Coefficients	**Value**	**SE**	**t-value**	**P**	
Intercept (Shetland)	1030.61	12.72	81.05	<0.01	*
Orkney	-18.13	14.87	-1.22	0.22	
Moray Firth	120.7	17.95	6.72	<0.01	*
SE Scotland	44.75	19.18	2.33	<0.05	*
Southern North Sea	-41.81	17.18	-2.43	<0.05	*
Outer Hebrides	52.48	17.73	2.96	<0.01	*
Inner Hebrides	-55.67	14.44	-3.86	<0.01	*
Harbour seal	56.46	9.58	5.90	<0.01	*
Spring/summer	19.45	9.32	2.09	<0.05	*

5.3.4.1 Harbour seals

The mean daily ingested prey weight required to meet the reported diet quality for each region ranged between 4.1 and 4.8 kg for harbour seals in SS (Table 5.6 A(i)) and 4.1 to 4.9 kg in AW (Table 5.6 B(i)). The mean daily ingested prey weight for harbour seals in SS and AW was very similar (4.4 and 4.5 kg, respectively).

Harbour seals in the Moray Firth and Shetland (4.1 kg) needed to eat the least prey by weight to attain their diet quality in SS, as did seals in the Moray Firth and Orkney (4.1 kg) in AW (5% less, relative to the seasonal mean, Table 5.6 A(i) and B(i)). In contrast, in SS, harbour seals in the Inner Hebrides (4.8 kg) and southern North Sea (4.7 kg) needed to eat the most prey by weight to attain their calorific density of diet, as did harbour seals in AW in SE Scotland (4.9 kg) and the southern North Sea, 4.8 kg (5% more than the seasonal mean, Table 5.6 A(i) and B(i)).

5.3.4.2 Grey seals

The mean daily ingested prey weight required to meet the estimated calorific density of the diet for grey seals in SS ranged between 4.2 and 5.7 kg (Table 5.6 A(ii)), and in AW between 4.7 and 5.6 kg (Table 5.6 B(ii)). As for harbour seals, the mean seasonal daily ingested prey weight for grey seals was very similar at 5.1 kg in SS and 5.3 kg in AW.

Grey seals in the Moray Firth (4.2 kg) and SE Scotland (4.5 kg) in SS and in the Moray Firth (4.7 kg) and Outer Hebrides (5.0 kg) in AW consumed less prey by weight (17 and 11% less, respectively, in SS and 11 and 6% less, respectively, in AW) compared to the seasonal average (Table 5.6 A(ii) and B(ii)). In contrast, seals in Shetland (5.7 kg), Orkney (5.7 kg) and the Inner Hebrides (5.4 kg) ate more prey by weight in SS (10% more than the seasonal average in Shetland and Orkney and 5% more in the Inner Hebrides, Table 5.6 A(ii)). Grey seals in the southern North Sea (5.6 kg) and Inner Hebrides in AW (5.6 kg) also ate more (more than 5%) relative to the seasonal average, Table 5.6 B(ii)).

Table 5.6: Estimated mean daily ingested prey weight (kg) required to attain the reported diet quality (Table 5.4) and the difference from the seasonal average: harbour seals SS = 4.4 and AW = 4.5 kg and grey seals SS = 5.1 and AW = 5.3 kg.

A)

Spring/Summer	(i) Harbour seal		(ii) Grey seal	
Region	**Mean prey weight (kg)**	**Seasonal difference (kg)**	**Mean prey weight (kg)**	**Seasonal difference (kg)**
S. North Sea	4.7	0.2	5.0	-0.1
SE Scotland	4.6	0.1	4.5	-0.6
Moray Firth	4.1	-0.4	4.2	-0.9
Orkney	4.5	0.0	5.7	0.6
Shetland	4.1	-0.3	5.7	0.6
Outer Hebrides	4.4	-0.1		
Inner Hebrides	4.8	0.3	5.4	0.3

B)

Autumn/Winter	(i) Harbour seal		(ii) Grey seal	
Region	**Mean prey weight (kg)**	**Seasonal difference (kg)**	**Mean prey weight (kg)**	**Seasonal difference (kg)**
S. North Sea	4.8	0.3	5.6	0.3
SE Scotland	4.9	0.4	5.4	0.1
Moray Firth	4.1	-0.4	4.7	-0.6
Orkney	4.1	-0.4	5.5	0.2
Shetland	4.4	-0.1	5.5	0.1
Outer Hebrides			5.0	-0.3
Inner Hebrides	4.7	0.2	5.6	0.2

5.4 Discussion

In this chapter, I use diet biodiversity, composition and quality metrics to investigate dietary niche overlap of sympatric harbour and grey seals around Britain. I used the established technique of analysing prey hard remains (fish otoliths and cephalopod beaks) to estimate diet (reviewed in Tollit *et al.*, 2010 and summarised in Chapter 3) and I have minimised sampling bias and uncertainty (reviewed in Bowen and Iverson, 2013, see also Chapter 3) through the use of seal species-specific and prey grade-specific digestion correction factors.

As with other sampling methods, scat analysis assumes that the data are representative of the population to which the results are extrapolated. I have minimised scat collection biases as far as possible by stratifying sample collection across four different times of the year, sampling at a range of haul-out sites throughout the regions and sampling over multiple days, where possible. Mitigation against scat collection bias and sampling bias is discussed in detail in Chapter 3.

The fish otoliths and cephalopod beaks found in scats reflect both, which species of prey were available for the seals to consume and which prey the seals did consume. I have used the individual diet metrics to explore if food is limiting for harbour seal populations that are currently in decline. I have compared this detailed information for both harbour and grey seals and set this in the context of the estimated population trajectories for each region/population (SCOS, 2012). To facilitate this complex comparison, I have simplified my results into a single summary comparison table (Table 5.7).

Only diet composition can be compared over time because previous estimates of diet diversity and diet quality are not available. For the diversity estimates, I am limited to comparisons between seal species within a region and season to maintain the integrity of the standardisation (rarefaction) process. For diet composition and quality (calorific density of the diet) comparisons can be made across regions, seasons and seal species.

Table 5.7: Summary comparison table of harbour and grey seal diet metrics. Harbour seals are annotated as Pv and grey seals as Hg. Trend displays the population trajectory of seals in each region (SCOS, 2013): **↗** = population increasing, **--** = population stable and **↘** = population declining. For species evenness: **H** = high (> 0.75), **--** = intermediate (0.3 - 0.75) and **L** = low (< 0.3). For diet quality (based on mean calorific density, cal.g-1): **H** = high (> 1,100), **--** = intermediate (1,000 – 1,099) and **L** = low (< 1,000).

			Evenness		**Quality**		**Prey type composition > 66.6%**			
	Trend		**SS**	**AW**	**SS**	**AW**	**SS**		**AW**	
Region	**Pv**	**Hg**	**Pv | Hg**	**Pv | Hg**	**Pv | Hg**	**Pv | Hg**	**Pv**	**Hg**	**Pv**	**Hg**
Southern North Sea	**↗**	**↗**	**H > L**	**H > L**	**-- = --**	**-- > L**	sandy benthic flatfish	sandeel	flatfish gadoids sandy benthic	sandeel scorpion fish flatfish
SE Scotland	**↘**	**↗**	**-- > L**	**-- > L**	**-- < H**	**L < --**	sandeel flatfish	sandeel	flatfish gadoids	sandeel gadoids
Moray Firth	**--**	**↗**	**L = L**	**L = L**	**H = H**	**H = H**	sandeel	sandeel	sandeel	sandeel
Orkney	**↘**	**--**	**L < --**	**-- = --**	**-- > L**	**H > L**	sandeel gadoids	gadoids sandeel pelagics	pelagics gadoids	gadoids sandeel pelagics
Shetland	**↘**	**--**	**-- < H**	**-- = --**	**H > L**	**H > --**	pelagics gadoids sandeel	gadoids scorpion fish	sandeel gadoids pelagics	gadoids sandeel sandy benthic
Outer Hebrides	**↗**	**--**	**--**	**--**	**H**	**--**	*Trisopterus* pelagics gadoids scorpion fish			sandeel gadoids pelagics
Inner Hebrides	**--**	**--**	**H = H**	**H = H**	**-- = --**	**-- > L**	gadoids pelagics	gadoids sandy benthic	gadoids pelagics	gadoids sandeel sandy benthic flatfish

5.4.1 The population status of British harbour and grey seals

The decline of harbour seal populations in some areas of Scotland has motivated a large programme of research around Britain; the main candidate drivers that may be responsible for the sharp declines include: changes in the quality or quantity of prey, uptake of marine toxins from harmful algae and unexplained or “corkscrew” seal deaths (SCOS, 2013). In this chapter I have explored the dietary niche of sympatric harbour and grey seals and used detailed information on the population status of both species to inform this discussion.

5.4.1.1 Population status: east coast of Britain/ North Sea

The harbour seal populations at each of the three regions on the east coast of Britain are experiencing different population trajectories. The population of harbour seals in the southern North Sea is increasing. Following a reduction of 22% due to the 2002 phocine distemper virus (PDV) epidemic (SCOS, 2013), the population showed no recovery until 2009, since when it has been increasing steadily (SCOS, 2013). The harbour seal population of the Rivers Tay and Eden (SE Scotland and the main sampling sites for this region) has suffered a major decline from around 600 adults to fewer than 100 in the most recent moult counts (SCOS, 2013). In contrast, the Moray Firth population has shown periodic increases and declines in abundance; declining by 50% before 2005, then remaining stable for 4 years before increasing by 40% in 2010 and declining again by 30% in 2011 (SCOS, 2013). The population now appears stable (SCOS, 2013).

Grey seal population trends are assessed from the counts of pups born during the autumn breeding season when females congregate on land to give birth. Trends in pup production up to 2010 show that there has been a continual increase in the North Sea since surveys began in the 1960s (SCOS, 2011). It is important to remember that the annually produced grey seal numbers may not reflect the abundance of grey seals in a particular region at other times of the year because up to 58% of female grey seals use different regions for breeding and foraging (Russell *et al.*, 2013).

5.4.1.2 Population status: Orkney and Shetland

Major harbour seal population declines have been documented since 2000 in Orkney (75%) and Shetland (30%, Lonergan *et al.*, 2007; SCOS, 2013). The declines are not thought to have been linked to the 2002 PDV epidemic that seemed to have had little effect on harbour seals in Scotland (SCOS, 2013). The grey seal population in Orkney (based on trends in pup production) has been stable for the last 10 years (SCOS, 2013). Information is scarcer for Shetland, which has a much smaller numbers of grey seals, and the population trend is considered to be equivalent to the Orkney grey seal population (SCOS, 2013).

5.4.1.3 Population status: west of Scotland, Outer and Inner Hebrides

The population of harbour seals in the Outer Hebrides has fluctuated over the last two decades. There was a decline of 35% reported between 1996 and 2008 and a subsequent increase of 50% in 2011 (SCOS, 2013). No population trend has been detected from harbour seal counts on the Scottish west coast (Inner Hebrides) and the population is considered stable (SCOS, 2013). Grey seal numbers are considered to be stable in both regions; pup counts have revealed no trend in the Outer Hebrides for approximately 20 years and 10 years in the Inner Hebrides (SCOS, 2013).

5.4.2 Dietary comparison: east coast of Britain/ North Sea

Grey seal diet was dominated by sandeels in all regions of the North Sea (southern North Sea, southeast Scotland and the Moray Firth). Although sandeels were also dominant in the diet of harbour seals in the Moray Firth (>75% in both seasons), in the southerly regions their diet was more varied in composition including: sandeel, flatfish, sandy benthic and large gadoid prey.

5.4.2.1 Southern North Sea

In the southern North Sea, harbour seals ate mostly sandy benthic prey, flatfish and sandeel in SS and flatfish, large gadoids and sandy benthic prey in AW. Grey seal diet was dominated in both seasons by sandeel but also included flatfish and large gadoids in SS and scorpion fish, sandy benthic, large gadoids and flatfish prey in AW. The number of prey species consumed by both species was similar in the region; however harbour seal consumption was spread much more evenly across the prey species in the diet. In this region the diet quality of seals overall was low and there was a high degree of overlap in the quality of both harbour and grey seal diets. The amount of prey that harbour seals in the region needed to eat to attain the estimated daily ingested prey quality was one of the highest in this region. Grey seals also had to eat more prey daily than the seasonal average to attain their estimated diet quality in AW.

A previous study of harbour seals in the southern North Sea estimated the main diet composition as; whiting and flatfish (50%), dragonet, sand goby and bullrout (approximately 33%) and gadoids (other than whiting, 12 %, Hall *et al.*, 1998). In this study, flatfish, sandy benthic prey and large gadoids remained important in harbour seal diet. However, sandeel made up a much greater proportion of the diet of harbour seals in SS than would be expected by the incorporation of complete digestion of otoliths, which was not used by Hall *et al.*, (1998) and it appears that this prey species is more important in the diet of harbour seals in the southern North Sea now than it was in the early 1990s.

The diet of grey seals in the southern North Sea has changed over the years. Sandy benthic and sea scorpions were more important and sandeel less important in the diet in 2002 compared to 1985 (Hammond and Grellier, 2006). The proportion of gadoid fish was similar, though the diet comprised less cod and more whiting in 2002 and less flatfish were consumed in 2002 than in 1985 (Hammond and Grellier, 2006). In this most recent study, grey seals consumed less sandy benthic/ scorpion fish compared to 2002 and sandeel was much more important in the diet. Gadoid contribution to the diet was also lower in this study and the contributions of cod and whiting was similar to the lower levels consumed of cod in 2002 and whiting in 1985 (Hammond and Grellier, 2006).

5.4.2.2 Southeast Scotland

In southeast Scotland, the diet of harbour seals was dominated by sandeel and flatfish in SS with lesser contributions of large gadoids. In AW, flatfish dominated harbour seal diet with the large gadoids, pelagic and cephalopod prey making up the remainder of the diet. Grey seal diet was dominated by sandeel in SS and to a lesser extent in AW; other important prey in AW included large gadoids and flatfish. Species richness in the diet was similar for both seal species in SS and grey seals slightly more prey in AW; however, grey seal diet was more uneven in both seasons than harbour seal diet. The quality of the diet of harbour and grey seals in SE Scotland ranged between moderate and low (Table 5.7) and overlapped in both seasons. However, the degree of overlap in SS was small and the confidence intervals for harbour seals were very large due to the small sample size. The only noteworthy deviation from the mean estimated daily ingested prey weight required to attain the reported diet quality was grey seal diet in SS.

Comparing the diet estimated in this study and results presented by Sharples *et al.*, (2009), flatfish appear more important in the diet and sandeel much less important in 2010 compared to the early 2000s. The dominance of flatfish and the reduction in sandeel contribution to the diet of harbour seals is unlikely to be affected by differences in the use of DCFs between the studies. However, this study had a much smaller sample sizes to estimate diet than Sharples *et al.*, (2009) and any variation should be interpreted with some caution.

Changes in grey seal diet were generally not large between 1985 and 2002; gadoids made up less of the diet and sandeel more of the diet in 2002 compared to the mid-1980s (Hammond and Grellier, 2006) and this trend continued in 2010/11. The contribution of cod declined markedly in 2002 and a significant increase was found in the amount of haddock consumed (Hammond and Grellier, 2006). In 2010/11, the proportion of cod was still very low and the proportion of haddock in the diet had declined. The amount of flatfish has been steadily increasing in the diet of grey seals, although the levels are still low relative to the amount of sandeel consumed.

5.4.2.3 Moray Firth

In the Moray Firth, the diet of both species was dominated by sandeel throughout the year (minimum contribution 67% harbour seals in SS). Flatfish were also important in the diet of harbour seals in SS and gadoids in the diet of grey seals in AW. The dominance of sandeel in the diet is reflected in the very low species diversity in the diet for both species. Diet quality in the Moray Firth was the highest of all the regions for both seal species. There was overlap in the confidence intervals in both seasons; however, this overlap in SS was very small. The high quality of the diet is reflected in the smaller than average mean daily ingested prey weight required by both species to attain the estimated diet quality in each season.

Sandeel has always been the main prey species for harbour seals in the Moray Firth (*e.g.*, Tollit and Thompson, 1996). However, other prey species do make up important seasonal contributions to the diet overall, including large gadoids and pelagic fish, and comparisons across the studies do indicate that flatfish are occurring more in the diet in recent years (Pierce *et al.*, 1990a; Thompson *et al.*, 1996a; Tollit and Thompson, 1996; Tollit *et al.*, 1997a).

Comparisons with the most recent diet estimates for grey seals cannot be made for the Moray Firth because diet was estimated combined with Orkney. This approach stems from the use of pup counts to estimate the population size of grey seals, and there being very few grey seal pups born in the Moray Firth (Hammond and Grellier, 2006). However, Prime and Hammond (1985) reported that gadoids and sandeels were the most important prey in the region in their study and Pierce *et al.*, (1991b) subsequently reported the dominance of sandeel in the diet in the 1980s (although no DCFs were applied) and cephalopods showed seasonal importance.

5.4.3 Dietary comparison: Orkney and Shetland

The diet of harbour and grey seals in Orkney and Shetland comprised mostly sandeel, large gadoids and pelagic prey across the seasons and, for grey seals, scorpion fish in Shetland in SS. The largest differences in the diet of the two species were in Orkney in SS where harbour seals ate more sandeel, and in Orkney AW and both seasons in Shetland where harbour seals ate more pelagic fish.

5.4.3.1 Orkney

In Orkney in SS, sandeel and pelagic prey dominated the harbour seal diet while grey seal diet comprised large gadoids, sandeel and pelagic prey. In AW, harbour seal diet was dominated by pelagic and large gadoid prey, although sandeel were also important and grey seals ate mostly large gadoids, sandeel and pelagic fish. Grey seal diet composition was much more evenly spread across prey species with no contributions to the diet greater than 20% in SS or 30% in AW. Overall grey seal diet was more diverse in Orkney than harbour seal diet. Grey seals had the greatest species richness in the diet in both seasons and harbour seal diet was more uneven. The diet of harbour seals in Orkney was better quality than that of grey seals in both seasons, and better for harbour seals in AW than in SS. However, there were no clear differences from the seasonal mean in the estimated daily ingested prey weight required to attain the estimated diet quality.

Based on frequency of occurrence, the diet of harbour seals in Orkney in the mid-1980s was dominated by sandeel, herring and gadoid fish (Pierce *et al.*, 1990a), a pattern similar to the diet of harbour seals in 2010/11 (Chapter 3).

Grey seal diet in Orkney (including some samples from the Moray Firth) saw a large increase in the percentage of gadoids in the diet and a decrease in the percentage of sandeel between 1985 and 2002 (Hammond and Grellier, 2006). In 2010/11, the proportion of gadoids in the diet had increased slightly, the proportion of sandeel had further declined and pelagic prey had become more important in the diet.

5.4.3.2 Shetland

The diet of harbour seals in Shetland in SS and AW was dominated by pelagic fish, sandeel and large gadoids. Grey seal diet was dominated by large gadoids and scorpion fish in SS and large gadoids and sandeel in AW. Both harbour and grey seals had similar species richness in the diet in SS, but grey seals had greater species richness in the diet than harbour seals in AW. However, in both seasons, harbour seal diet was more uneven than grey seal diet. Diet quality in Shetland was significantly lower for grey seals than harbour seals in both seasons. In SS, the high calorific content of prey in the diet of harbour seals required them to eat less prey by weight than the seasonal average to attain their daily diet quality. In contrast, grey seals in SS had to eat more prey by weight than the seasonal average to attain their daily energy quality.

In Shetland, comparison of the diet of harbour seals in 2010/11 to the mid-1990s (Brown and Pierce, 1998) revealed few changes in the dominant prey types. The variation seen in the seasonal pattern of importance (mainly for sandeel and pelagic prey) is most likely a result of with the lack of use of Number Correction Factors (NCFs) to account for complete digestion of otoliths in the earlier work, because both these prey types have poor recovery rates due to the fragility of their otoliths. There was, however, a noticeable change in the proportion of whiting in the diet, which decreased from one quarter of the diet composition in the 1990s (Brown and Pierce, 1998) to less than 1% in 2010/11.

The diet of grey seals in Shetland was previously estimated in 2002, when it was heavily dominated by sandeel with large gadoids making up the rest of the diet (Hammond and Grellier, 2006). In 2010/11, the proportion of sandeel in the diet of grey seals had decreased and the contribution of gadoids had increased.

5.4.4 Dietary comparison: west of Scotland; Outer and Inner Hebrides

Large gadoid prey were important in the diet of both harbour and grey seals on the west of Scotland. Pelagic fish were also important in harbour seal diet and sandeel and sandy benthic prey in grey seal diet.

5.4.4.1 Outer Hebrides

In the Outer Hebrides, only SS harbour seal diet and AW grey seal diet was able to be estimated in this study. Harbour seal diet was split across five main prey groups; *Trisopterus* species, pelagic fish, large gadoids, scorpion fish and sandeel. Grey seal diet in AW was dominated by sandeel and large gadoids with the remaining prey groups generally contributing less than 10% of the diet over all.

Harbour seal diet in the Outer Hebrides has not previously been described so no comparisons are possible.

Sandeel was the dominant prey of grey seals in the Outer Hebrides in 2002, although herring and large gadoids were also important in the diet (Hammond and Harris, 2006). Only limited variation in grey seal diet composition was detected between 1985 and 2002 in the Hebrides as a whole (Hammond and Harris, 2006). The main differences were fewer sandeel and more pelagic prey in the diet in 2002 compared to 1985 (Hammond and Harris, 2006). In 2010/11 there was a slight increase in sandeel contribution, but not back to the level recorded in 1985, and a slight drop in the contribution of pelagic and gadoid prey to the diet.

5.4.4.2 Inner Hebrides

In SS in the Inner Hebrides, harbour seals ate mostly gadoids and some pelagic fish and *Trisopterus* species. Grey seal diet was dominated by large gadoids and sandy benthic prey with important contributions of *Trisopterus* species. In AW, harbour seals ate predominantly large gadoids and pelagic fish while grey seals ate mostly large gadoids and sandeel. Harbour seals had greater species richness in the diet in SS and dietary species richness was similar in both species in AW. The diet of both species was diverse (high level of evenness), reflected in the diet composition estimates in which no one prey species dominated the diet in either seal species or season. At a regional level, diet quality in the Inner Hebrides was significantly lower than average. The diet quality of grey seals was lower than harbour seals in AW but more similar in

SS. Reflecting the low calorific density of their diet, harbour seals in the Inner Hebrides in SS and grey seals in both seasons needed to eat more prey by weight than the seasonal average to attain their estimated energy density.

A previous study of harbour seals in the Inner Hebrides in the mid-1990s revealed a diet dominated by large gadoids with a minimal contribution of sandeel and seasonal pulses of pelagic prey in summer (Pierce and Santos, 2003). In 2010/11, gadoids still dominated but pelagic prey and sandy benthic prey also contributed more to the diet.

In the Inner Hebrides, sandeel and large gadoids dominated the diet of grey seals in 2002; dragonet was important in the north of the region and sprat in the Minch (Hammond and Harris, 2006). In 2010/11, the estimated proportion of gadoids in the diet had not changed since 2002 but the proportion of sandeel had declined markedly. The proportion of pelagic prey in the diet also seems to have declined but sandy benthic prey and scorpion fish appear to have increased.

5.4.5 The role of major prey in regional differences in harbour and grey seal foraging, diet and population trends

All organisms require resources to survive, grow and reproduce and so competition for resources is expected unless partitioning occurs at some level (*e.g.*, foraging niche, dietary niche). A commonly accepted hypothesis when studying diet is that diversity of diet increases as food becomes limiting (*e.g.*, Krebs *et al.*, 1977; Thompson and Colgan, 1990). A strong link between decreasing diet diversity and population decline has been described in Steller sea lions, *Eumetopias jubatus* (Merrick *et al.*, 1997; Trites *et al.*, 2007a) followed by a subsequent increase in diet diversity in regions showing the strongest population growth (Sinclair *et al.*, 2013). Furthermore, the quality of sea lion diet has also been shown to have large effects of the amount of food that needs to be consumed (Winship and Trites, 2003). However, recent biological opinion reports have suggested that the scientific evidence does not support the nutritional stress hypothesis and proposed that the hypothesis be scientifically rejected (NOAA Fisheries, 2010; Bowen, 2012; Stewart, 2012; Stokes, 2012; NOAA Fisheries, 2014). Though the cause(s) of the decline of Steller sea lions remains uncertain a large body of peer-reviewed research does indicate that the decline is a direct result of changes in the availability of suitable prey (Merrick *et al.*, 1987; Springer, 1992; Rosen and Trites, 2000; Trites and Donnelly, 2003; Rosen, 2009; Sinclair *et al.*, 2013).

Around Britain, many fish stocks have been exposed to high levels of fishing mortality and as a consequence stocks have declined and/or undergone a marked change in distribution (*e.g.*, cod, whiting and sandeel, ICES, 2008a; 2011b). However, there is evidence of recovery of stocks. For example, the North Sea cod stock has remained outside of safe biological limits since approximately 1998, but the spawning stock biomass (SSB) has been increasing since approximately 2006 (ICES, 2013). In addition, following a decline in sandeel populations in the North Sea, since 2000 the central western North Sea has seen an increase, probably as a result of the fishery closure (ICES, 2011b). Some of these stocks, including cod, whiting and sandeel, are important prey of harbour and grey seals (Tollit and Thompson, 1996; Hall *et al.*, 1998; Hammond and Grellier, 2006; Hammond and Harris, 2006). The abundance of these higher predators has also changed over the decades.

Since surveys first began in the 1960s, grey seals numbers in the North Sea have continued to increase while the populations in Orkney, Shetland and Outer and Inner Hebrides have stabilised in recent years (assessed from the counts of pups born during the autumn breeding season, SCOS, 2013). Up until 2000, harbour seal populations around Britain were stable or increasing; since then, however, declines have been observed in Shetland (down 30%), Orkney (down 75%) and Firth of Tay in southeast Scotland (down 85%, SCOS, 2013). In the Moray Firth, following a period of decline the population has since stabilised and in the southern North Sea, following a period of decline associated with the 2002 Phocine Distemper Virus (PDV) epidemic, harbour seals numbers are continuing to increase (SCOS, 2013). On the west coast of Scotland in the Outer and Inner Hebrides populations of harbour seals have remained stable (SCOS, 2013).

The population of grey seals as a whole is much larger than that of harbour seals. Based on annually monitored colonies in 2010, the UK population of grey seals was estimated as 111,300 (95 % CI 90,100 - 137,700, SCOS, 2012) and harbour seals 36,500 (95 % CI 29,900 - 48,650, SCOS, 2012). As a consequence of the overall increasing numbers of seals in British waters and low levels of their main prey species (ICES, 2011a; b; 2013) it is very likely that there is competition among individuals of the same species (intra-specific competition) and/or between species (inter-specific competition) for fewer prey. One of the central questions driving research into the decline of harbour seals around Britain is: do grey and harbour seals compete for food, and is the decline of harbour seals in some areas linked to this competition for prey (SCOS, 2009)?

However, a consistent picture relating harbour and grey seal diet diversity, composition and quality with population trajectories cannot be drawn from this study (Table 5.7). What is clear is that some prey are more important in the diet than others. For example, sandeel and large gadoids are important prey groups in the diet of grey seals now as they have been over the last three decades (1985-2014, Hammond and Grellier, 2006; Hammond and Harris, 2006). These prey are also important in the diet of harbour seals around Britain (*e.g.*, Thompson *et al.*, 1996b; Brown and Pierce, 1998; Sharples *et al.*, 2009, Chapter 3) alongside the increasing importance of pelagic prey in the diet of both species (*e.g.*, Brown *et al.*, 2001; Hammond and Grellier, 2006, Chapter 3).

Differences in diet are expected to be strongly influenced by the abundance and availability of prey in different regions as well as the physiological requirements of individuals and by the different foraging distributions of the two seal species. Given the general importance of sandeel, pelagic prey and large gadoids in the diet of both harbour and grey seals around Britain, I explored each prey group in turn focusing on: species characteristics, changes in abundance/distribution, availability to each species of seal and how changes in these parameters may have affected seal diet.

5.4.5.1 Sandeel

Sandeel is an important prey type for many predators including large gadoids, seabirds and mammals (Harwood and Croxall, 1988). Sandeel are largely stationary after settlement and are dependent on suitable sandy sediment types (Lewy *et al.*, 2004) from which they emerge infrequently (Wright and Begg, 1997) in large schools. Sandeels have a relatively high calorific density (1367 cal/g, Murray and Burt, 1977) The majority of sandeel stock biomass is in the central and southern North Sea (ICES, 2012) see Figure 5.8, however, sandeels are also found in abundance around Orkney and Shetland and in the northeast and northwest of the Outer Hebrides (SNH).

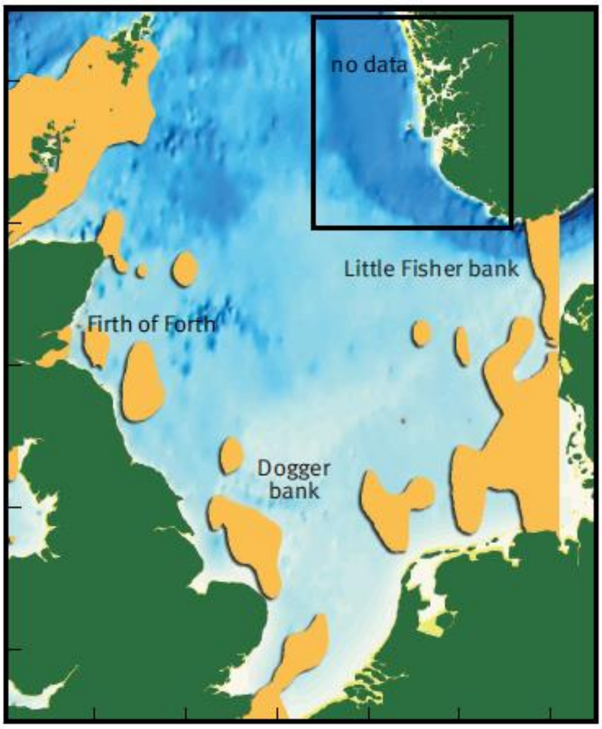


Figure 5.8: Distribution of sandeel spawning grounds in the North Sea. Reproduced from (Fisheries Research Services, 2001b).

Up until the early 2000s, sandeel were the target of the largest single species fishery in the North Sea (ICES, 2004) and, as a consequence, stocks declined and underwent marked changes in distribution causing concerns about localised depletions (ICES, 2011b). Off Scotland, small sandeel fisheries operate around Shetland and off the west coast (Marine Scotland, 2014c). Localised sandeel closures have taken place in Scotland, principally to protect seabird populations. The sandeel fishery in the Firth of Forth was closed in 2000 (ICES, 2012) and around Shetland the stock is closely managed with all fishing restricted to small inshore grounds (Fisheries Research Services, 2001a). Since 2002, the majority of the fishing banks in the central western North Sea have been closed and this area has seen an increase in stock in recent years, furthermore, in the southern North Sea (Dogger Bank fishing area) the sandeel stock was expected to be at full capacity due to a large recruitment in 2009 and reduced fishing since 2005 (ICES, 2011b).

Reduced availability of sandeel can have serious consequences for some predators. For example, in Shetland, variability in seabird breeding success has been closely linked to sandeel in the diet (*e.g.*, Hamer *et al.*, 1993; Furness and Tasker, 2000). Sandeel are found in both offshore and coastal waters (<30 m depth) around Britain (*e.g.*, Figure 5.8) in areas which are accessible to both harbour and grey seals (Figure 5.1).

Sandeel are an important prey type for harbour and grey seals around Britain (Table 5.7, Chapter 3) and have become increasingly important in the diet of both species in some areas (Hall *et al.*, 1998; Hammond and Grellier, 2006; Hammond and Harris, 2006). It is likely, therefore, that fluctuations in the abundance and distribution of sandeel are driving diet changes in harbour and grey seals.

Sandeel has increased in importance the diet of both harbour and grey seals in the southern North Sea, in the diet of grey seals in the central North Sea and remained consistently important in the diet of grey and harbour seals in the Moray Firth (Pierce *et al.*, 1991b; Hammond and Grellier, 2006). In southeast Scotland, the importance of sandeel in the diet of harbour seals has declined while flatfish have increased in importance (Sharples *et al.*, 2009). In the southern North Sea, the increase in sandeel in the diet is very likely driven by reduced fishing and large 2009 recruitment of sandeel at Dogger bank (ICES, 2011b) an area frequented during foraging trips by both species of seal (Figure 5.1). In southeast Scotland, the closure of the Firth of Forth sandeel fishery may have benefited grey seals more than harbour seals. The principle haul-out sites for both species in this region are in the Firth of Tay/ St Andrews Bay area. The Firth of Forth sandeel banks are probably more accessible to grey seals that make longer distance and duration foraging trips (Thompson *et al.*, 1996a; McConnell *et al.*, 1999; Jones *et al.*, 2013) than harbour seals (Thompson *et al.*, 1996a; Cunningham *et al.*, 2009; Sharples *et al.*, 2012; Jones *et al.*, 2013).

In the Moray Firth, the harbour seal population has shown periodic increases and declines in abundance (SCOS, 2013) and it is possible that this may be linked to the reliance of harbour seals on one primary prey type. Detailed information on prey availability and variation in diet is not available to explore this suggestion further, but it is reasonable to consider that at times of low prey availability (low sandeel abundance), there may be greater competition for prey within the harbour seal population itself (intra-specific competition) and/or between harbour and grey seals (inter-specific competition). Increased competition could have had detrimental effects on harbour seal individual growth, reproduction and survival and led to population fluctuations (Cody and Diamond, 1975; Eccard and Ylönen, 2003). However, it is also likely that other causes of population fluctuation may exist, particularly in this region, which maintains an important commercial rod and line salmonid fishery. Thompson *et al.*, (2007) cited evidence that substantial numbers of seals in the Moray Firth have been shot to reduce the interactions with the fishery. Variety in prey types in the diet has been suggested by Merrick *et al.*, (1997) as important for increasing foraging efficiency and buffering against significant changes in abundance of any single dominant prey species. The Moray Firth is a region which presents an opportunity to investigate this further, should time series of seal diet and fish abundance data become available.

In the Northern Isles, sandeel has remained an important part of the diet of harbour seals since the mid-1990s (Brown and Pierce, 1997; Brown and Pierce, 1998; Brown *et al.*, 2001). However, studies by Brown and Pierce (1997 and 1998) did not account for complete digestion of otoliths and so the contribution of sandeels to the diet of harbour seals in their study will have been underestimated. Taking this into account it is likely that the contribution of sandeel to the diet has declined in harbour seals in Shetland particularly in spring and summer (Chapter 3). There are no comparable biomass estimates for Orkney, although sandeel did dominate the diet there based on frequency of occurrence in the mid-1980s (Pierce *et al.*, 1990a). Over this same time period the proportion of sandeel in the diet of grey seals has declined in both Shetland and Orkney (Hammond and Grellier, 2006; Hammond and Harris, 2006).

The importance of sandeel in the diets of harbour and grey seals in the North Sea and Northern Isles does indicate that competition for this prey resource is likely. Comparing dietary overlap results with a more detailed analysis of bio-logging data from grey and harbour seals around Britain and more detailed fishery information would allow the possibility of foraging niche overlap/ separation to be explored in greater detail.

5.4.5.2 Pelagic prey

Pelagic prey such as herring, mackerel and sprat are some of the highest quality prey (greatest calorific density) that seals around Britain eat. They are highly mobile species with seasonal migrations in British waters following the main circulation patterns of the North Atlantic Drift, Slope Current and associated Atlantic Inflow (Figure 5. 9). A study of abundance and geographic distribution of North Sea herring in the early-1990s linked the distribution of this pelagic species to dynamic environmental factors (Maravelias, 1997) and the winter migration of western mackerel has also been associated with the environmental factors along the shelf edge to the west of Britain (Reid *et al.*, 1997).

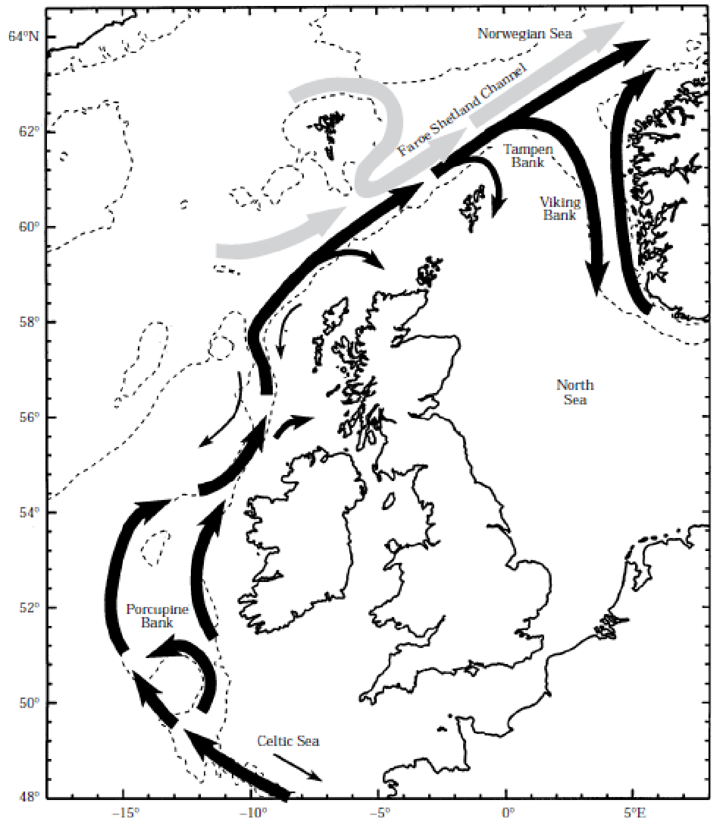


Figure 5. 9: Map of the European shelf around Britain showing the main circulation patterns of the North Atlantic Drift (grey arrows) and the Slope Current and associated Atlantic Inflow (black arrows). Reproduced from Reid *et al.*, (1997).

In July, the main feature of the northern North Sea is the Slope Current which is responsible for the input of nutrient rich water west of Shetland and Orkney. Some of this water enters the North Sea flowing down the east coast of Shetland or between Orkney and Shetland via the East Shetland Atlantic Inflow and the Fair Isle currents, respectively (Figure 5.10).

In the North Sea, ICES Area IV, which includes the Northern Isles, herring spawning stock biomass (SSB, 2010 estimate ~ 2,000,000 t) has been gradually increasing since an historical low SSB in the mid-1970s (ICES, 2014d). Over this same time period, catches of herring have fluctuated but remained lower than average (catch records 1947 - present, ICES, 2014d). In western Scotland, herring SSB is stable at around 100,000t (ICES, 2014c) and landings have remained constantly below average since approximately 1990 (ICES, 2014c).

Considered the most abundant pelagic fish in Scottish waters, changes have been documented in the mackerel migrations around Scotland since the 1970s (Marine Scotland, 2014b). The western stock of mackerel during the 1970s-1980s migrated in late summer and autumn and fish passed through the Minch. Currently, migration occurs later in the year and is further offshore, west of the Outer Hebrides (Marine Scotland, 2014b).

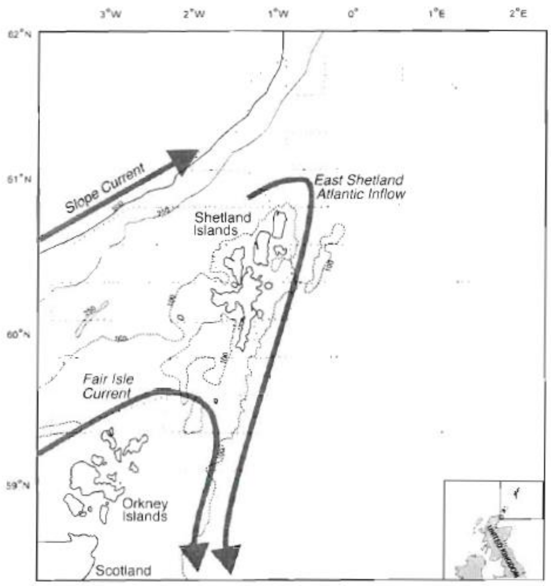
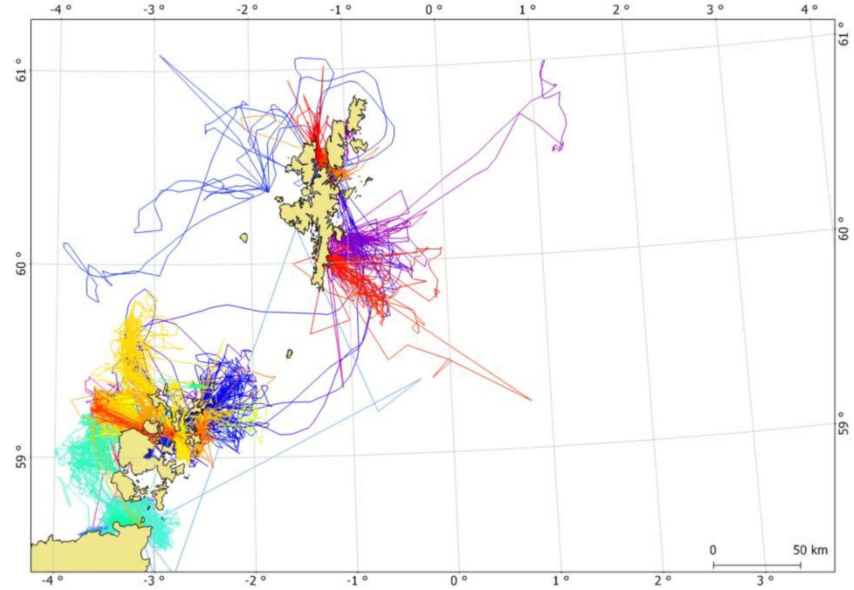
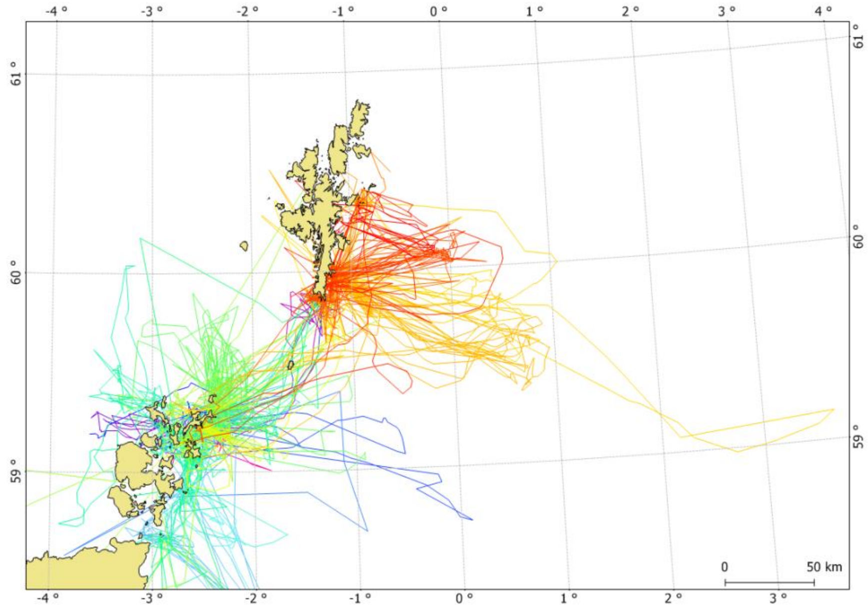


Figure 5.10: Arrows indicate the main currents and water movements in the northern North Sea (ICES Division Iva), bottom topography in metres. Reproduced from Maravelias (1997).

The at-sea distribution of harbour and grey seals around the west coast of Scotland and Shetland and Orkney brings them into the dynamic boundary zones which influence the temporal distribution patterns of pelagic prey in these regions (see Figure 5.11 for telemetry tracks of harbour and grey seals around Shetland and Orkney). Although both seal species do make repeated trips to discrete local foraging areas (Thompson and Miller, 1990; McConnell *et al.*, 1999), harbour seals tend to have a more coastal at-sea distribution (Cunningham *et al.*, 2009; Sharples *et al.*, 2012; Jones *et al.*, 2013) than grey seals, which make longer distance and duration foraging trips (McConnell *et al.*, 1992; McConnell *et al.*, 1999; Jones *et al.*, 2013).



A)



B)

Figure 5.11: Telemetry tracks of (A) 61 harbour seals (Shetland; n = 15 from 2003 and 2004, Orkney; n = 15 from 2003 and 2004, n = 31 from 2011 and 2012) and (B) 24 grey seals (Shetland; n = 7 from 1998 and Orkney n = 2 from 1993, n = 8 from 1996 and n = 7 from 1998). Shetland and Orkney 2003 – 2004 reported in Sharples *et al.*, (2012) the remaining SMRU unpublished telemetry data.

Despite differences in apparent foraging locations and the stable (Hebrides) and increasing (Northern Isles) stocks of pelagic prey, an increase in importance of these prey in the diet of grey seals was only observed in Orkney and the Outer Hebrides (Hammond and Grellier, 2006). Pelagic prey remained unimportant in the diet of grey seals in Shetland (Hammond and Grellier, 2006) and decreased in importance in the diet of grey seals in the Inner Hebrides (Hammond and Harris, 2006). The contribution of pelagic prey to the diet of harbour seals in Shetland and The Hebrides does not appear to have changed much and this prey group has remained abundant in the diet since the 1980s-1990s (Pierce *et al.*, 1990a; Brown and Pierce, 1997; Brown and Pierce, 1998; Brown *et al.*, 2001; Pierce and Santos, 2003). However, complete digestion of otoliths was not taken into account in the previous diet estimates and it is possible that the contributions of prey with fragile otoliths, such as pelagic fish and sandeel will have increased in the diet.

Pelagic fish could be considered a substitute prey in the diet of grey seals in Orkney, the contribution of which has increased while sandeel decreased. Pelagic fish are generally considered to be highly mobile and stocks are more dispersed as fish conduct long annual migrations to spawning grounds (Maravelias, 1997; Reid *et al.*, 1997). Despite the higher calorific content of these prey (1587 cal/g, Murray and Burt, 1977) it will likely require more energy to locate and capture them. By ‘switching’ to pelagic prey grey seals may be able to still meet their energetic demands however, harbour seals may be less able to cope with the change in foraging tactics required and the population may have been impacted as a result.

From a purely dietary perspective it would seem that, despite harbour seals consuming a diet higher in pelagic prey (better quality) than grey seals, that harbour seals may not be finding enough food to maintain their cost of living. As mentioned earlier this may be driven by decline in sandeel in their diets, consumption of which presumably costs individuals less energy than locating and catching highly mobile pelagic prey. If grey seals are better adapted to prey switching and balancing their energy budget than the smaller harbour seals this species may struggle to get enough food and become nutritionally stressed.

5.4.5.3 Large gadoid fish

Gadoid fish are some of the most heavily exploited for human consumption world-wide and the seas around Britain are no exception. The main demersal fisheries around Scotland are for cod, haddock, whiting and saithe. In 2002, the west of Scotland cod and whiting stocks were considered to be outside safe biological limits as was the haddock stock to the west and north of Scotland (Gordon *et al.*, 2002).

The decline in the west of Scotland cod spawning stock biomass (SSB) has been dramatic over the last 30 years but, since approximately 2006, the stock has plateaued and appears stable though at historically low levels (ICES, 2014a). Since the early 2000s, catches of cod in this region have also been at historically low levels and the proportion of the catch which is discards has increased due to landing restrictions (ICES, 2014a). Since the mid-2000s, the SSB of cod in ICES Area IV (North Sea) Division VIId (Eastern Channel) and Division IIIa West (Skagerrak) has been increasing from historically low levels, although catches in these regions remain low (ICES, 2013).

Haddock SSB has been much more dynamic over the last 40 years, with peaks and troughs in abundance and recruitment evident in the North Sea, Skagerrak and West of Scotland (ICES, 2014b). Catches of these stocks have mirrored the periods of high and low stock abundance, but are currently at historical lows for the region (ICES, 2014b).

The SSB of saithe in ICES Area IV (North Sea) Division IIIa West (Skagerrak) and Area VI (West of Scotland and Rockall) experienced a dramatic peak in biomass (~ 550,000 t) in the mid-1970s; otherwise the stock has been relatively stable at lower SSB (around 200,000 t) for 30+ years (ICES, 2014e). Landings of saithe have remained relatively constant (100,000 t) in these regions since the early 1990s (ICES, 2014e).

Whiting stocks in the west of Scotland have shown some recovery in recent years from historically low levels reported in 2005 - 2010 (ICES, 2014f). The trend in catches in this region reflect the stock biomass over the decades and remain currently at very low levels (2,000 t, ICES, 2014f).

In Scotland, juvenile Atlantic cod and whiting occupy the near shore environment for most of their first year of life, and move into deeper water as age-1 fish during their first winter and second summer (Bailey *et al.*, 2001). Haddock are present in the near shore only sporadically, and exhibit no consistent use of the near shore (Bailey *et al.*, 2001). In the coastal waters of Scotland, surveys of juvenile cod indicate that the highest densities are found within 60 km of the coast (Gibb *et al.*, 2007).

Although there are differences in the distances and durations of foraging trips of harbour and grey seals around Britain, it is likely that foraging occurs throughout the at-sea range of these higher predators (Thompson and Miller, 1990; Thompson *et al.*, 1991a; McConnell *et al.*, 1999; Cunningham *et al.*, 2009; Sharples *et al.*, 2012; Jones *et al.*, 2013). Based on the over-arching perceptions of foraging behaviour of each species, one might expect small gadoids to dominate the diet of harbour seals, the species considered to have the more coastal at-sea distribution (Thompson *et al.*, 1996a; Cunningham *et al.*, 2009; Sharples *et al.*, 2012; Jones *et al.*, 2013). However, despite the low SSB of the main commercial gadoid stocks in the waters around Scotland, large gadoid fish still make up a large proportion of the diet of harbour and grey seals.

In the Inner Hebrides the diet of both harbour and grey seals is particularly dominated by large gadoid prey, though the diet itself is very varied and not dominated by any prey species in particular. In the Northern Isles, grey seals have experienced a shift in diet from sandeel to large gadoid dominance (Hammond *et al.*, 1994a; Hammond and Grellier, 2006). Fine scale prey availability data are not available at a level which could be used to inform harbour/ grey seal foraging niche overlap or segregation. But it does seem likely that differences in the proportions of different prey species reflect the distribution and abundance (SSB) of the prey species and this in turn will affect availability at the foraging grounds and present differences in the diet of both seal species across space and time. For example, the gadoid contribution to the diet of both harbour and grey seals in the Northern Isles roughly reflected the stocks of fish which are reportedly stable or increasing (ICES, 2013; 2014e).

The calorific density of large gadoid prey (approx. 730 cal/g, Murray and Burt, 1977) is low compared to pelagic prey (approx. 1,600 cal/g, Murray and Burt, 1977) and sandeels (approx. 1,350 cal/g, Murray and Burt, 1977) and the consumption of low-energy prey can affect food requirements (Winship and Trites, 2003). This has been linked to population decline in Steller sea lions where populations that consumed higher proportions of low-energy prey experienced the highest rates of population decline (Winship and Trites, 2003). However, the lack of any trend in grey seal pup production over the last 10 years in Orkney, Shetland or The Hebrides combined with the decreased importance of sandeel in the diet and overall low consumption of pelagic prey by grey seals does not fit this model. For harbour seals that are consuming higher proportions of high-energy prey, this model would predict a stable or increasing population, but this is not the case in Orkney and Shetland where harbour seals consume greater quantities of higher calorific prey than grey seals.

The stability of the seal populations on the west coast of Scotland may reflect the availability of the prey within close range of haul-out sites. Harbour seal foraging trips in the Inner Hebrides are short. Mean travel-trip extent was 10.5 km and 50 % of trips were within 25 km of the haul-out site and mean trip duration was between 25 h and 35 h (Cunningham *et al.*, 2009). However, the trip parameters are similar for harbour seals in the Outer Hebrides, Shetland and Orkney; yet despite a diet made up of less calorific prey (fewer sandeel and pelagic prey) the population of harbour seals on the west coast of Scotland remains stable. Alternatively, Merrick *et al.* (1997) and Trites *et al.* (2007a) both made links between diet diversity and regional population trajectories in Steller sea lions; as diet diversity decreased, populations decreased. Trites *et al.* (2007a) were not clear on the consequences of this relationship; that is, whether diversity was acting as a proxy for energy content of the diet as previously suggested by Winship and Trites (2003) or whether it captured some other biologically meaningful measure of nutrition.

In this study I have examined diversity, composition and quality of the diet of seals which are in populations undergoing different population trajectories and I have not identified any other biologically meaningful measure of nutrition for which diversity could be a proxy. However, for seals on the west coast of Scotland a more simple explanation may suffice. It may be that prey are more accessible due to the local habitat and that harbour seals in particular with their more coastal distribution have a much lower cost of living, allowing them to eat a less calorific diet and still maintain basal metabolism plus other life history functions.

5.5 Final Remarks

Resource use often is a logical first hypothesis when investigating interspecific competition because all organisms require resources to survive, grow and reproduce. I have explored the dietary niche of sympatric marine higher predators, the harbour and grey seal, looking for dietary overlap or separation which may be linked to population trajectories. Comparisons have been made in predator diet diversity, composition and quality in spring/summer and autumn/winter around Britain. However, differences in each of these diet metrics have tended to be small and, where they exist, have tended to be contrary to my expectation that some component of diet may be influencing the population trajectory of the different populations.

Based on these initial findings I examined in more detail the three main prey groups consumed by harbour and grey seals and explored how prey availability might be driving seal diet and foraging behaviour around the coast of Britain. In some regions, sandeel is very important in the diet and, in the Northern Isles, changes in the population trajectories of seals may be linked to declines in sandeel in the diet. It is possible that prey switching may be occurring in this area as seals compensate for the lack of moderate-high calorie sandeel in the diet by increasing the contribution of pelagic prey. However, this does not appear to be supporting the energy requirements of harbour seals which continue to decline in this region despite consuming a better quality diet than grey seals. But this supposition is only relevant if diet and prey availability are the cause of the decline of harbour seals in the region. On the west of Scotland the importance of sandeel is minimal compared to the contribution of lower quality gadoid prey and there has been no evidence of a decline in harbour seal abundance. Though I have not directly tested the competition hypothesis in terms of energy intake relative to requirements I propose that differences in diet may not be the biologically meaningful driver behind the observed differences in seal trajectories around Britain.

It is possible that population size is regulated by other extrinsic factors. One possible explanation may be the availability of pupping sites which may be affected by natural processes or anthropogenic actions. In the North Sea, the increase in the population of grey seals is mostly a result of the relatively recent colonisation of the southern North Sea. Prior to 1990, hardly any grey seal pups were born in at Donna Nook (Duck and

Morris, 2013) and the other colonies including Blakeney Point (sampled in this study) were only established since 2000 (Duck and Morris, 2013).

The role of this Chapter was to examine the dietary niche of harbour and grey seals and look for overlap or separation which might provide some evidence for competition for prey between the two species. In the context of the equivocal results, it is important to note that the dietary niche of any consumer is only one element of a complex interaction between predator and prey and a much wider perspective is required to explore this question fully. Other aspects to include should involve the distribution of seals at-sea and on-land and spatial and temporal trends in diet foraging behaviour and prey distribution.

Appendix 5.1: Seasonal and regional variation in the number of otoliths and beaks recovered for the 20 most abundant species or higher taxon prey.

A) Harbour seal

i) Southern North Sea

Species	**SS**	**AW**	**Total**
Goby	1768	1130	2898
Sandeel	600	229	829
Plaice	627	143	770
Dragonet	494	190	684
Whiting	34	603	637
Unidentified flatfish	178	129	307
Dab	220	59	279
Dover sole	80	42	122
Sprat	4	102	106
Flounder (Butt)	33	8	41
Lemon sole	10	28	38
Pout whiting (Bib)	14	13	27
Lesser weever	14	11	25
Bullrout	5	17	22
Cod	14	7	21
Sea Scorpion	1	19	20
Herring		18	18
Smelt	12	1	13
Unidentified roundfish	7	6	13
Sepiolids	9	2	11

ii) SE Scotland

Species	**SS**	**AW**	**Total**
Goby		2522	2522
Sandeel	1261		1261
Plaice	373	649	1022
Whiting	126	515	641
Unidentified flatfish	82	277	359
Dab	136	50	186

Sprat	14	82	96
Loligo	1	33	34
Cod	8	19	27
Flounder (Butt)	13	10	23
Haddock		11	11
Dragonet		10	10
Unidentified gadid	1	7	8
Saithe		6	6
Eelpout		3	3
Lemon sole		3	3
Mackerel		3	3
Long rough dab		2	2
Sea trout	2		2
Snake blenny		2	2

iii) Moray Firth

Species	**SS**	**AW**	**Total**
Sandeel	15143	3168	18311
Plaice	773	28	801
Unidentified flatfish	411	23	434
Dab	345	14	359
Sprat	75	93	168
Cod	51	31	82
Flounder (Butt)	59	8	67
Whiting	32	23	55
Saithe	21	30	51
Unidentified gadid	17	20	37
Bullrout	22	3	25
Loligo	21	3	24
Goby	3	15	18
Haddock	17	1	18
Poor cod	2	11	13
Flounder or Plaice	11		11
Eelpout	6	3	9
Long rough dab	9		9

Herring	2	4	6
Dragonet	2	2	4

iv) Orkney

Species	SS	AW	Total
Sandeel	3467	1039	4506
Cod	578	94	672
Unidentified gadid	258	31	289
Herring	37	152	189
Saithe	138	31	169
Poor cod	108	20	128
Dab	47	16	63
Plaice	51	9	60
Dragonet	29	22	51
Haddock	12	38	50
Unidentified Trisopterus	34	11	45
Sea Scorpion	38	3	41
Unidentified flatfish	29	6	35
Mackerel	5	29	34
Rockling	19	2	21
Ling	10	6	16
Butterfish	14		14
Whiting	6	7	13
Flounder (Butt)	12		12
Goby	9		9

v) Shetland

Species	SS	AW	Total
Sandeel	1092	1415	2507
Saithe	41	651	692
Norway pout	520	49	569
Poor cod	72	228	300
Herring	115	45	160
Unidentified gadid	73	65	138
Dragonet	124	7	131

Unidentified Trisopterus	44	54	98
Garfish		37	37
Mackerel	4	24	28
Cod	12	10	22
Plaice	18	2	20
Ling	11	4	15
Whiting	2	6	8
Dab	1	4	5
Lemon sole		5	5
Goby	3	1	4
Unknown Species	1	3	4
Eledone	1	2	3
Rockling	3		3

vi) Outer Hebrides

Species	**SS**	**Total**
Norway pout	798	798
Sandeel	250	250
Poor cod	201	201
Unidentified Trisopterus	54	54
Unidentified gadid	45	45
Whiting	34	34
Cod	33	33
Dragonet	28	28
Horse mackerel (Scad)	22	22
Mackerel	20	20
Norway pout or Poor cod	19	19
Herring	17	17
Unidentified Cottidae	16	16
Haddock	14	14
Eledone	10	10
Plaice	7	7
Saithe	3	3
Wrasse	3	3
Ling	2	2

Rockling	2	2

vii) Inner Hebrides

Species	SS	AW	Total
Poor cod	1378	2342	3720
Norway pout	2440	850	3290
Whiting	2285	744	3029
Blue whiting	890	329	1219
Unidentified gadid	700	284	984
Sandeel	354	570	924
Haddock	502	365	867
Unidentified Trisopterus	596	193	789
Dragonet	171	512	683
Norway pout or Poor cod	443	169	612
Herring	140	352	492
Mackerel	91	188	279
Cod	121	140	261
Saithe	86	60	146
Silvery pout	74	49	123
Horse mackerel (Scad)	18	66	84
Plaice	36	48	84
Witch	40	34	74
Rockling	18	44	62
Ling	28	19	47

B) Grey seal

i) Southern North Sea

Species	SS	AW	Total
Sandeel	3821	2368	6189
Whiting	199	171	370
Dover sole	58	157	215
Dragonet	65	101	166
Sea Scorpion	8	126	134
Rockling	2	97	99
Plaice	57	19	76

Unidentified flatfish	33	39	72
Bullrout	10	31	41
Cod	36	4	40
Goby	2	27	29
Hooknose (Pogge)	4	22	26
Pout whiting (Bib)	19	7	26
Lemon sole	11	12	23
Butterfish	14	7	21
Poor cod	21		21
Dab	14	4	18
Unidentified gadid	12	4	16
Unidentified Cottidae		15	15
Herring		14	14

ii) SE Scotland

Species	**SS**	**AW**	**Total**
Sandeel	4471	3969	8440
Whiting	30	378	408
Plaice	68	139	207
Unidentified flatfish	33	92	125
Unidentified gadid	18	83	101
Sprat		86	86
Cod	5	63	68
Dab		49	49
Hooknose (Pogge)		44	44
Bullrout	3	37	40
Lemon sole	13	14	27
Unidentified Trisopterus	1	26	27
Haddock	1	25	26
Poor cod	5	13	18
Dragonet	4	9	13
Long rough dab		13	13
Norway pout		13	13
Goby	1	11	12

Herring	9		9
Eelpout	1	4	5

iii) Moray Firth

Species	SS	AW	Total
Sandeel	2702	7417	10119
Poor cod		97	97
Haddock		92	92
Unidentified flatfish	7	52	59
Plaice	11	41	52
Rockling		49	49
Cod	5	39	44
Bullrout		30	30
Flounder (Butt)		26	26
Unidentified Trisopterus	1	24	25
Saithe		22	22
Dragonet		16	16
Unidentified gadid	1	15	16
Whiting	3	13	16
Dab	3	11	14
Sprat		9	9
Lumpsucker		7	7
Goby		5	5
Hooknose (Pogge)		4	4
Lesser weever	3	1	4

iv) Orkney

Species	SS	AW	Total
Sandeel	332	5906	6238
Norway pout	318	1036	1354
Poor cod	83	962	1045
Saithe	56	721	777
Unidentified Trisopterus	84	435	519

Cod	14	489	503
Haddock	20	367	387
Rockling	177	161	338
Plaice	39	290	329
Bullrout	13	228	241
Unidentified gadid	9	227	236
Herring	10	192	202
Unidentified flatfish	15	158	173
Sea Scorpion	2	142	144
Ling	2	118	120
Loligo	5	101	106
Whiting	8	98	106
Goby	72	24	96
Dab	26	69	95
Lemon sole	2	84	86

v) Shetland

Species	**SS**	**AW**	**Total**
Sandeel	119	1820	1939
Saithe	108	442	550
Poor cod	70	240	310
Goby		260	260
Norway pout	50	184	234
Dragonet	2	145	147
Unidentified gadid	39	50	89
Cod	17	53	70
Bullrout	26	32	58
Unidentified Trisopterus	7	43	50
Sepiola spp		45	45
Dab	1	38	39
Ling	1	35	36
Rockling	18	7	25
Lemon sole	4	20	24
Plaice	2	19	21

Sea Scorpion	9	10	19
Unidentified flatfish	6	12	18
Unidentified Squid		17	17
Loligo		15	15

vi) Outer Hebrides

Species	Total	AW
Sandeel	2904	2904
Norway pout	787	787
Poor cod	446	446
Unidentified		
Trisopterus	323	323
Unidentified gadid	91	91
Herring	83	83
Saithe	71	71
Dragonet	59	59
Whiting	52	52
Cod	48	48
Unidentified flatfish	46	46
Megrim (Whiff)	45	45
Ling	40	40
Eledone	34	34
Haddock	30	30
Lemon sole	30	30
Rockling	28	28
Loligo	26	26
Mackerel	21	21
Hake	14	14

vi) Inner Hebrides

Species	SS	AW	Total
Sandeel	10	1278	1288
Norway pout	34	1040	1074
Poor cod	16	627	643
Unidentified	6	372	378

Trisopterus			
Dragonet	12	205	217
Unidentified gadid	6	186	192
Blue whiting		152	152
Ling	5	97	102
Cod		97	97
Unidentified flatfish	1	87	88
Whiting	6	79	85
Eledone	1	72	73
Saithe		72	72
Rockling		57	57
Haddock	3	53	56
Witch	2	39	41
Thickback sole		39	39
Lemon sole		36	36
Sea Scorpion		32	32
Topknot		30	30

Appendix 5. 2: Harbour and grey seal diet listed according to prey type for each region and season (expressed as the percentage of each prey type in the diet by weight).

A) Southern North Sea

	Spring/ Summer		Autumn/ Winter	
Prey type	**harbour**	**grey**	**harbour**	**grey**
Gadid	3.8	11.5	29.5	10.6
Trisopterus	1.1	0.9	0.5	0.2
Sandeel	20.8	70.5	6.4	45.3
Flatfish	29.0	10.6	31.2	9.7
Sandy benthic	43.5	4.5	18.6	10.8
Scorpion fish	1.0	1.5	6.9	18.9
Pelagic	0.3	0.0	3.6	4.5
Salmonid	0.0	0.0	0.0	0.0
Cephalopod	0.0	0.5	2.9	0.0
Other	0.4	0.1	0.2	0.0

B) SE Scotland

	Spring/ Summer		Autumn/ Winter	
Prey type	**harbour**	**grey**	**harbour**	**grey**
Gadid	10.3	1.7	16.9	13.7
Trisopterus	0.0	0.1	0.0	0.4
Sandeel	44.4	86.1	0.0	60.7
Flatfish	38.6	6.1	49.7	12.5
Sandy benthic	0.0	1.0	5.9	1.1
Scorpion fish	0.0	0.5	1.3	8.3
Pelagic	1.1	4.3	13.4	2.1
Salmonid	1.4	0.0	0.2	0.0
Cephalopod	4.2	0.2	11.4	0.5
Other	0.0	0.0	1.3	0.7

C) Moray Firth

	Spring/ Summer		Autumn/ Winter	
Prey type	**harbour**	**grey**	**harbour**	**grey**
Gadid	2.2	0.2	5.9	11.6
Trisopterus	0.0	0.0	0.2	0.5
Sandeel	67.1	97.4	72.3	75.6
Flatfish	24.5	1.1	7.6	4.1
Sandy benthic	0.1	0.1	1.0	1.8
Scorpion fish	2.3	0.0	3.4	6.0
Pelagic	1.6	0.9	5.5	0.1
Salmonid	0.5	0.0	3.0	0.0
Cephalopod	1.7	0.0	0.5	0.1
Other	0.1	0.2	0.5	0.1

D) Orkney

	Spring/ Summer		Autumn/ Winter	
Prey type	**harbour**	**grey**	**harbour**	**grey**
Gadid	30.2	37.3	34.5	30.4
Trisopterus	1.0	10.0	0.2	3.2
Sandeel	52.2	19.4	15.5	31.1
Flatfish	5.9	3.2	5.4	7.4

Sandy benthic	1.1	2.2	2.9	1.7
Scorpion fish	2.7	7.8	0.1	9.0
Pelagic	6.2	16.5	39.2	13.8
Salmonid	0.0	0.0	0.0	0.0
Cephalopod	0.4	2.0	1.6	3.0
Other	0.3	1.7	0.5	0.2

E) Shetland

	Spring/ Summer		**Autumn/ Winter**	
Prey type	**harbour**	**grey**	**harbour**	**grey**
Gadid	21.5	35.3	26.0	32.7
Trisopterus	7.7	4.5	5.6	2.9
Sandeel	21.3	18.8	29.7	31.9
Flatfish	1.2	6.5	3.7	5.2
Sandy benthic	9.1	0.3	0.8	11.0
Scorpion fish	0.0	33.6	0.0	5.8
Pelagic	38.4	0.0	24.6	4.0
Salmonid	0.0	0.0	0.0	1.3
Cephalopod	0.8	0.9	0.2	1.8
Other	0.0	0.0	9.4	3.4

F) Outer Hebrides

	Spring/ Summer		**Autumn/ Winter**	
Prey type	**harbour**	**grey**	**harbour**	**grey**
Gadid	16.7			28.9
Trisopterus	23.9			6.0
Sandeel	12.7			37.0
Flatfish	1.9			5.9
Sandy benthic	2.7			3.1
Scorpion fish	15.8			0.5
Pelagic	22.3			11.5
Salmonid	0.0			0.0
Cephalopod	3.7			3.0
Other	0.3			4.2

G) Inner Hebrides

	Spring/ Summer		Autumn/ Winter	
Prey type	**harbour**	**grey**	**harbour**	**grey**
Gadid	53.2	38.2	33.3	31.1
Trisopterus	13.7	14.6	7.8	7.4
Sandeel	3.1	8.0	4.0	22.6
Flatfish	2.6	3.1	4.8	8.0
Sandy benthic	3.7	32.0	15.0	10.8
Scorpion fish	2.9	0.0	1.5	4.7
Pelagic	18.4	2.8	32.2	3.7
Salmonid	0.1	0.0	0.0	0.0
Cephalopod	2.2	1.2	1.0	3.9
Other	0.1	0.0	0.4	8.0

Appendix 5.3: 95% Confidence Limits (CL) for harbour seal diet composition expressed as the percentage of each prey type in the diet by weight (Appendix 5.2).

A) Southern North Sea

	95% CL			
	Spring/ Summer		**Autumn/ Winter**	
Prey type	**harbour**	**grey**	**harbour**	**grey**
Gadid	0.7-8.1	3.2-25.1	17.5-42.1	3.7-23.2
Trisopterus	0-3	0.1-2.6	0-1.3	0-0.7
Sandeel	6.2-39.4	47.1-85.7	1.6-14.7	8.9-72.6
Flatfish	17-39.1	5-19.7	18.4-44.4	3.9-20.5
Sandy benthic	30.4-62	1.4-10.4	12.5-30.6	4.5-21.4
Scorpion fish	0-3.5	0.4-4.2	2-14.5	5.9-47.9
Pelagic	0-0.7		1-7.6	0.8-11.6
Salmonid				
Cephalopod	0-0.1	0-1.5	0.5-6.8	
Other	0-1.3	0-0.3	0-0.8	

B) SE Scotland

	95% CL

	Spring/ Summer		Autumn/ Winter	
Prey type	**harbour**	**grey**	**harbour**	**grey**
Gadid	0.6-31.2	0.2-4.3	6.8-35.3	7-23.8
Trisopterus		0-0.5		0.1-0.8
Sandeel	9.6-76.6	70.9-93.9		37.6-77.2
Flatfish	8.7-70.3	2.2-15.4	17.2-70	6.4-22.3
Sandy benthic		0-3.3	0.3-14.9	0.2-2.7
Scorpion fish		0-2.4	0-6.9	2.6-20.1
Pelagic	0-4.1	0.9-11.5	2.7-39.7	0.3-5.6
Salmonid	0-6.2		0-0.7	
Cephalopod	0-13.3	0-0.6	0-37.7	0-1.5
Other		0-0.1	0-4.8	0-2.4

C) Moray Firth

	95% CL			
	Spring/ Summer		**Autumn/ Winter**	
Prey type	**harbour**	**grey**	**harbour**	**grey**
Gadid	1-5.8	0-1.1	2-22.8	2.3-32.4
Trisopterus	0-0.1	0-0	0-0.8	0.1-1.4
Sandeel	47.6-81.9	89.8-99.3	47-87	47.4-90.6
Flatfish	11.9-40.8	0.2-3.9	3.1-14.2	1.3-9.9
Sandy benthic	0-0.7	0-0.5	0-3.8	0.2-5.2
Scorpion fish	0.3-6.7		0-13.2	1.3-18.9
Pelagic	0.5-4.4	0-4.8	1.6-14.5	0-0.5
Salmonid	0-1.9		0-10.7	
Cephalopod	0-5.5		0-1.7	0-0.5
Other	0-0.2	0-1.3	0-1.5	0-0.2

D) Orkney

	95% CL			
	Spring/ Summer		**Autumn/ Winter**	
Prey type	**harbour**	**grey**	**harbour**	**grey**
Gadid	16.3-56.1	15.9-76.1	20.7-51.8	18.6-51.7
Trisopterus	0.3-2.1	2.1-19.6	0.1-0.4	1.5-5
Sandeel	25.1-71.6	1.4-51.3	6.2-29.5	14-53.5

Flatfish	1.6-12.2	0.7-7.2	1.1-12.6	3.9-11.3
Sandy benthic	0.4-2.5	0.3-6.6	0.4-8.7	0.8-2.9
Scorpion fish	0.3-10.7	0.4-23.2	0-0.5	4-17.2
Pelagic	1.6-13.9	2.5-34.5	23.2-56	6.4-23.2
Salmonid				
Cephalopod	0-1.3	0.2-5.1	0-3.7	1.6-4.4
Other	0-0.7	0.1-4.5	0-2.2	0.1-0.4

E) Shetland

	95% CL			
	Spring/ Summer		Autumn/ Winter	
Prey type	**harbour**	**grey**	**harbour**	**grey**
Gadid	7.7-47.8	16.1-74.2	8.3-68.0	15.7-65.7
Trisopterus	3.2-13.1	1.6-9.9	1.4-11.9	1.1-5.1
Sandeel	7.1-39.5	3.3-44.1	8.9-51.9	11.3-54.9
Flatfish	0-4.1	0.8-17.2	0.5-11.1	2.1-9.3
Sandy benthic	2.8-22.6	0-1.3	0-2.5	3.7-19.4
Scorpion fish		7.9-60.2		1.5-13.2
Pelagic	18.6-57.4		8.5-45.9	1.4-7.6
Salmonid				0-5.7
Cephalopod	0-2.3	0.1-2.6	0-0.7	0.6-3.4
Other	0-0.1		1.8-26.3	0.6-8.0

F) Outer Hebrides

	95% CL			
	Spring/ Summer		Autumn/ Winter	
Prey type	**harbour**	**grey**	**harbour**	**grey**
Gadid	7.2-33.6			15.1-51.0
Trisopterus	11.9-38			2.9-9.8
Sandeel	1.3-32.2			16.7-60.8
Flatfish	0.1-5.9			2.9-9.4
Sandy benthic	0-9.6			1.1-5.9
Scorpion fish	2.1-35.4			0-1.7
Pelagic	9.5-42.2			5.3-19.8
Salmonid				

Cephalopod	0.4-10.0			1.4-4.9
Other	0-0.8			0.2-13.3

G) Inner Hebrides

	95% CL			
	Spring/ Summer		**Autumn/ Winter**	
Prey type	**harbour**	**grey**	**harbour**	**grey**
Gadid	40.8-65.9	11.1-66.7	22.4-50.7	20.3-44.2
Trisopterus	8.9-17.4	4.8-34.1	4.2-11.4	4.2-11.4
Sandeel	1.2-6.9	0.7-30.2	1.0-9.3	9.1-45.5
Flatfish	1.4-4.3	0-6.4	2.1-8.8	4.5-12.0
Sandy benthic	1.2-8.5	5.7-56.3	6.3-29.6	5.0-17.7
Scorpion fish	0.2-8.2		0.5-3.1	0.9-13.0
Pelagic	9.8-33.8	0-12.4	17.8-48.7	1.5-7.3
Salmonid	0-0.2			
Cephalopod	0.8-3.9	0-5.0	0.3-1.9	2.2-6.0
Other	0-0.2		0-0.9	0.4-21.0

Appendix 5.4: The 95% Confidence Limits (CL) for harbour seal diet composition expressed as the percentage of each prey species in the diet by weight (Table 5.3).

A) Southern North Sea

	95% CL			
	Spring/ Summer		**Autumn/ Winter**	
species	**harbour**	**grey**	**harbour**	**grey**
Cod	0-6.0	0.3-14.5	0-3.0	0-9.4
Whiting	0.5-2.7	1.5-14.4	16.1-40.6	2.1-13.1
Plaice	2.5-17.1	1.4-8.1	2.8-17.5	0.2-3.2
Lemon sole	0.2-4.8	0-1.5	1.2-16.1	0.1-4.9
Dover sole	3.4-14.0	1.6-7.5	1.1-18.5	2.3-13.5
Sandeel	6.2-39.4	47.1-85.7	1.6-14.7	8.9-72.6
Dragonet	25.8-57.7	1.2-10.0	10.1-28.9	4.4-21.1
Goby	2.4-7.9	0-0	0.7-3.6	0-0.1
Bullrout	0-3.0	0.2-2.7	0.7-11.7	0.7-20.5

Sea Scorpion	0-0.7	0.1-1.8	0.2-6.1	2.5-39.6

B) SE Scotland

	95% CL			
	Spring/ Summer		**Autumn/ Winter**	
species	**harbour**	**grey**	**harbour**	**grey**
Cod	0-7.2	0-2.2	0.1-9.7	2.0-12.4
Whiting	0.1-27.6	0-2.4	0.6-22.9	1.9-7.9
Plaice	0.8-44.6	0.7-4.4	8.9-54.6	2.8-11.9
Flounder (Butt)	0.2-20.9		0-10.8	0-0.4
Dab	1.7-21.6		0.8-10.2	0.8-6.5
Mackerel		0-0.4	0-24.3	
Sprat	0-3.6		0-25.5	0.3-5.6
Sandeel	9.6-76.6	70.9-93.9		37.6-77.2
Bullrout		0-2.4	0-6.9	1.8-17.2
Loligo	0-13.3	0-0.6	0-37.7	0-1.5

C) Moray Firth

	95% CL			
	Spring/ Summer		**Autumn/ Winter**	
species	**harbour**	**grey**	**harbour**	**grey**
Haddock	0-1.7		0-0.1	0.1-24.5
Plaice	3.1-14.1	0.1-1.8	0.5-2.9	0.3-1.9
Dab	3.3-21.0	0-1.9	0.6-4.4	0.1-1.6
Sandeel	47.6-81.9	89.8-99.3	47.0-87.0	47.4-90.6

D) Orkney

	95% CL			
	Spring/ Summer		**Autumn/ Winter**	
species	**harbour**	**grey**	**harbour**	**grey**
Cod	8.1-32.5	1.3-19.8	13.2-39.1	7.1-22.1
Haddock	0-1.9	2.2-9.2	0.8-6.5	0.5-11.5
Saithe	0.7-39.1	2.3-68.2	0.2-13.2	0.9-32.7
Norway pout	0-0	1.0-15.3		0.5-2.6
Mackerel	0.1-4.7	0-2.9	1.9-21.2	0-1.1

Herring	0.6-11.9	1.2-32.1	16.1-48.5	5.7-22.2
Sandeel	25.1-71.6	1.4-51.3	6.2-29.5	14-53.5
Bullrout	0.1-2.4	0-21.5		2.6-15.0

E) Shetland

	95% CL			
	Spring/ Summer		Autumn/ Winter	
species	**harbour**	**grey**	**harbour**	**grey**
Cod	0-0.3	2.8-17.3	0.3-4.0	2.0-16.5
Saithe	0.7-39.5	2.6-66.0	3.9-66.5	2.5-57.1
Ling	1.2-17.4	0-3.2	0-1.9	1.4-7.1
Poor cod	0.4-2.3	0.8-5.3	1.0-11.3	0.6-3.2
Norway pout	2.2-11.2	0.4-5.2	0-1.3	0.2-2.3
Mackerel	0-5.2		1.8-31.2	0-2.1
Herring	17.8-55.2		4.1-26.8	0.6-6.2
Sandeel	7.1-39.5	3.3-44.1	8.9-51.9	11.3-54.9
Dragonet	2.8-22.6	0-1.3	0-2.5	3.6-19.3
Bullrout		5.6-54.2		1.2-12
Sea Scorpion		0.5-17.9		0.1-2.7
Garfish			1.7-26.3	0-0.3

F) Outer Hebrides

	95% CL			
	Spring/ Summer		Autumn/ Winter	
species	**harbour**	**grey**	**harbour**	**grey**
Cod	1.0-7.4			2.3-20.2
Ling	0-9.6			2.6-13
Norway pout	8.8-31.6			1.6-6.5
Mackerel	3.2-33.2			0.1-3.1
Herring	1.9-15.4			4.8-18.5
Sandeel	1.3-32.2			16.7-60.8
Unidentified Cottidae	2.1-35.4			

G) Inner Hebrides

	95% CL

	Spring/ Summer		Autumn/ Winter	
species	**harbour**	**grey**	**harbour**	**grey**
Cod	4.8-14.1		2.4-8.8	5.3-17.9
Whiting	7.5-16.0	0-14.5	2.8-8.3	0.5-2.2
Haddock	5.5-12.8	0-8.8	4.6-13.0	0.6-2.8
Ling	1.8-7.6	2.7-57.6	0.9-5.9	4.3-14.4
Blue whiting	4.0-16.3		1.4-6.4	0.2-3.6
Poor cod	3.4-8.1	0.7-9.9	2.9-8.4	1.3-3.6
Norway pout	4.4-9.3	2.0-29	0.8-2.7	2.4-8.3
Mackerel	3.1-26.0	0-12.4	4.1-33.6	0-0.1
Herring	3.7-12.0		7.6-22.8	1.4-7.0
Sandeel	1.2-6.9	0.7-30.2	1.0-9.3	9.1-45.5
Dragonet	1.2-8.5	5.7-56.3	6.3-29.6	5.0-17.7
Ballan wrasse	0-0		0-0.4	0.1-20.7

Chapter 6

GENERAL DISCUSSION

To understand inter-specific competition between harbour (*Phoca vitulina*) and grey (*Halichoerus grypus*) seals around Britain, and whether this may be a contributing cause to the observed declines in harbour seal abundance, requires knowledge of many aspects of their ecology including at-sea and on-land distribution and habitat use, population abundance and trends, and spatial and temporal variation in diet composition and foraging. Our knowledge is good for some of these aspects, especially trends in on-land distribution and abundance, but less good for others. In particular, there is little information on changes over time in either the diet of harbour seals or the foraging distribution and behaviour of both grey and harbour seals.

Around Britain, grey seals have much greater abundance than harbour seals (SCOS, 2013) and each species is experiencing different population trajectories in different regions. Grey seal numbers are either increasing or remain stable (SCOS, 2013) while harbour seal populations are increasing, stable or declining (Lonergan *et al.*, 2007; SCOS, 2013), depending on the area. Availability of prey resources can have large effects on consumers. In pinnipeds, insufficient quality and/or quantity of prey has adversely influenced population abundance (Trites and Donnelly, 2003), body size (Majluf, 1991), reproduction (Trillmich and Limberger, 1985), birth weight (Lunn *et al.*, 1994), pup survivorship (Trillmich and Limberger, 1985) and physiology (*e.g.*, through metabolic depression, Rosen and Trites, 1999).

An extensive list of the potential causes of harbour seal population declines was proposed in Hall and Kershaw (2012) and included: infectious disease (*e.g.*, bacterial infections, viral infections, parasites and protozoans), non-infectious disease (*e.g.*, persistent organic pollutants), biotoxin exposure (*e.g.*, domoic acid), nutritional stress, prey quality, prey quantity, trauma, shooting, ecological overlap with other species (*e.g.,* competition with grey seals and direct exclusion), human disturbance, predation and fisheries interactions (*e.g.*, by-catch). The most likely candidates which could be causing localised harbour seal population declines were expected to involve prey (changes in quality or quantity of prey and uptake of marine toxins from harmful algae) or trauma (the impact of unexplained or "corkscrew" deaths).

Hall and Kershaw (2012) also conducted a review of ongoing (now completed) studies on harbour seals, which showed that there were no differences in pup mortality across areas with contrasting population dynamics (Hanson *et al.*, 2013), and that in the Moray Firth, harbour seals had high survival rates (Mackey *et al.*, 2008; Cordes, 2011; Cordes *et al.*, 2011) and high fecundity rates that were indicative of a population in recovery (Cordes and Thompson, 2014). There is no information on survival and fecundity rates from other populations.

Between 2008 and 2010, 76 dead seals washed ashore (mostly in Norfolk, England and Fife, Scotland) with injuries that were consistent with the animals having been drawn through the ducted propellers of ships (trauma consisting of a single continuous curvilinear skin laceration spiralling down the body, Bexton *et al.*, 2012). Assuming that not all carcasses wash ashore, this could be an important cause of mortality and could have significant impacts on the abundance of seals in some areas.

This thesis was motivated by questions concerned with potential prey-related drivers of the observed harbour seal declines. Have harbour seal populations been affected by changes in prey quality and/or quantity and does inter-specific competition for prey with grey seals play any role? The main objectives were: to generate digestion correction factors for accurate estimation of harbour seal diet, to use faecal analysis to determine the diet of harbour seals around Britain, to examine sex-specific variation in the diet of harbour seals, and to compare the diet of harbour and grey seals around Britain to explore whether there is evidence that these species compete for food and whether the decline of harbour seals in some areas can be linked to competition for prey.

To estimate accurately the size and number of prey consumed using faecal analysis, digestion correction factors (DCFs) must be applied to measurements and counts of fish otoliths and cephalopod beaks. I conducted 100 whole prey feeding trials on the 18 prey species most commonly found in the diet of harbour seals around Britain (Chapter 2). I developed digestion coefficients (DCs) to account for partial digestion of otoliths and recovery rates/number correction factors to account for complete digestion of otoliths/beaks. Recovery rates were broadly similar to those for grey seals, but harbour seal species- and grade-specific DCs were generally smaller (Grellier and Hammond, 2006). Differences in partial and complete digestion rates among prey species and between harbour (Tollit *et al.*, 1997b) and grey seals (Grellier and Hammond, 2006) highlighted the importance of applying predator- and prey-specific digestion correction factors when reconstructing diet and I used these new DCFs to estimate diet accurately in the subsequent chapters.

Regional and seasonal differences in the diet of harbour seals around Britain appear to reflect a qualitative association with the distribution, abundance and seasonal patterns (feeding, spawning and migrations) of their prey (Chapter 3). Large changes in the diet of harbour seals compared to earlier studies (Pierce *et al.*, 1990a; Thompson *et al.*, 1996b; Tollit and Thompson, 1996; Brown and Pierce, 1998; Hall *et al.*, 1998; Pierce and Santos, 2003; Sharples *et al.*, 2009) were not observed and the size of prey eaten by harbour seals appears to have remained relatively consistent, with the majority of prey eaten less than 30 cm in estimated length (Hall *et al.*, 1998). In regions that are currently undergoing serious population declines, limited changes in the diet were observed between this and previous studies undertaken at times of high harbour seal abundance. Unfortunately, large sample sizes were difficult to obtain in regions where the population of seals has been declining (southeast Scotland, Orkney and Shetland) and a full seasonal and regional comparison was not possible.

I explored sex-specific variation in the diversity, composition and quality of the diet of harbour seals. Overall differences in the diet metrics between males and females tended to be small except in The Wash in winter, when the diet quality of female seals was significantly higher than males and this difference was large enough to result in a difference in diet quality across all seasons (Chapter 4). Consumption of pelagic prey, which are higher in calorific density, appeared to be driving this change and I associated the increased diet quality in this season with the reproductive condition and energy requirements of female seals; that is, their need to recover body condition following lactation and moult and to support rapidly growing foetuses and neonates in the following seasons (Bowen *et al.*, 1992; Greig, 2002; Paterson *et al.*, 2012). The Wash is the only area around Britain where harbour seals are increasing in abundance (SCOS, 2013). This finding may therefore be important and its detectability may only have arisen because of the large sample sizes obtained in this region. The declining population trend of harbour seals in southeast Scotland, Orkney and Shetland may indicate that in these regions female seals are not getting this critical energy boost at an important life stage. Unfortunately, large enough sample sizes for male-female diet comparisons were not obtained in other regions but this could be an important area of future work.

I used the same diet metrics to investigate the degree of overlap in the dietary niche of sympatric harbour and grey seals (Chapter 5). Differences in the diet metrics between species, regions and seasons tended to be small and I found no clear evidence that diet reflected inter-specific competition (Chapter 5). Examination of the distribution and abundance of the three main prey types in the diet of both species (sandeel, pelagic fish and large gadoids) revealed the importance of sandeel in the North Sea and there was some evidence that changes in the proportion of sandeel in the diet of harbour seals may be affecting population dynamics *e.g.*, in southeast Scotland. On the west of Scotland however, where both harbour and grey seals eat a wider range of prey species sandeel made up only a minor proportion of the diet (Chapter 5). As such, it is not possible to infer that sandeel is the dominant prey species influencing seal population dynamics around Scotland.

Quantifying inter-specific competition is challenging and studies tend to focus on partitioning or overlap of resource/habitat use to try to understand the coexistence of two potential competitors (Schoener, 1968; Whitehead *et al.*, 2003; Page *et al.*, 2005a; Jeglinski *et al.*, 2013).

In Orkney and Shetland, two regions that have undergone substantial declines in harbour seal numbers, the diet remains similar to that proposed by (Brown and Pierce, 1998; Brown *et al.*, 2001), though it is possible that the proportions of pelagic and sandeel prey have increased as the previous diet estimates did not take into account complete digestion of otoliths. The biggest changes in these regions however, appear in the diets of grey seals. It is possible that intra-specific competition for resource may be self-limiting this species in these regions where the population has remained stable for approximately 10 years (SCOS, 2013). I propose in Chapter 5 that declines in harbour seals in these regions may be linked to the greater energy requirements required to locate and capture pelagic prey which is prevalent in the diet. Though this prey type has also increased in grey seal diet, these larger predators may be more able to balance the cost/benefit of their foraging activities.

In southeast Scotland, sandeel contribution to the diet of harbour seals has declined (Sharples *et al.*, 2009) while its contribution to the diet of grey seals has increased (Hammond and Grellier, 2006). At the same time the population of grey seals in the region is increasing as a whole (SCOS, 2013). Flatfish were the dominant prey of harbour seals in this region (Chapter 3) and it is possible that harbour seal net energetic gain from the diet is not enough to support individual survival. The flatfish prey group (specifically: plaice, dab and long rough dab) has also been highlighted for their importance in trophic transfer of toxins from harmful algae to pinnipeds (S. Jensen, Pers. Comm.). However, scat and fish sample sizes available for estimating diet and biotoxin transfer were small and no firm conclusions can yet be drawn about changes in prey abundance in the diet and the impact of biotoxins. Southeast Scotland may be the only region in which diet was examined where harbour seals may be declining possibly as a consequence of competition for prey with grey seals, however, increased sampling effort over the longer term would be necessary to validate this proposition.

In the West coast regions, where sandeel is much less important in the diet and lower quality gadoid fish dominate, I propose that seals need to use less energy to find their prey, despite exhibiting similarities in foraging trip distances and durations with seals in Orkney and Shetland (*e.g.*, harbour seals, Cunningham *et al.*, 2009; Sharples *et al.*, 2012). It is currently not possible to estimate foraging success including; where, when or how often prey are captured and eaten and so this proposal is unverified. Using telemetry data, foraging is often inferred from dive shape with square bottom dives and time being indicative of foraging (Baechler *et al.*, 2002). However, this does not provide information on feeding success (ingestion).

Techniques do exist, however, to measure prey ingestion. Animal borne video (*e.g.*, CRITTERCAMS) have been used on a range of marine animals including harbour seals and Antarctic fur seals (*Arctocephalus gazella*) to reveal information on animal foraging (Marshall, 1998; Hooker *et al.*, 2002; Heaslip *et al.*, 2014). Liebsch *et al.* (2007) used a Hall sensor-magnet system and inter-mandibular angle sensors attached to an animal's jaw to identify feeding events. Based on captive experiments with a harbour seal and

Australian sea lion (*Neophoca cinerea*), feeding events were clearly distinguishable from other jaw movements except for small prey (Liebsch *et al.*, 2007). More recently fast movements of the head and jaws have provided reliable feeding cues in harbour seals with small low-power accelerometers mounted on the head (Ydesen *et al.*, 2014). This newer method detected both raptorial and suction feeding (Ydesen *et al.*, 2014). As such, this method may have more potential for detecting consumption of smaller prey items such as sandeel and therefore be a more relevant method for investigating feeding success in harbour seals. Telemetry studies incorporating new technology such as this would be beneficial in furthering our understanding of the cost of foraging activities for both harbour and grey seals in the different regions.

As a cause of the decline of harbour seals, competition with grey seals is a prominent working hypothesis. However the nature of such competition is not clear and it may not be prey related. In some areas around the coast there have been marked changes in the abundance of grey and harbour seals hauled-out on land. For example, at the Mousa Special Area of Conservation (SAC) for harbour seals off Shetland's southeast mainland, the number of harbour seals counted has declined (reported in, SNH, 2006) and the number of grey seals has increased (personal observation and K. Grellier Pers. Comm.). Changes in the haul-out distributions of grey seals outside of the breeding season are not monitored *per se*, and it is possible that grey seals due to their greater abundance are impacting the behaviour and physiology of harbour seals through disturbance at, or displacement from, their traditional resting places. The consequences of this may be increased cost of living, which they may be unable to meet during their coast foraging activities.

Overlap or change in the at-sea distribution of harbour and grey seals should provide insight into the complexities of dietary niches between these two seal species. Telemetry data for both species has been collated over a number of years at the Sea Mammal Research Unit (SMRU) and an upcoming project investigating temporal and spatial variation in trip metrics may provide evidence of any at-sea disturbance or displacement of foraging activities between the seals.

Grey seals may also be impacting the harbour seal population in other ways, such as direct predation. In Chapter 4 I introduced killer whales as a predator of harbour seals particularly in the Northern Isles (Weir, 2002; Bolt *et al.*, 2009; Foote *et al.*, 2010;

Deecke *et al.*, 2011) where seasonal sightings of killer whales peak during the harbour seal pupping period (Bolt *et al.*, 2009). Grey seals have recently been identified as predators and/or scavengers of harbour porpoises (*Phocoena phocoena*) in the North Sea/English Channel (Haelters *et al.*, 2012; Bouveroux *et al.*, 2014). Though predation on harbour seals by grey seals has not been directly observed, grey seals have been seen behaving aggressively towards and scavenging dead grey seal pups (M. Bivins, Pers. Comm.).

In this study the sample sizes were not always adequate to conduct seasonal comparisons in diet metrics. Larger samples sizes over a longer time period would allow for a much more detailed appraisal of diet and potential dietary change in these higher predators. If such work could be linked with long-term individual-based studies of key life parameters (*e.g.*, survival and fecundity) this would provide better understanding of diet, body condition and individual reproductive success. Fatty acid analysis may provide a better means of linking diet and individual parameters. Blubber collected from individual seals (ideally remotely) could be used to assess body condition (core depth, Boyd, 1984) and diet over weeks to months using quantitative fatty acid signature analysis (Budge *et al.*, 2006; Iverson, 2009).

The environment in which harbour and grey seals exist has a major influence on the diet and foraging behaviour of these and other higher predators. Over the last 50 years, there has been an overall decline in commercial fish spawning stock biomass (SSB) in the North Sea including cod, whiting and sandeel, (ICES, 2011b; 2014a; f). All commercially exploited stocks are still considered to be in a seriously depleted condition, although there are signs of increasing SSB in recent years (ICES, 2011b; 2014a; f). Furthermore, the abundance of large fish has decreased and numbers of small fish significantly increased (Daan *et al.*, 2005; Marty *et al.*, 2014). Smaller fish body size has also been proposed as a universal outcome of warming temperatures (Daufresne *et al.*, 2009) and, in the North Sea, six of eight commercial fish species underwent reductions in body size over the last 40 years coinciding with a 1-2 °C increase in water temperature (Baudron *et al.*, 2014). Further consequences of warming sea temperatures are the deepening of fish assemblages by ~ 3.6m decade^{-1}, (Dulvy *et al.*, 2008) and an increase in fish species with typically more 'southern' distributions (*e.g.*, red mullet, anchovy and pilchard) in the northern North Sea (Beare *et al.*, 2004).

A marked difference in harbour porpoise distribution in the European Atlantic, including the North Sea, has also been documented with higher densities in northern areas in 1994 and more southerly areas in 2005 (Hammond *et al.*, 2013). Although the pattern was less clear, there was also a suggestion in the data of the same pattern for minke whale (*Balaenoptera acutorostrata*, Hammond *et al.*, 2013). Reasons behind the cetacean distribution changes include shifts in prey availability (Hammond *et al.*, 2013).

Studies of seabirds indicate that population level responses have a close correlation with fish prey abundance (Furness and Tasker, 2000; Rindorf *et al.*, 2000). Overall, seabirds numbers in Britain have increased over the last century as a direct result of increased protection from hunting and persecution (Mitchell *et al.*, 2004). However, fluctuations in abundance do occur; for example, declines in the breeding populations of seabirds in Shetland have been linked to the 1985-1990 collapse of the sandeel stock in local waters (Mitchell *et al.*, 2004).

Overlap in trophic, temporal and spatial niches may result in competition within and/or between species which may affect the health (Trillmich and Limberger, 1985; Majluf, 1991) or survival of individuals (Trillmich and Limberger, 1985; Mair, 1998) and could be an important factor in changing community structure (Trites and Donnelly, 2003). Full exploration of niche differentiation requires an understanding of several niche dimensions such as diving depth, activity budget, at-sea movement and haul-out behaviour alongside dietary parameters which may include analysis of prey hard remains, fatty acids, faecal DNA or stable isotope analysis. Individual studies combining these parameters provide an interesting snapshot of foraging niche overlap or separation (*e.g.*, Clarke *et al.*, 1998; Lynnes *et al.*, 2002; Whitehead *et al.*, 2003; Page *et al.*, 2005a). However, long term studies of these niche dimensions carried out contemporaneously are needed to provide a clearer understanding of existing or changing niche dynamics between species (e.g., Reid and Arnould, 1996; Croxall *et al.*, 1999; Barlow *et al.*, 2002).

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