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The diet of the grey seal [*Halichoerus grypus* (Fabricius, 1791)] in Ireland and potential interactions with commercial fisheries

Martha Gosch, BSc. MSc.



A thesis submitted in fulfilment of the requirements for the degree of Doctor of Philosophy

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Declaration

This is to certify that the work I am submitting is my own and has not been submitted for another degree, either at University College Cork or elsewhere. All external references and sources are clearly acknowledged and identified within the contents. I have read and understood the regulations of University College Cork concerning plagiarism.

Martha Gosch

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ABSTRACT

Grey seal populations have steadily increased in recent decades, across their range. Concurrently, interactions between grey seals and fisheries have seemingly increased, with high levels of by-catch occurring in set-net fisheries and high incidents of depredation reported by fisheries. The latter, along with a perception that grey seals are competing for commercial fish stocks, has led to increasing calls from the fishing industry within Ireland to introduce a seal cull. Grey seals are protected under national and EU legislation, including under Annex II of the Habitat's Directive (Council Directive: 92/43/EEC) and very little is known about their diet and foraging ecology. The extent to which commercial species contribute to grey seal diet composition has not been recently quantified. As apex predators, grey seals likely play a fundamental role in the structuring and functioning of an ecosystem. Investigating their diet can therefore provide valuable insights into the trophic interactions that are occurring within a region. Grey seals are widely acknowledged as displaying a generalist feeding strategy, taking advantage of those prey species which are locally and seasonally abundant. The presence of prey species within the diet is thought to broadly reflect fish distribution and abundance within a region. The biologically productive areas along the west and south western coast support numerous fish and cephalopod species that may form an important component of grey seal diet in Ireland. This study aimed to investigate prey species assemblages occurring within grey seal diet in Ireland, particularly with regards to the presence of commercial species, and provide current baseline data on diet composition. To describe prey species contribution to the seals diet, the traditional method for diet reconstruction was used. A number of approaches under this methodology were tested, such as using the "all structures" approach versus using otoliths alone for prey identification, and whether the application of correction factors improved prey biomass estimates. Prey detection increased substantially when "all structures" were included, while a deficit of correction factors for non-otolith/beak structures tended to under-estimate the biomass contribution of certain prey species. To assess whether grey seals in Ireland alter their diet with time, faecal (scat) samples were collected from a colony of national importance on the southwest coast over a period of just under five years. Results highlighted significant seasonal and inter-annual variations occurring within the diet. *Trisopterus* species and sandeels (Ammodytidae) were found in the highest abundances with their relative proportions

contributing significantly to the observed temporal effects within the diet. In order to study spatial variation in diet, scat samples collected from a major haul-out site on the southeast coast of Ireland were compared to samples collected over the same time period from the southwest coast sample site. Findings indicated that significant regional differences in diet occurred between geographic locations. Differences in prey assemblages are assumed to be related to foraging habitat type surrounding each haul-out site. Higher abundances of pelagic species were found within samples collected from the southwest coast with seals that haul-out on the southeast coast consuming larger quantities of flatfish. While commercial species were found in relatively low abundances at both sites, haddock/pollock (*Melanogrammus aeglefinus/Pollachius pollachius/ P. virens*) species were substantial contributors in terms of biomass to grey seal diet in Ireland. Stomach samples from juvenile by-caught seals obtained from the west and south coast of Ireland indicate that this cohort are not primarily responsible for the reported levels of depredation occurring. Low quantities of fishery target species were recovered from forty-four samples, with only one fish clearly depredated, and lengths from a total of four prey fish overlapping with sizes targeted by the fisheries. The findings from this study are discussed in relation to results from other geographical areas of the grey seals distribution, with potential mitigation measures and future recommendations considered.

CHAPTER 1

General Introduction

1.1 INTRODUCTION

Ocean ecosystems provide important and valuable resources for humans and marine predators. Top marine predators, including seabirds and marine mammals, play a vital role in ecosystem structure and functioning, and their absence can lead to declines in local species diversity, with the system shifting towards simplicity as single species start to monopolise resources (Paine, 1966). As a result, higher predators are often used as indicators of ecosystem condition and change (e.g. Harris & Wanless, 1990; Furness & Camphuysen, 1997; Reid & Croxall, 2001; Weimerskirch *et al*., 2003).

In order to understand how apex predators and their populations respond to changing ecological and environmental conditions, together with their functional roles in the marine ecosystem, information on their foraging ecology, including diet, is necessary (Heithaus *et al*., 2008; Barnett *et al*., 2010; Pompanon *et al*., 2012; Bowen & Iverson, 2013; Bromaghin *et al*., 2016).

Predator dietary investigations are additionally beneficial for providing insights into niche width that animals occupy (Berg, 1979); inter-specific competition between marine mammals (e.g. Spitz *et al.,* 2006); resource competition between marine mammals and human fisheries (Butler *et al*., 2006); area-specific or global food consumption (Pauly *et al*., 1998); foraging habitat preferences (Pauly *et al*., 1998); determining dependence on high trophic level species of economic importance, or lower trophic level prey such as invertebrates (Hobson *et al*., 1996), and contaminant loading within an ecosystem (Hobson *et al*., 2002). The estimation of resource use is achieved by combining estimates of marine mammal energy requirements with empirically determined estimates of their diet composition and the energy content of the prey (e.g. Trites *et al.* 1997; Boyd, 2002).

Ecological modelling approaches such as "Ecopath with Ecosim" (EwE), enables the interactions between predator and prey to be analysed. Amongst many other applications, predator consumption rates and diet can be used to assess mortality impacts on particular prey groups, or to estimate predator population consumption rates. By gathering as much information on the components of an ecosystem (e.g. exploitation, interactions), Ecopath has the ability to illustrate how the energetic flow,

the biomasses and their corresponding utilisation may function in a particular study system (Christensen & Walters, 2004).

While ecological modelling tools can provide insights into the energy requirements of predators and their annual food consumption, the bioenergetics outputs supply no indication as to the specific prey species being consumed (Jobling, 1987). The primary information gained from diet studies therefore reveals details on the feeding behaviour of the studied predator, although, understanding the complexities within a food web is complicated if the predator is a generalist (Pompanon *et al*., 2012).

The majority of trophic models group prey species into larger categories, however, for accurate diet composition description, prey items should ideally be identified to their highest taxonomic resolution. This is particularly true when investigating potential competition for resources between marine mammals and fisheries as high value species, e.g. plaice (*Pleuronectes platessa*) may appear similar to others of far less economic value e.g. dab (*Limanda limanda*).

Challenges of reconstructing marine mammal diet:

In order to address gaps in our knowledge, and to determine the role top predators play in their ecosystem, assessing the diet of marine mammals requires accurate estimations of prey composition (Casper *et al*., 2006). These descriptive estimations can then elucidate as to which prey species are particularly dominant within the diet, and whether predators are selecting fish resources also targeted by local fisheries. However, as marine mammals are free-ranging and foraging takes place underwater, opportunities for direct observation of prey consumption are limited (Pierce & Boyle, 1991; Bowen & Iverson, 2013).

The traditional method of diet analysis through the identification of prey hard parts (mainly otoliths and cephalopod beaks) is, to date, the most commonly employed technique due to its practicality in terms of economic and material costs, together with the relative ease of access to samples and is non-invasive (Bowen & Sniff, 1999; Hamill *et al*., 2005; Hückstädt *et al*., 2007). Samples generally consist of faecal (scat) material (e.g. Pierce *et al*., 1991; Kavanagh *et al*., 2010; Geiger *et al*., 2013), stomach (e.g. Bowen *et al*., 1993; Spitz *et al*., 2006; Hernandez-Milian *et al*., 2016) or regurgitate content (Harvey & Antonelis, 1994; Votier *et al*., 2003). Prey remains can generally be identified to a high taxonomic resolution (i.e. species level), with the

content reflecting the diet composition of the previous few days, unlike many molecular methods which rely on analysis of predator tissue samples (such as stable isotope analysis of fatty acid signatures), which are indicative of trophic level interactions only (Williams *et al*., 2012). Regression methods based on the relationship between otolith/beak size and prey size enable length and biomass estimates to be derived that are based on realistic assumptions (Pierce & Boyle, 1991).

There are however, several limitations associated with this methodology (Jobling & Breiby, 1986). Prey-specific differential rates of passage and differential erosion rates of diagnostic structures are widely acknowledged sources of bias (Olesiuk *et al*., 1990; Tollit *et al*., 1997; Orr & Harvey; Staniland, 2002; Yonezaki *et al*., 2003; Grellier & Hammond, 2006). To combat the degradation of otoliths, there exists within the literature some correction factors accounting for both partial and complete erosion (e.g. Murie & Lavigne, 1985; da Silva & Neilson, 1985; Jobling, 1987; Dellinger & Trillmich, 1988; Harvey, 1989; Harvey & Antonelis, 1994; Tollit *et al*., 1997; Bowen, 2000; Grellier & Hammond, 2006). The use of otoliths only for the identification of fish prey has also been shown to reduce prey detectability particularly for species containing fragile and/or small otoliths (Boyle *et al*., 1990), and otoliths may be lost during sampling (Iverson *et al*., 2004). Related to this is the lack of otoliths contained within cartilaginous fish, which has led to such species being substantially underestimated within marine mammal diet (Pierce *et al.*, 1993). Furthermore, particularly large prey are often not consumed in their entirety and instead have bites removed from the flesh, thereby leaving behind the head containing the otoliths (Lundström *et al*., 2010; Cosgrove *et al*., 2015). Differentiating between secondarily ingested prey may also introduce potential bias when enumerating prey items contained within the diet of animals that feed on large carnivorous fish. Otoliths identified within predator diet samples may have originated from the digestive tracts of fish prey (Arnett & Whelan, 2001; BIM, 2001; Moore, 2003). While not yet wide spread in aquatic predator diet analysis, the identification of non-otolith diagnostic structures alongside otoliths for prey detection (termed "all structures") increases the probability of improved quantitative prey estimation within the diet (Olesiuk *et al*., 1990; Pierce *et al*., 1991a; Cottrell *et al*., 1996; Tollit *et al*., 1997; 2003; Fernandez *et al*., 2009; Hernandez-Milian & Rogan, 2011).

Molecular techniques to facilitate the detection of prey identities and their proportions have been used in marine mammal diet analysis with some success for over 50 years (Tollit *et al*., 2010; Pompanon *et al*., 2012). Certain caveats do however exist in relation to DNA based methods. While conventional PCR techniques are valuable tools for detecting target species (e.g. salmon, *Salmo salar*) from hard remains in scats and stomach contents (Purcell *et al*., 2004; Parsons *et al*., 2005; Wright *et al*., 2007) they can lack resolution, are often labour intensive, and provide qualitative rather than quantitative estimates (Tollit *et al*., 2010; Pompanon *et al*., 2012). To improve prey detection, real-time PCR (qPCR) methods have proven successful when analysing samples that are limited in quantity and quality (e.g. Matejusová *et al*., 2008) and Taqman qPCR assays have the capacity to determine the species and sex of the source predator (Matejusová *et al*., 2012). However, predator and prey species need to be distinguished and issues arise regarding secondarily ingested prey (Méheust *et al*., 2015). Furthermore, while relative quantities of prey can be established, DNA degradation during digestion, particularly when analysing the diet of predators containing mixed prey species remains a problem (Matejusová *et al*., 2008). This can lead to potential biases similar to those that affect traditional hard part analysis diet studies, when attempting to quantitatively estimate prey abundance (Tollit *et al*., 2010). However, molecular techniques are continually being refined and new methods are being developed e.g. DNA barcoding (e.g. Méheust *et al*., 2015), next generation sequencing (e.g. Deagle *et al*., 2009), and near infrared spectroscopy (e.g. Kaneko & Lawler, 2006; Rothman *et al*., 2009), leading to a reduction in costs and an expansion in the availability of sequence databases (Pompanon *et al*., 2012).

Many dietary indices are available to facilitate diet study comparisons, however some are more widely used than others (Ahlbeck *et al.,* 2012). Numerical percentage (%N) is the most commonly used index as it takes into account potential food availability and ingested food (Berg, 1979). However differential passage rates of prey may bias estimates (Pillay, 1952). While the percentage frequency of occurrence (%F) can provide substantial information regarding the variety of prey species consumed and consistently relied on, it provides no indication of prey weight or their subsequent contribution to the diet (Bowen *et al*., 1993). The percentage biomass (%B) describes the nutritional value associated with specific prey and the assessment of predator impact on prey populations (Ahlbeck *et al*., 2012), however it may over-estimate the

importance of individual large prey, and prey of low calorific value in energetic studies (Pierce & Boyle, 1991). Composite indices, such as the relative index of relative importance (Piankas *et al*., 1971), incorporate values of different methods and may facilitate comparative regional diet studies (Windell, 1971; Cortés, 1997). However, as composite indices are based on multiplication methods, this can introduce various biases thereby increasing the chances of potential errors (Hyslop, 1980; Bigg & Perez, 1985; Hansson, 1998; Ahlbeck *et al*., 2012).

Grey seals:

The grey seal (*Halichoerus grypus*) is an apex marine predator. It is a large seal of the family Phocidae or "true seals". The species occurs exclusively in the Northern hemisphere, in cold temperate and sub-polar waters (Abt *et al*., 2002) with three main populations recognised (Figure 1.1) (Davies, 1957). The smallest of the populations occurs in the northern and central Baltic Sea (Kokko *et al*., 1999), stretching from the Gulf of Finland down through the eastern coasts of Sweden, Estonia, Latvia and Lithuania, with the largest concentration occurring in the Gulf of Bothnia (Kauppinen *et al*., 2005). The north western Atlantic stock comprises the largest population of grey seals with the highest numbers found at Sable Island and the Gulf of St. Lawrence (Breed, 2008). Grey seals that occur along the northeast Atlantic are considered to be part of one metapopulation (Boskovic *et al*., 1996). Their distribution extends southwards from the Barents Sea to their southern limit in France with the highest concentrations located around the British Isles (Härkönen *et al*., 2007). The large gaps between populations and differences in breeding seasons have resulted in the Baltic Sea population remaining relatively isolated while the western and eastern stocks are genetically distinct from each other (Davis, 1957; Boskovic *et al*., 1996).

The grey seal is the largest of the two species of seals native to Ireland, the other being the harbour seal (*Phoca vitulina vitulina*), and the species is widely distributed in Irish waters. Most terrestrial haul-out sites are located on islands off the western seaboard, with smaller colonies off the south-east and east coast. The first reliable breeding population estimate for grey seals in Ireland was established in 2005 (Ó Cadhla *et al*., 2005) and the population is currently estimated at 7,284 – 9,365 individuals (Ó Cadhla *et al*., 2013).

Under the EU Habitats Directive (Council Directive: 92/43/EEC) grey seals are listed as an Annex II species of community interest, which requires the designation of Special Areas of Conservation (SACs). Within Ireland, ten SACs are currently designated for grey seals, located around known grey seal breeding and moulting colonies (Ó Cadhla & Strong, 2007). As grey seals are gregarious, they may form large groups of up to several thousand animals during the moulting and breeding seasons (Lyons, 2004). The haul out sites utilised by grey seals in Ireland tend to be remote locations such as offshore rocky skerries, isolated cliff-bound beaches and uninhabited islands (Ó Cadhla & Strong, 2007; Ó Cadhla *et al.*, 2008). Site use varies across the annual cycle and some of the sites are particularly important during both the breeding and moulting periods. The largest of the grey seal colonies are situated along Irelands western and south western coast, at the Inishkea and Blasket Islands (Ó Cadhla *et al*., 2013). Both of these sites are used during the breeding and moulting periods. The annual breeding season typically occurs from approximately August to December (Ó Cadhla *et al*., 2013), with peak pupping taking place during October and November (Cronin *et al*., 2007). Grey seal moulting season in Ireland tends to begin as early as November for females and can continue up until April for large males (Kiely, 1998), although peak numbers for seals coming ashore to moult occurs in February and March (Kiely *et al*., 2000; Ó Cadhla & Strong, 2007).

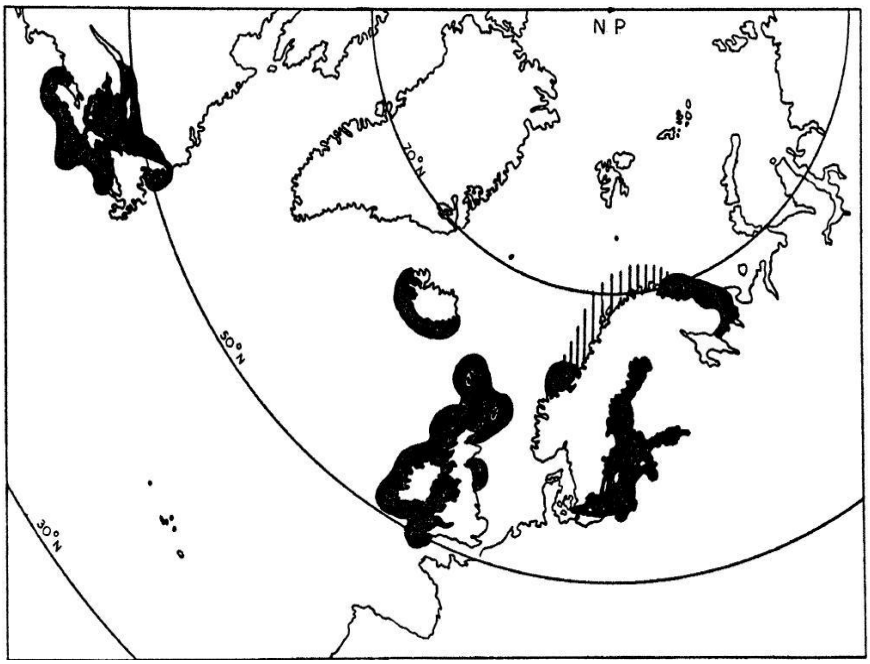


Figure 1.1: Map showing the worldwide distribution of grey seals (Davies, 1957).

Grey seal diet:

At the end of the breeding season, seals may undergo extensive foraging trips to replenish their lipid stores (Beck *et al*., 2007). Given their high levels of philopatry they often return to the site of their birth to breed (Bowen *et al*., 2003). While they can range from the continental shelf to inland seas (Bowen *et al*., 2007), telemetry studies in Ireland have demonstrated that grey seal foraging effort is primarily concentrated inshore within 50 km of haul-out areas (Cronin *et al*., 2013). The extent and duration of foraging trips varies seasonally, with seals foraging more locally in summer months prior to the breeding season (Cronin *et al*., 2013).

As generalists, grey seals are known to exploit a wide range of prey as species become locally and seasonally abundant (Benoit & Bowen, 1990; Hammond *et al*, 1994a; Bowen *et al*., 2006). Furthermore, grey seals are thought to forage on or near the sea bed, consuming mostly demersal or benthic prey (Pierce *et al*., 1990; Thompson & Hammond, 1991; Fedak, 1996; McConnell *et al*., 1999). Diet studies have shown how grey seals along the northeast Atlantic will feed primarily on sandeels (*Ammodytes* spp.), gadoids (whiting *Merlangius merlangus*, *Trisopterus* species) and to a lesser extent flatfish (Pleuronectiformes) and Cephalopoda species (Prime & Hammond 1990; Pierce *et al*., 1990; Hammond *et al*, 1994a; 1994b; McConnell *et al*., 1999; Trzcinski *et al*., 2006; Grellier & Hammond, 2006; Ridoux *et al*., 2007). Previous studies on the diet of grey seals in Ireland are limited in geographical coverage and span relatively short sampling time frames (BIM 1997; 2001; Kiely *et al*., 2000, McKibbon, 2000; Philpott, 2001; Gosch *et al*., 2014). However, key prey species recovered within these studies are consistent with diet descriptions for grey seals across their distribution range in the northeast Atlantic.

Seal-fishery interactions:

Detailed information on diet and feeding habitat is becoming increasingly necessary to evaluate potential impacts of seals on fish stocks (Meynier *et al*., 2008). With major declines in the worlds' fish stocks over the last few decades (FAO, 2016) there has been increased interest in the extent of competition for resources between commercial fisheries and top marine predators (Trites *et al*., 1997). By producing detailed robust data on predator diet, it is possible to investigate the degree to which local marine

predator populations may be impacting marine stocks (e.g. Houle *et al*., 2016), thereby quantifying the level of marine mammal-fisheries interactions.

Biological interactions between mammals and fisheries are typically indirect, in that they do not occur at the nets but at a population level where both compete for shared resources (Northridge and Hofman, 1999). Operational interactions involve marine mammals (usually odontocetes or pinnipeds) actively removing fish from fishing gear (termed depredation), damaging gear, or dying from entanglement in fishing gear (termed by-catch) (Northridge and Hofman, 1999; Kaschner and Pauly, 2005; Cronin *et al*., 2014; González *et al*., 2015).

There are several categories of depredation, however seal damage to catch generally exhibit certain key characteristics. In many cases, it can be relatively rare for the whole fish to be consumed (Northridge *et al*., 2013). Seals may often take bites out of the belly, removing soft parts such as viscera or flesh, and regularly leaving behind the main body of the fish. Marks left in the abdomen attributed to canines testify to the fish having been killed by a seal. It is thought that this type of depredation generally occurs with larger fish. Damage to smaller fish is often characterised by the posterior half being removed, leaving the anterior end behind in the net. The most typical form of seal depredation is the entire removal of the body with only the head and sometimes partial spine, remaining in the net. Such damaged has been shown to occur with both small and large fish and is attributed to there being little flesh within the head, thus making it less appealing to the seal. Finally, in many cases fish remain fully intact with no flesh removed, however deep gashes in the abdomen are made from clawing actions by seal fore-flippers, or alternatively, the skin of the fish has been completely removed yet the body remains undamaged (Moore, 2003; Rafferty *et al*., 2012; Northridge *et al*., 2013; Cosgrove *et al*., 2015).

Accidental capture of marine mammals typically occurs when; animals are removing fish from fishing gear and are caught themselves in the attempt; if the animal does not perceive the gear in the water; or it does not recognise the threat the gear poses (Northridge & Hofman, 1999). As animals most often become entangled below the surface, it is difficult to determine the reason why they became caught and the exact time of the incident and death. As marine mammals require air to breath, death may be immediate as a result of drowning. Alternatively, death may be slower if the animal

escapes the nets with "cryptic" mortality from prolonged injuries, starvation or infection problematic to assess. By-catch is therefore of international concern, particularly when the conservation of vulnerable populations become threatened (Tudela, 2004). Seal by-catch in tangle-net gear is generally considered to occur to a greater extent in nets that comprise of larger mesh sizes (Bonner, 1990; Sjare *et al*., 2005) and within Irish waters most incidents of by-caught animals relate to juveniles (Cosgrove *et al*., 2016).

As large, locally abundant piscivores, conflict between grey seals and inshore fisheries over shared resources is common and particularly prevalent in Ireland and the Baltic Sea (Moore, 2003; Matthiopoulos *et al*., 2004; Fjälling, 2005; Kauppinen et al., 2005; Jounela *et al*., 2006; Cronin *et al*., 2014; Cosgrove *et al*., 2015; Oksansen *et al*., 2015). Ireland's Seafood Sector is of substantial economic importance, with both Irish and foreign landings into Ireland valued at €344 million in 2015 (Peter Tyndall, BIM, *pers. comm*.). Two-thirds of landings at the largest fishing ports in the country consist of demersal species, primarily gadoids such as cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), pollock (*Pollachius pollachius*), and whiting (*Merlangius merlangus*), the important prey of grey seals in many regions (Hammond *et al*., 1994a; 1994b; Kiely *et al*., 2000; Brown *et al*., 2012). Inshore set-net fisheries in Ireland mainly comprises tangle -, trammel- and gill-nets (Gabriel *et al*., 2005). The few studies on depredation within Irish waters have indicated that grey seals appear to be the primary species responsible for catch damage within commercial fisheries (McCarthy, 1985; Collins *et al*., 1993; BIM, 1997; Kiely *et al*., 2000; Cosgrove *et al*., 2015). However, while problem or "rogue" seals that specialise in raiding fishing gear are known to occur (Königson *et al*., 2013), it is not clear whether operational interactions in Irish waters occurs as a result of random or learned seal behaviour. Losses and damage to target catch appears to occur year round and is highest within fisheries targeting the pollock (*Pollachius* spp.), cod (*Gadus morhua*), hake (*Merluccius merluccius*), monkfish (*Lophius* spp.) and turbot (*Scophthalmus maximus*) as described by Cronin *et al*. (2014). A recent study off the west coast of Ireland estimated that between 10-59% of the catch in gill-net and tangle-net fisheries targeting pollock, hake and monkfish is damaged by seals (Cosgrove *et al.*, 2015). The scale of these interactions can have severe economic implications for small scale fisheries and may lead to some local inshore fisheries becoming unsustainable.

Furthermore, as seal damaged fish are typically discarded, they are not included when evaluating catch per unit effort which is therefore likely underestimated. Consequently, depredation may have further implications regarding fish stock management issues.

Background to the project:

In areas where seals are perceived to compete with fisheries, the priorities of fishers and wildlife managers sometimes conflict, and resolution requires quantitative information on the intensity of competition (assessed by estimating resource use by top predators and man, and calculating the overlap between them). However, gaps in our knowledge and understanding of seal diet and foraging ecology are one of the greatest obstacles to resolving this problem. Both intrinsic and extrinsic factors including prey size, the timing of prey consumption, the location of feeding, predator age, sex, reproductive status, and body condition can influence diet composition and foraging strategies (McConnell *et al*., 1999; Beck *et al*., 2005; Ahlbeck *et al*., 2012; Cronin *et al*., 2013).

Prior to this study, information on grey seal diet in Ireland was limited in spatial and temporal coverage, thus robust data on diet composition are lacking. This study aimed to address gaps in our knowledge regarding grey seal diet feeding ecology by undertaking a detailed long term diet study. Determining the extent to which geographical and seasonal variation may be occurring within the diet and between individual predators can be confounded by low sample size, sampling effort restricted to short time scales, and inappropriate sampling design (Benoit & Bowen, 1990). By acquiring large numbers of samples collected over consecutive years, appropriate dietary analysis approaches were applied to address specific questions regarding overall diet composition, and potential geographic and temporal variation in diet.

The first data chapter of this thesis (Chapter 2) investigates the consequences to seal diet composition when applying different approaches using the traditional method of pinniped diet analysis. The approaches that are deemed to minimise potential biases while attempting to describe the diet composition as accurately as possible are therefore adopted for the remaining data chapters (Figure 1.1).

It is acknowledged that higher predators will forage over spatially variable habitat boundaries, shifting their diet as different resources become available (McMeans *et*

al., 2015). Variations in diet may be attributed to the differing energy requirements of seals in relation to their life history strategies. Furthermore, as a result of reproductive condition, the energy content of prey species will also exhibit seasonal changes. To determine whether grey seals in Ireland display significant seasonal and inter-annual variation in their diet, diet is examined over an extended time period of five years (Chapter 3). In Chapter 4 regional variation in the diet of grey seals reconstructed from scat samples collected during the same time from two geographically distinct colonies off the southwest and southeast coast of Ireland was examined.

Due to the growing concern regarding seal-fishery interactions and the increasing demand within the Irish fishing industry for a cull of grey seals (Cronin *et al*., 2014; Cosgrove *et al*., 2015, 2016), it is essential to evaluate the extent to which grey seals in Ireland may be selecting species of economic value and whether prey fish sizes overlap with those targeted by fisheries. Using by-caught seals recovered from two tangle-net fisheries operating on the west and south coast of Ireland, the issue of seals depredating the nets prior to their entanglement is investigated (Chapter 5). Potential overlap with the fisheries is further explored by comparing the lengths of commercial prey species recovered from seal digestive tracts with the length of fish species targeted by the fisheries.

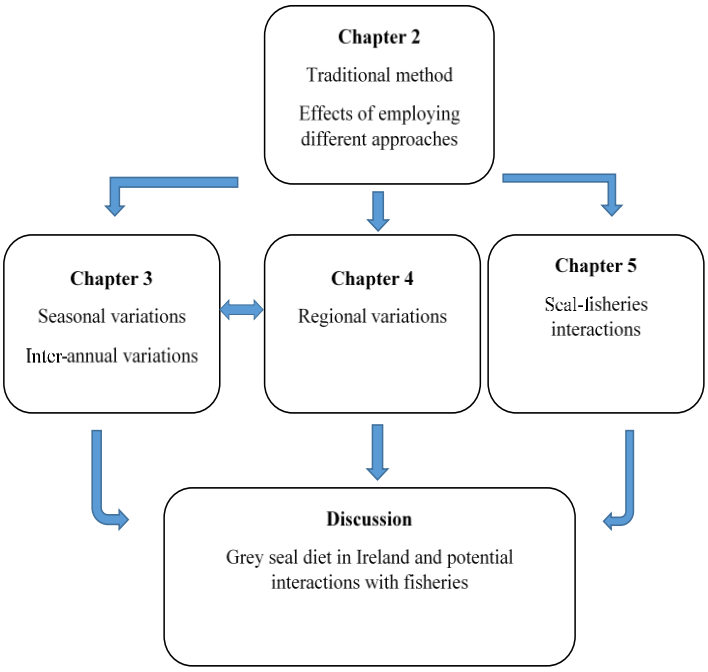


Figure 1.1: Simplified flow chart outlining the thesis contents.

1.2 Objectives

The overall objectives of this thesis were to:

i. Obtain robust baseline data on Irish grey seal diet composition and investigate the most appropriate dietary assessment approaches;

ii. Determine the extent to which seasonal and inter-annual variation in seal diet occurs, using a five-year dataset from a colony of national importance;

iii. Investigate regional variation in diet across a wide geographic range using samples collected over the same time period;

iv. Examine the extent to which grey seals may be relying on particular key prey species;

v. Test the assumption that by-caught juvenile seals are depredating set-nets prior to becoming entangled by comparing stomach contents of by-caught seal with net contents.

CHAPTER 2

A multifaceted approach to diet reconstruction using prey hard parts



2.1 ABSTRACT

Robust dietary composition information is fundamental to investigating the role of top marine predators. The traditional method of prey hard part analysis from scat or digestive tract contents remains the most widespread technique used when investigating pinniped diet composition. Though this method is relatively inexpensive and non-invasive, number of caveats exist using this approach. Most noticeably, differences in inter- and intraspecific differential passage rates of structures can lead to prey being over- or under-represented in the diet, and the effects of erosion on hard parts like otolith can have implications on prey length and biomass estimations. A number of methods, such as use of diagnostic structures in addition to the traditional otolith/beak analysis, and application of correction factors to account for partial or complete erosion of structures have been developed to address the limitations of traditional hard part analysis. However, regression equations for teleost prey size reconstruction from non-otolith structures, and correction factors for partial or complete erosion are not available for all species, leading to new potential biases. In this study, diet composition using prey identified solely from otoliths/beaks was compared with an all diagnostic structures approach. This resulted in the identification of four additional prey taxa with an overall increase of 35% in prey item detection, including substantial contributors to prey biomass. Uncorrected prey sizes were also compared to sizes obtained using correction factors. The application of digestion coefficients was limited to 61% of prey items and while lengths of all commercial species increased noticeably, biomass contribution of gadoids tended to be over-represented. Numerical correction factors were only applicable to 59% of prey items, with sandeel biomass over-represented relative to decreases in biomass contribution from otherwise important prey. It is therefore recommended that correction factors are not used unless they can be applied to all prey items within the diet.

Keywords: pinniped diet analysis, traditional method, otoliths, all structures, correction factors, regression equations, biomass estimations.

2.2 INTRODUCTION

Our understanding of how ecological processes structure ecosystems is based on two fundamental concepts; that the structure and function of a community is strongly shaped by the interactions among organisms within and, that the sizes and identities of the organisms govern the nature of these interactions (Elton, 1927 cited in Trebilco *et al*., 2013). The feeding habits and relationships between organisms (trophic interactions) can also provide insights into ecosystem health (Arim & Naya, 2003; Christensen & Walters, 2004; Williams *et al*., 2012; Bowen & Iverson, 2013; de la Vega *et al*., 2016). As predator prey interactions within a complex system ultimately have implications for the wider food web, bio-energetic models are important tools for estimating consumption and biomass removal by top predators (Pauly *et al*., 2000). However, to quantify trophic interactions, together with supporting further ecological research, predator diet most first be described in terms of composition (Tollit *et al*., 2010). One of the benefits of diet reconstruction is that it can allow predators to be classified on the generalist-specialist spectrum, thereby elucidating the ecological niche a species may occupy (Machovsky-Capuska *et al*., 2016). Generalists are typically characterised as consuming a large variety of prey taxa (i.e. broad dietary niche breath), while specialists typically consume a narrower range of prey taxa (i.e. narrow dietary niche breath) and may often specialise on particular species. Understanding feeding ecology can thus help predict potential competition between other ecosystem components (e.g. Kruuk *et al*., 1994; Spitz *et al*., 2006) including humans (e.g. Medina-Vogel *et al*., 2004; Cronin *et al*., 2016).

Reconstruction of diet to acquire accurate estimates of prey composition initially requires the application of appropriate dietary investigation methods (Casper *et al*., 2006). A number of methods for piscivore diet analysis are available, though each methodology has its own merits and disadvantages (see Tollit *et al*., 2006). Marine mammal diet estimation has traditionally relied on indirect methods of assessment such as the analysis of prey remains found within stomach and scat contents (Prime & Hammond, 1990; Pierce *et al*.,1991a; 1993; Trites & Joy, 2005). The traditional method is mainly reliant on teleost fish otolith and cephalopod beak identification, though the inclusion of other skeletal structures is increasingly being used (Pierce & Boyle, 1991; Pierce *et al*., 1991a; 1993; Browne *et al*., 2002; Tollit *et al*., 2003; Trites

et al., 2007; Hernandez-Milian *et al*., 2011; Pierce *et al*., 2011; Spitz *et al*., 2015). Indeed, studies have demonstrated how the rate of prey detection can significantly increase when using "all structures" as opposed to otoliths alone (Olesiuk *et al*., 1990; Pierce *et al*., 1991a; Cottrell *et al*., 1996; Tollit *et al*., 2003).

Possibly the greatest advantage to using the traditional method for diet analysis is the ability to quantify prey species and for the majority, to reconstruct original prey size from recovered hard structures. While published regression equations enabling size reconstruction from otolith/beak dimensions are widely available for the vast majority of commonly consumed prey species (Casper *et al*., 2006), there is a deficit of regression equations for size reconstruction from non-otolith structures. Additionally, when species level identification is not possible, general regression equations based on family or genus level are often utilised (e.g. Brown & Pierce, 1998), or average prey sizes derived from the same prey type previously identified in samples are applied. However, Pierce *et al*. (1991b) caution that the calculated weight of prey items can vary substantially depending on the regression equation used. Therefore, the application of general equations when reconstructing predator diet, may have ramifications for prey biomass estimates.

Scat sample analysis has several further acknowledged limitations typically associated with differential rates of prey species retention times, structural digestion times, and erosion (Harvey 1989; Pierce & Boyle, 1991; Bowen, 2000; Tollit *et al*., 2003). This is primarily due to the variety of factors that can influence the degree of degradation hard structures undergo during the digestion process (Harvey, 1989; Marcus *et al*., 1998). While many studies have calculated correction factors to account for partial and full erosion (Murie & Lavigne, 1985; da Silva & Neilson, 1985; Jobling, 1987; Dellinger & Trillmich, 1988; Harvey, 1989; Harvey & Antonelis, 1994; Tollit *et al*., 1997; Bowen, 2000; Grellier & Hammond, 2006), they are only applicable to certain fish otoliths and cephalopod beaks. This may have an unintended consequence of further biasing diet estimations by not correcting all individuals in the diet for erosion.

Furthermore, when analysing the diet of a predator that displays a generalist feeding strategy, the identification of numerous prey species can be difficult. A single sample can contain many different bones in various states of erosion, which may confound prey identification, quantification and size reconstruction. Therefore, specialised

identification skills, and a very good reference collection, in conjunction with a high level of experience is required (Cottrell & Trites, 2002). Failing this, there is the potential for misidentifying prey species, which in turn can have implications in relation to the predators' overall diet composition estimate.

The outcomes of a dietary study may therefore be highly influenced by selecting one approach over another. To evaluate the degree to which dietary estimates can be impacted depending on the approach taken, the diet of grey seals (*Halichoerus grypus*) from a colony of national importance in southwest Ireland was investigated. The biologically productive waters off the south and west coast of Ireland (ICES, 2003) are important foraging grounds for grey seals (Cronin *et al*., 2012). This region also supports important spawning and nursery grounds for many fish species of both non-commercial and economic value, such as haddock (*Melanogrammus aeglefinus*) and pollock spp. (*Pollachius pollachius/P. virens*), along with anadromous salmonids like Atlantic salmon (*Salmo salar*) and sea trout (*Salmo trutta*) (Anon, 2009; Brennan & Rodwell, 2008). A recent study identified salmonids within the diet of grey seals in Ireland (Gosch *et al*., 2014). However, subsequent revision of the samples found that the bone originally identified as salmonid premaxillae was in fact a misidentified gadoid bone. This has provided an opportunity to re-analyse those data and determine the consequences of the misidentification of a potentially large contributor to diet, as well as to investigate the effect of applying general regression equations/average prey sizes, using the 'all structures' approach and the application of correction factors to our understanding of seal diet. This study specifically investigates how prey composition, prey importance and overall contribution to diet in terms of abundance and/or biomass varies in relation to using:

- Traditional fish otolith and cephalopod beak prey identification versus the all structures approach
- Correction factors versus no correction factors
- Misidentified species versus correct identification
- Genus/family level regression equations and average prey sizes

2.3 METHODS

2.3.1 Study site and scat collection

The Great Blasket Island grey seal colony, on the southwest coast of Ireland, is the second largest breeding and moulting grey seal colony in Ireland (Ó Cadhla & Strong, 2007; Ó Cadhla *et al*., 2013). It is located 1.5 km west of the Dingle Peninsula, Co. Kerry (10° 30’53’’W, 52°06’15’’N, Figure 2.1), and is the largest of the 15 islands that make up the Blasket Islands. The site supports a mixed (sex and age) haul out group of grey seals, with up to 1,413 individuals observed on the broad sandy beach (An Trá Bán) during the moulting period of December to April (Ó Cadhla *et al*., 2013). To minimise potential effects of seasonal variability in diet, scat sample collection was limited to Spring months (February and April) in 2009 (n=83) and 2010 (n=53). All samples were stored in separate polythene bags, labelled, and frozen at -20°C until further processing could take place.

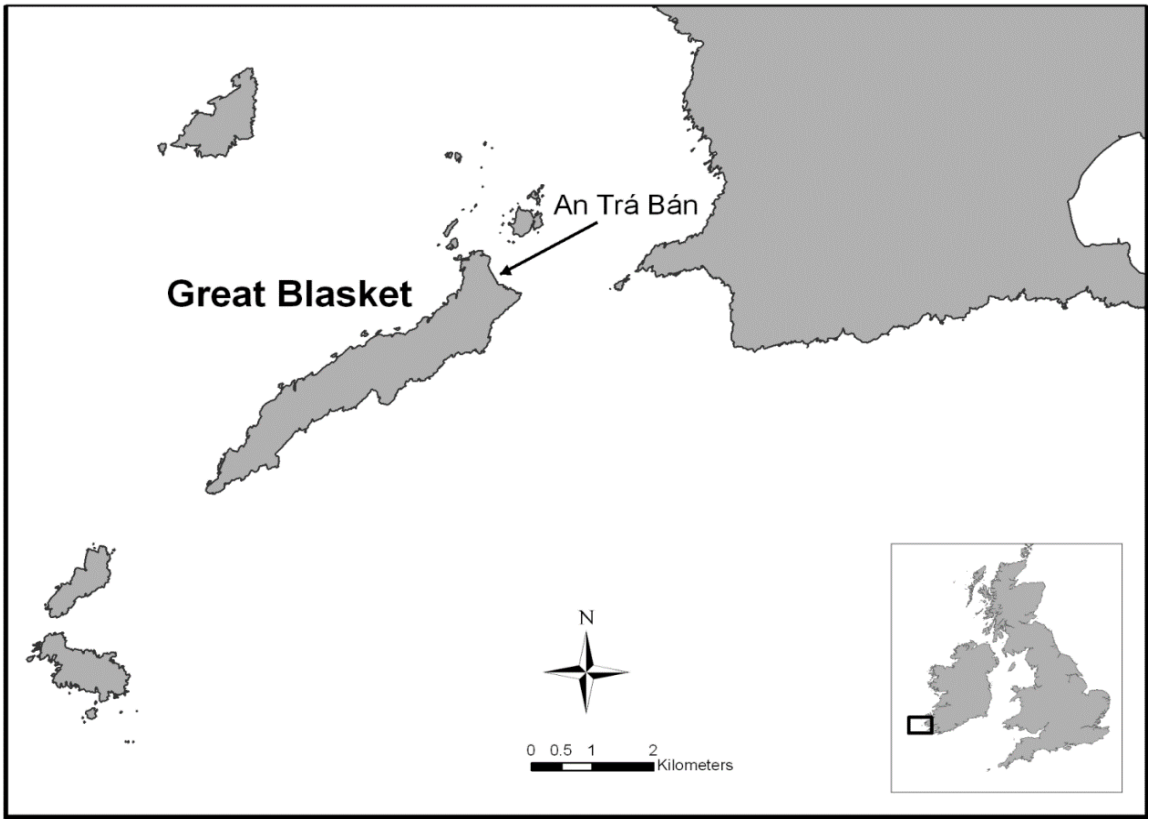


Figure 2.1: Map of Ireland showing the sampling site, An Trá Bán, located on the Great Blasket Island, Co. Kerry.

2.3.2 Dietary analysis

Following standard methodology (Murie & Lavigne, 1985; Pierce *et al*., 1991a; Pierce & Boyle, 1991), scat samples were initially washed through a nest of sieves ranging from 0.25 to 5mm (mesh size). This facilitated the removal of soft waste material with hard remains of prey then transferred into 70% ethanol for sterilization. All diagnostic structures apart from cephalopod beaks were then left to dry for 48 hours after which they were stored pending identification. All hard prey remains (otoliths, bones, and beaks) were measured. Prey remains less than 1 cm were measured using an eye-piece graticule fitted to a Zeiss 200S binocular dissecting microscope at x40 magnification, while prey items larger than 1 cm were measured using a digital callipers (accuracy ±0.01mm). Using the "all structures" approach (e.g. Tollit *et al.,* 2003) all prey were identified to their lowest taxonomic level when possible using reference collections and published guides (e.g. Clarke 1986; Härkönen, 1986; Watt *et al*. 1997; Tuset *et al*. 2008).

Due to similarities between prey morphologies, particularly when structures have undergone erosion, identification to species level was not always possible. In these cases, prey were grouped together e.g. haddock/pollock species (*Melanogrammus aeglefinus/P. pollachius/P. virens*), classified as unidentified fish, or identified to a genus level (e.g. *Trisopterus* spp.), family level (e.g. Ammodytidae), or order level (e.g. unidentified Pleuronectiformes). Following McConnell *et al*. (1984) and Pierce & Boyle (1991), highly eroded structures and crustacean remains were considered secondarily ingested items and were excluded from further analysis. Length and weight reconstruction for each species were based on published regression equations (Appendix I). Dragonets (*Callionymus* spp.) identified from preoperular bones were assigned lengths using university reference material (source: Gema Hernandez-Milian). Where prey could not be identified to species level, then genus/family regressions were applied (e.g. *Trisopterus* spp., haddock/pollock/saithe spp.). When regression equations were not available for prey identified from particular diagnostic structures such as dentaries', maxillae, preopercular bones etc., average lengths/weights were assigned to the prey item from either FISHBASE (Froese & Pauly, 2013) or from the average sizes obtained from similar species. For example, a lemon sole (*Microstomus kitt*) identified from an urohyal was assigned the average size of all lemon soles identified within the same sample/month/year. Propercular

To account for partial erosion, species-specific digestion coefficients (DC) were applied when possible as multipliers to otoliths/beaks following Grellier & Hammond (2006). Numerical correction factors (NCF) were also applied as a multiplier to prey body mass following Tollit *et al*. (1997) to account for complete erosion of prey during the digestive process (see Appendix II for correction factors used). Tollit *et al*. (1997) provides an average DC that can be applied to otoliths when no species-specific DC is available and this was used for prey species identified from otoliths for which no DC exist. Correction factors are only available for otoliths and not for other diagnostic structures. Furthermore, no correction factors exist for octopus beaks.

2.3.3 Diet quantification

Quantification of prey species was accomplished using a number of methods. The minimum number of species per scat was determined by counting the highest numbers of paired structures present (e.g. left or right otoliths/beaks/premaxillae etc.) or single diagnostic structures such as an urohyal or vertebrae atlas (e.g. Ammodytidae). Various head bones can be used for prey identification (see Figure 2.2). While only a limited number can be used for species level identification (depending on the species) and for prey size reconstruction (see Figure 2.3a, b), many other bones enable the identification of prey items to a coarse taxonomic resolution (Figure 2.4a-l). Minimum numbers of prey individuals identified from vertebrae were established by differentiating anterior caudal vertebrae through their size, colour and degree of erosion. The anterior caudal vertebrae were used as opposed to other vertebrae as these are less variable in size according to Watt *et al*. (1997) (see Figure 2.5a and 2.5b for associated measurements). As multiple structures from the same prey individual will often be present within scats when employing the "all structures" method, diagnostic structures were matched according to colour and degree of erosion, and then through length measurements (original lengths within ± 1mm were deemed to originate from the same individual). Diet quantification was conservatively estimated so as to avoid duplication of prey items, and all measurements were taken from otoliths as opposed to bones when they were present. Finally, diet composition was expressed in terms of percentage frequency of occurrence (%F), percentage by number (%N), and percentage by biomass (%B), as described in Pierce & Boyle (1991).

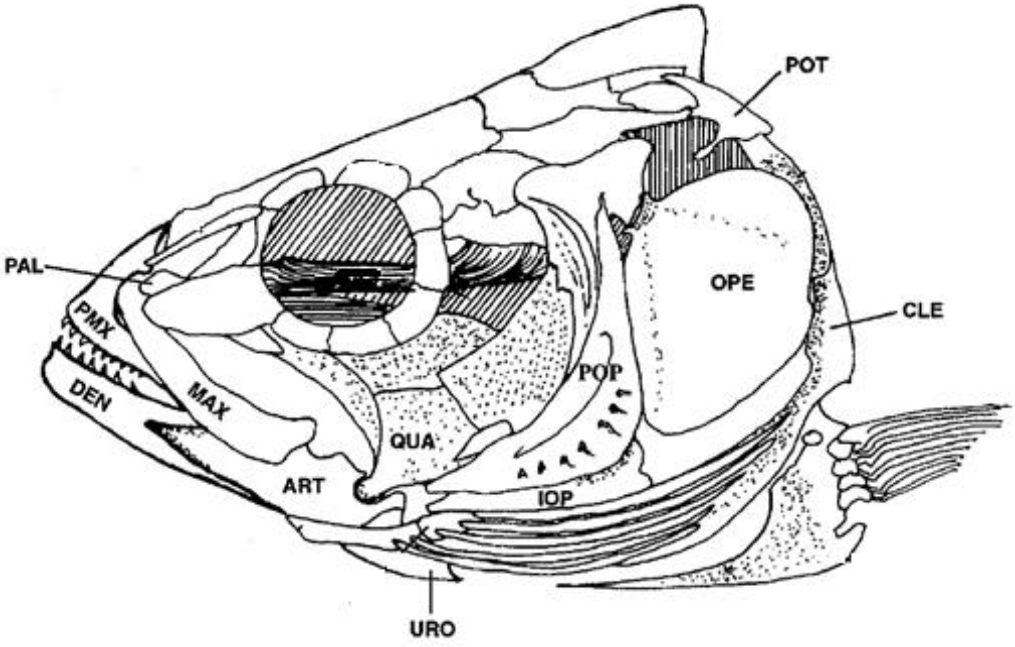


Figure 2.2: Bones used for prey prey identification (generalised teleost fish). ART, articular; CLE, cleithrun; DEN, dentary; IOP, interopercular; MAX; maxilla; OPE, opercular; PAL, palatine; PMX; premaxilla; POP, preopercular; POT, post-temporal; QUA, qauadrate; URO, urohyal. (Source: Watt *et al*., 1997).

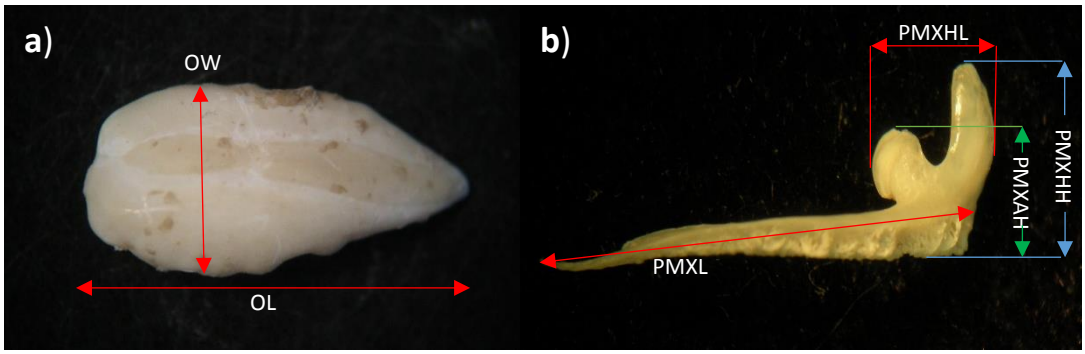


Figure 2.3: a) *Trisopterus luscus* otolith and b) *T. luscus* premaxilla displaying the measurments used for prey size reconstuction. OW, otolith width; OL, otolith length, PMXL, total premaxilla length; PMXHL, head length; PMXHH, head height; PMXAH; articular height.

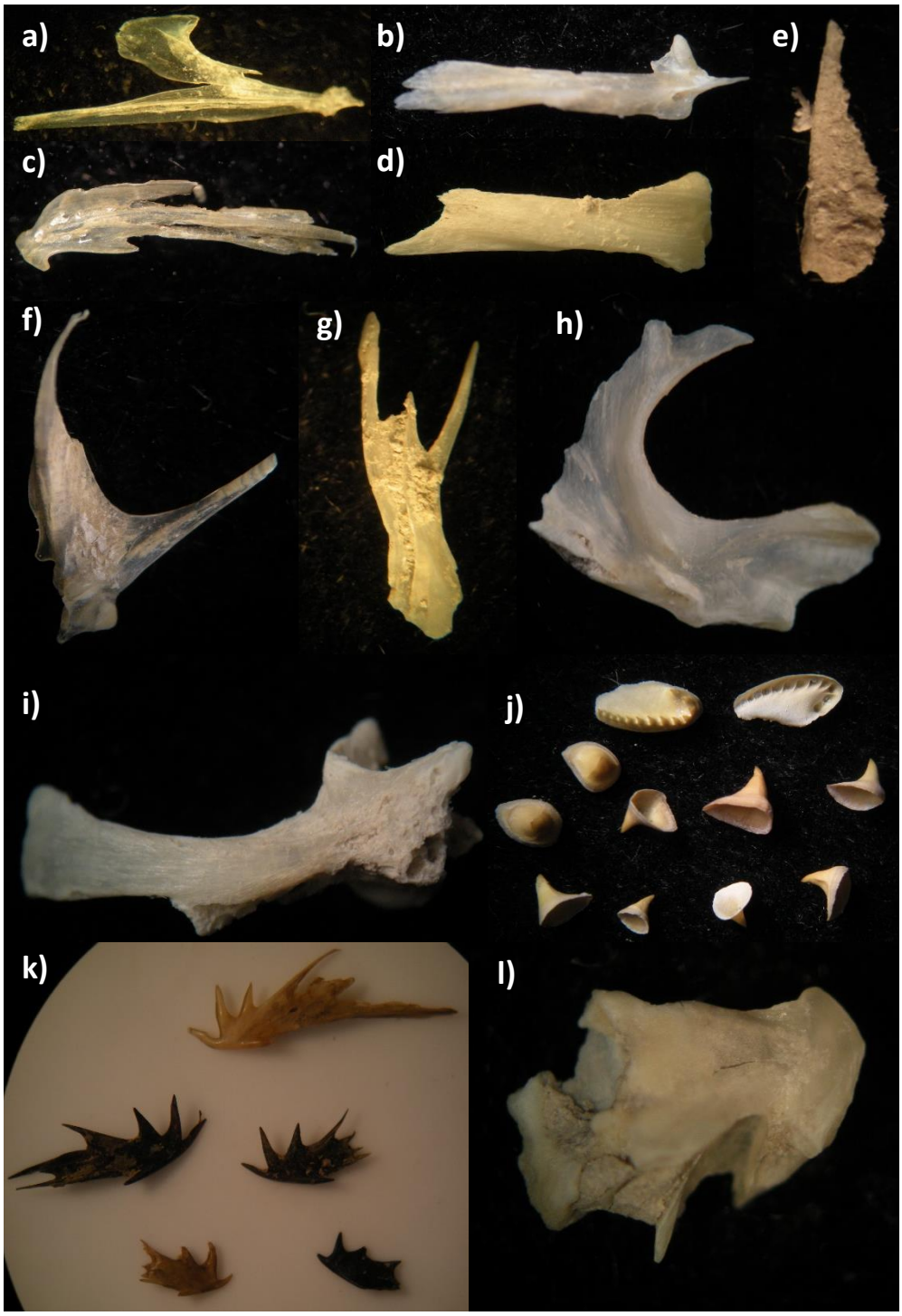


Figure 2.4: Examples of diagnostic structures used for prey identification. a) Lesser sandeel (*Ammodytes marinus*) dentary, b) Greater sandeel (*Hyperoplus lanceolatus*) dentary; c) Flatfish dentary; d) Gadoid dentary; e) *Trisopterus* spp. palatal teeth; f) Cuckoo wrasse (*Labrus mixtus*) post-temporal; g) Lesser sandeel post-temporal; h) Dab (*Limanda limanda*) urohyal; i) flatfish maxilla; j) Lampry (*Petromyzon marinus)* teeth; k) Dragonet (*Callionymus* spp.) preoperculars; l) Gadoid interopercular (previously identified as salmonid premaxilla).

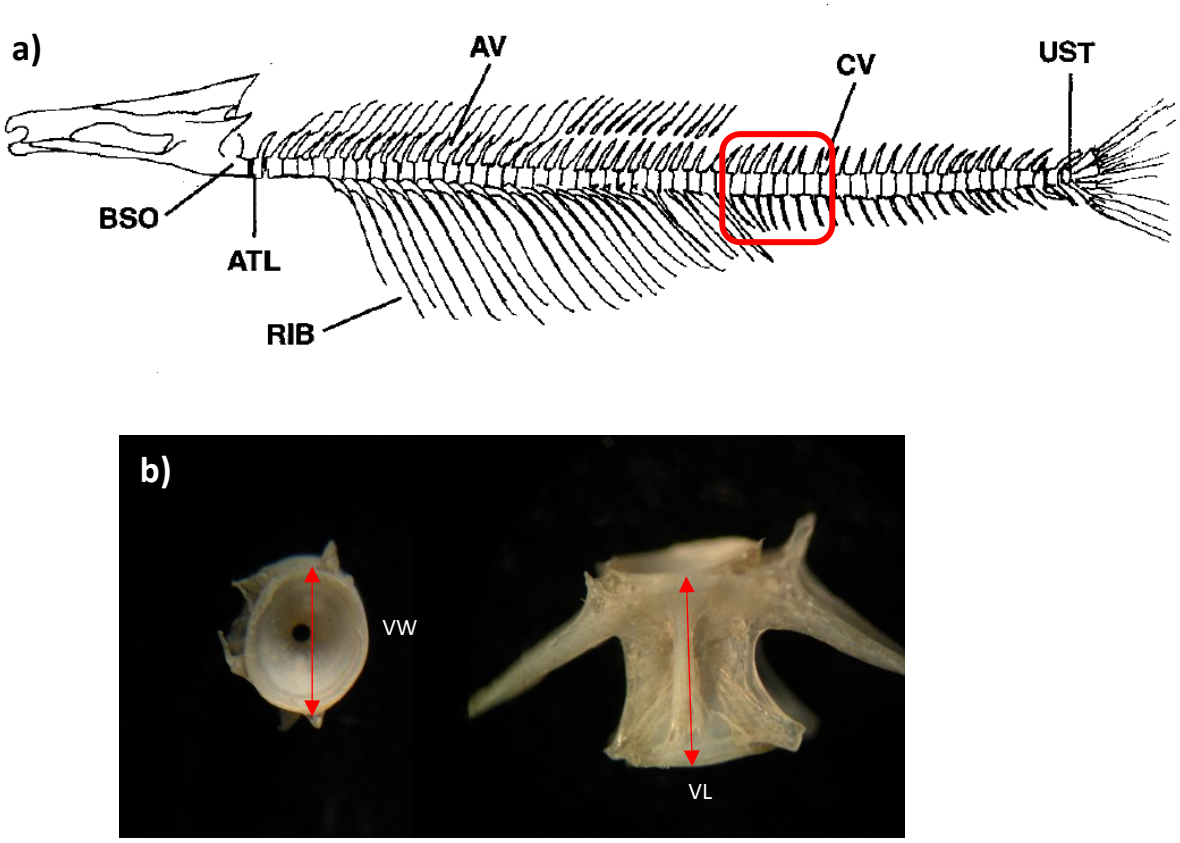


Figure 2.5: a) Neurocranicum and vertebral column of a teleost fish. BSO, basioccipital; ATL, atlas vertebra; RIB, ribs; AV; abdominal vertebrae; CV, caudal vertebrae; UST, urostyle. Area in red highlights the anterior caudal vertebrae used for prey size reconstruction. (Source: Watt *et al*., 1997), b) Greater sandeel (*H. lanceolatus*) vertebrae depicting the measurements used for prey size reconstruction. VW, vertebra width; VL, vertebra length.

2.3.4 Methodologies investigated

Regression equations for prey size reconstruction are available for otoliths, bones and beaks of a limited number of species, however correction factors cannot be applied to non-otolith/beak structures. Table 2.1 summarises the diagnostic structures that regression equations and correction factors can be applied to, and highlights the hard parts that are only employed for prey quantification.

The effects of employing different techniques for the refinement of pinniped diet reconstruction was assessed in four ways: 1) comparing reconstructed diet using only otoliths versus the all structures approach; 2) comparing reconstructed diet with and

without the use of DC and NCF correction factors to prey lengths and weights; 3) comparing reconstructed diet using misidentified salmonid bones with correct prey identification; and 4) comparing reconstructed diet using genus/family level regression equations and average body size estimates, with species level regression equations.

2.3.5 Diet variability in relation to methods employed

To examine the extent of grey seal diet variability depending on the methodologies employed, modified Costello graphs were created following Amundsen *et al*. (1996). A predator population and the individuals within may display different food niches, with niche width being the sum of two components, the within-phenotype component and the between-phenotype component (Giller, 1984 cited in Amundsen *et al*., 1996). A population displaying a high within-phenotype component (WPC) consists of many generalists that each exploit a variety of overlapping resources with particular prey species occurring in high frequencies, although each accounts for only a small proportion of the diet. Populations that exhibit a high between-phenotype component (BPC) are comprised of specialist individuals who exhibit little or no overlap in resource use. In this case different prey species occur rarely although they account for a much larger proportion of the diet. While predator populations that display narrow dietary niches are comprised of individuals with narrow and specialised niches, populations displaying broad dietary niches may be composed of individuals exhibiting either wide or narrow niches or both (Amundsen *et al*., 1996 and references therein). Prey-specific abundance and biomass of species identified within the diet depending on the methodology used were plotted against their frequency of occurrence (as a fraction rather than a percentage) on a two-dimensional graph.

Table 2.1: Diagnostic structures used to identity prey items and their associated advantages & disadvantages in pinniped diet analysis.

Diagnostic Structure	Species identification	Prey Quantification	Regression equations	Susceptibility to erosion	Correction factors	Dietary indices	Pros/Cons
Otolith	Yes	Yes	Yes	Low to high	Yes	%F, %N, %B	Dietary estimations including the effects of erosion possible/Regression equations & correction factors not available for all spp.
Premaxillae	Yes	Yes	Yes	Low to high	No	%F, %N, %B	Sp. counts attainable & regression equations /High level of taxonomic experience required when eroded
Anterior Caudal Vertebrae	Yes	Yes	Yes	Medium to high	No	%F, %N, %B	Minimum sp. counts attainable & regression equations available so dietary estimations possible/High level of taxonomic experience required
Dentaries	Rarely	Yes	No	Low to high	No	%F, %N	Prey counts possible but usually not to sp. level (e.g. gadoid, flatfish only)/Size reconstruction not achievable
Maxilla	Rarely	Yes	No	Medium to high	No	%F, %N	Prey counts possible but usually not to sp. level (e.g. gadoid, flatfish only)/Size reconstruction not achievable
Preopercular	Dragonets	Yes	No	Low to high	No	%F, %N	Prey counts possible but usually not to sp. level (e.g. gadoid, flatfish only), apart from *Callionymus* spp. /Size reconstruction not achievable
Opercular	No	Yes	No	Low to high	No	%F, %N	Prey counts possible but usually not to sp. level (e.g. gadoid, flatfish only)/Size reconstruction not achievable
Post-temporal	Occasionally	Yes	No	Low to high	No	%F, %N	Prey counts possible, often to a spp. level/ Size reconstruction not achievable
Urohyal	Flatfish	Yes	No	Low to high	No	%F, %N	Prey counts possible, often to a spp. level/ Size reconstruction not achievable
Quadrate	No	Yes	No	Medium to high	No	%F, %N	Prey counts possible but usually not to sp. level (e.g. gadoid, flatfish only)/Size reconstruction not achievable
Cleithrum	No	Yes	No	Low to high	No	%F, %N	Prey counts possible but usually not to sp. level (e.g. gadoid, flatfish only)/Size reconstruction not achievable
Otic bulla	Clupeids	Yes	No	Low	No	%F, %N	Clupeid minimum counts possible but not to a sp. level/ Size reconstruction not achievable
Pharyngeal Teeth	Labrids/lamprey	Yes	No	Low	No	%F, %N	Labrid & lamprey minimum counts possible/ Size reconstruction not achievable
Scales	Sometimes	Yes – 1 item per sample	No	Low to high	No	%F, %N	Certain sp. level counts possible/ Size reconstruction not achievable & high level of taxonomic experience required
Denticles/Spines	Rajidae spp.	Yes – 1 item per sample	No	Low to medium	No	%F, %N	Minimum counts of Rajidae spp. possible/ Size reconstruction not achievable
Cephalopod Beak	Yes	Yes	Yes	Low	Squid only	%F, %N, %B	Dietary estimations possible/Regression equations not available for all spp. & correction factors not available for Octopus.
Cephalopod Eye Lens	No	Yes	No	Low to medium	No	%F, %N	Minimum Cephalopoda counts possible/ Size reconstruction not achievable

Alterations in prey selectivity and importance were then interpreted by examining the distribution of prey points along the axes and diagonals on the diagram (Figure 2.6).

Prey-specific abundance is expressed by:

$$P_i = (\sum S_i / \sum S_{ti}) \times 100$$

P_i represents the prey-specific abundance/biomass of prey *i*, S_i signifies the total contribution of prey *i* to the scat content, and S_{ti} denotes the total abundance/biomass of all prey within all samples containing prey *i*.

Frequency of occurrence as a fraction is expressed as:

$$Fi = Ni/N$$

Where N*i* is the sum of all samples containing prey *i* and N is the total number of scat samples containing all prey within the diet.

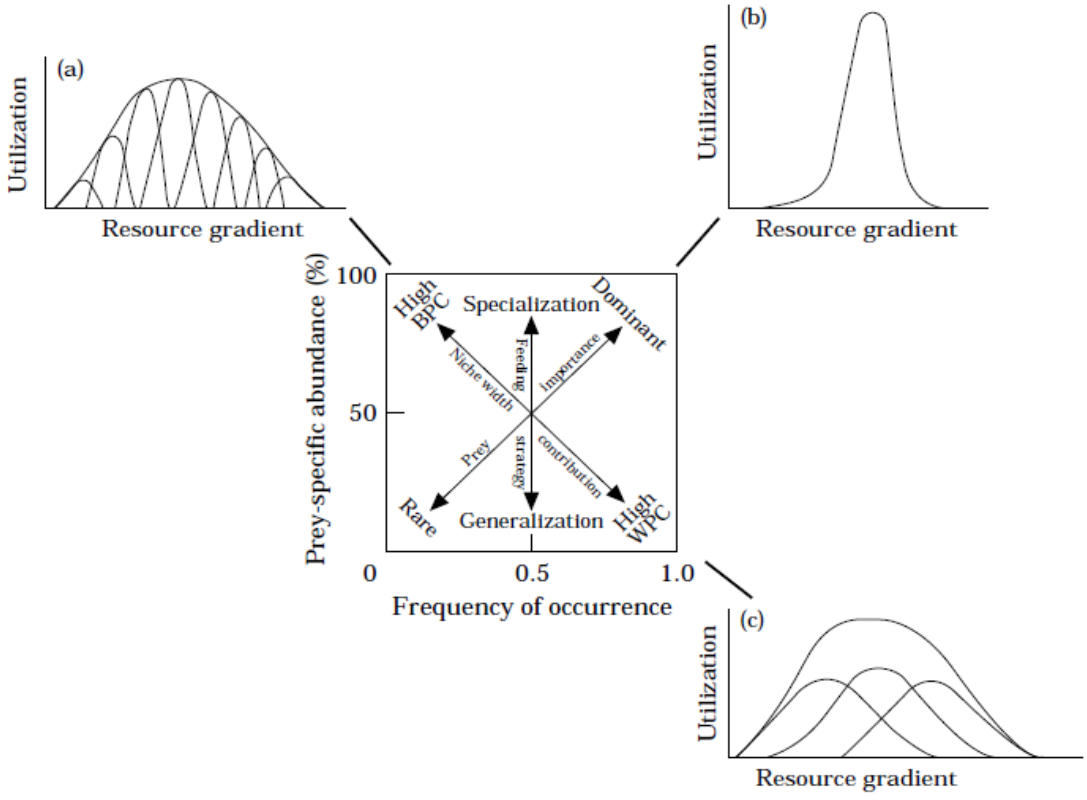


Figure 2.6: Diagram from Amundsen *et al*. (1996) interpreting the feeding strategy of a predator population. (a) High between-phenotype component to niche width, (b) narrow niche width and (c) high within-phenotype component. Prey importance increases along the diagonal (lower left to upper right) with feeding strategy (generalist-specialist dichotomy) represented on the vertical axis as described by Amundsen *et al*. (1996).

2.4 RESULTS

2.4.1 Overall diet composition

Out of a total of 136 samples, 132 scats contained identifiable prey remains. Scat samples were collected in February 2009 (n = 57), February 2010 (n = 40), April 2009 (n = 26) and April 2010 (n = 13).

Using all structures, 893 prey individuals were identified, representing a minimum of 37 separate species. Teleost fish were the main prey component and comprised 98% by number (98%N) of the entire diet. Other prey consisted of Cephalopoda, lamprey (*Petromyzon marinus*) and rays (Rajidae spp.) which combined, represented 2%N of all prey consumed. The Gadidae family was the most important prey group within the diet with *Trisopterus* spp. displaying the highest values across all dietary indices within this family (Appendix III). While not numerically abundant, haddock/pollock spp. were the second largest gadoid contributors to the diet in terms of biomass (6.5%B). Sandeels were also amongst the most important prey in the diet, occurring frequently (38%F) and in high abundances (33%N), although their biomass contribution was less than that of other core prey groups (5.4%B). Both flatfish and Cephalopoda occurred in relatively low abundances but were substantial contributors to the diet in terms of weight (14%B and 31%B, respectively). Squid (*Loligo* spp.) were by far the largest contributors within this class (29%B), with five individuals exhibiting weights of between 1-10kg.

2.4.2 Effect of using "all structures" as opposed to otoliths/beaks alone.

From 602 otoliths recovered within scat samples, 99.5% were identifiable to at least family level, with the remaining 0.5% exhibiting high levels of erosion and therefore assumed to be secondarily ingested. These were excluded from subsequent analyses. All Cephalopoda were identified from beaks to a genus level, with eye lenses only occurring when beaks were present. A further 315 prey items (35% of all prey) were identified using other diagnostic structures such as spines, preopercular, dentaries' etc., with four taxa (lamprey, rays, Triglidae spp., and eelpout, *Zoarces viviparus*) solely identified through the use of these structures. In 5% of cases, it was not always possible to identify prey to species level using otoliths alone. In these instances, additional diagnostic structures were matched with otoliths thereby facilitating species identification to their highest taxonomic resolution. The most important diagnostic structures for prey detection (apart from otoliths) were vertebrae, premaxillae, and dentaries' which enabled the identification of 10.2%, 6.1%, and 5.9% of all prey species in the diet, respectively. Thirteen types of bones were used in conjunction with otoliths and beaks to identify prey. While nine prey groups were identified using only otoliths, the percentage increase of the number of prey detected within most groups increased markedly when other diagnostic structures were included in the identification process. Most noticeably, abundances in the unidentified fish group increased by 463%, while dragonet (*Callionymus* spp.) abundance increased by 336% as a result of preopercular detection within scat samples. Other groups to experience substantial increases in abundance included unknown gadoids (increasing 186%, due to high numbers of dentaries', vertebrae, and post-temporal bones), and flatfish (increasing 180%, mainly due to the presence of vertebrae and premaxillae). *Trisopterus* spp., sandeels, haddock/pollock spp., blue whiting (*Micromesistius poutassou*), whiting (*Merlangius merlangus*), horse mackerel (*Trachurus trachurus*) and Labridae spp. detection within the diet also increased after the inclusion of other non-otolith structures.

Diet variability – effects of using otoliths/beaks v all structures

Prey-specific abundance and biomass were plotted against frequency of occurrence (as a fraction) using prey items identified from otoliths/beaks alone compared to when all structures (including otoliths and bones) were included in the identification process (Figure 2.7). When all structures were used to identify prey, unidentified gadoids, sandeels, flatfish and dragonets were consumed with greater regularity by the entire "population" as opposed to infrequently as suggested using otoliths alone. No single species dominated the diet, however, *Trisopterus* spp. were consumed by the majority of the population along with myriad of other prey. Their importance in the diet did not alter substantially when using otoliths or all structures for their identification.

Triglidae, eelpout (*Zoarces viviparous*) and lamprey emerged as prey that only occurred in a small number of scats, while not being encountered in the diet at all when using otoliths alone. When excluding non-otoliths structures in the identification process, perch (*Perca fluviatilis*) appeared to occur rarely but accounted for a large proportion of the diet (top left corner). Regardless of which structures are used for identification, certain other species such as *Eledone* spp., *Loligo* spp., ling (*Molva molva*), rocklings, and mackerel (*Scomber scombrus*) also occurred rarely in samples but again represented a substantial proportion of the diet.

While for the most part the general feeding strategy of grey seals remained unchanged, the inclusion of all structures facilitated a more accurate account of which key prey e.g. sandeels, flatfish, dragonets, are utilised regularly most predator individuals at the study site.

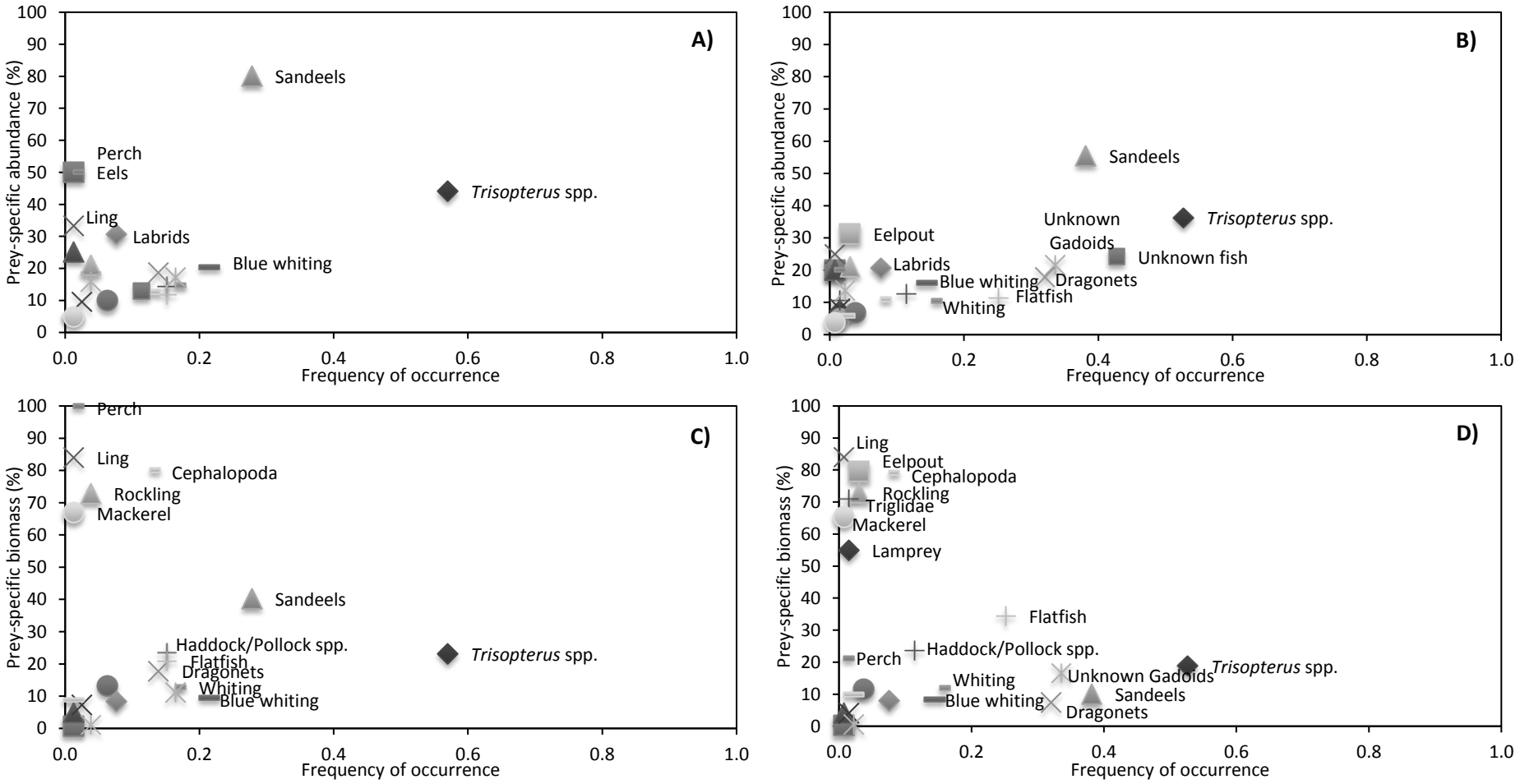


Figure 2.7: Costello-Amundsen feeding plots displaying prey of grey seals off southwest Ireland, constructed using otoliths/beaks alone versus the inclusion of all structures. A) otolith/beak species-specific abundance, B) all structures species-specific abundance, C) otolith/beak species-specific biomass, and D) all structures species-specific biomass. See Appendix III for unlabelled prey.

2.4.3 Effects of applying correction factors

DC were applied to 61% of all prey items recovered from the diet. No DC exist for octopus (*Eledone* spp.) beaks or prey identified solely from bones within the diet (n = 5 and n = 336, respectively). All prey increased in length after the application of DC (Table 2.2), with sandeel, dragonet, unknown gadoids, haddock/pollock spp., hake, Labridae spp., *Trisopterus* spp., blue whiting, and whiting all displaying significant increases (Paired T-test, $P < 0.01$). Mean length increased from 16.8 cm (± 3.2 SE) to 24.6 cm (± 5.2 SE), thereby exhibiting an overall percentage increase of 46%. Commercial species consumed by seals all displayed substantial increases in length (Figure 2.8) with whiting, haddock/pollock spp. and hake (*Merluccius merluccius*) increasing by 48%, 54%, and 72%, respectively. However, with the application of DC, the maximum length of certain prey species (e.g. herring *Clupea harengus*, rocklings, sandeels, dragonets) exceeded their maxima according to published information (Froese & Pauly 2016).

Table 2.2: Reconstructed prey lengths with and without the application of DC (n=549).

Species	N	Uncorrected Length (cm)		Corrected Length (cm)	
		Range	Mean ± SD	Range	Mean ± SD
Eels	1	-	1.7	-	2.1
Conger eel	1	-	6.9	-	8.6
Herring	2	16.5 – 25.2	20.9 ± 6.2	26.6 – 86.3	56.4 ± 42.2
Haddock/Pollock spp.	19	14.1 – 38.8	28.4 ± 6.1	31.2 – 58.0	43.7 ± 8.6
Whiting	20	14.7 – 25.1	20.0 ± 2.7	22.2 – 36.2	29.4 ± 4.3
Blue whiting	27	8.9 – 27.4	17.6 ± 4.0	15.8 – 33.3	23.5 ± 4.1
Trisopterus spp.	150	3.1 – 28.1	15.1 ± 5.0	3.9 – 36.3	19.6 ± 6.6
Rocklings	4	38.2 – 66.4	53.3 ± 15.2	62.9 – 106.2	86.0 ± 23.5
Ling	1	-	49.1	-	97.6
Unknown Gadidae spp.	20	7.2 – 21.2	15.2 ± 3.8	14.4 – 36.0	26.2 ± 5.9
Hake	5	20.3 – 31.0	26.4 ± 4.6	33.8 – 54.7	45.5 ± 9.1
Perch	1	-	13.1	-	17.3
Horse mackerel	1	-	26.4	-	33.6
Wrasse	12	16.8 – 27.2	21.3 ± 2.7	21.1 – 34.2	26.7 ± 3.4
Sandeels	249	8.3 – 55.2	15.2 ± 60.0	12.0 – 85.0	22.6 ± 9.3
Dragonets	14	12.7 – 26.4	19.4 ± 40.0	24.4 – 50.8	36.9 ± 7.6
Scaleless worm goby	3	6.9 – 9.9	9.0 ± 1.9	12.4 – 20.0	16.7 ± 3.9
Mackerel	1	-	59.9	-	73.9
Long rough dab	2	22.2 – 24.6	23.4 ± 1.7	30.7 – 33.8	32.2 ± 2.3
Lemon sole	1	-	17.0	-	41.9
Witch	1	-	15.1	-	19.1
Sole	4	31.1 – 38.8	35.1 ± 3.1	39.2 – 48.8	44.2 ± 3.9
Solenette	1	-	17.2	-	21.5
Unknown flatfish spp.	3	9.5 – 23.8	15.3 ± 7.5	12.5 – 30.4	19.7 ± 9.4
Squid	6	21.1 – 80.1	48.9 ± 24.0	21.6 – 81.7	50.0 ± 24.5

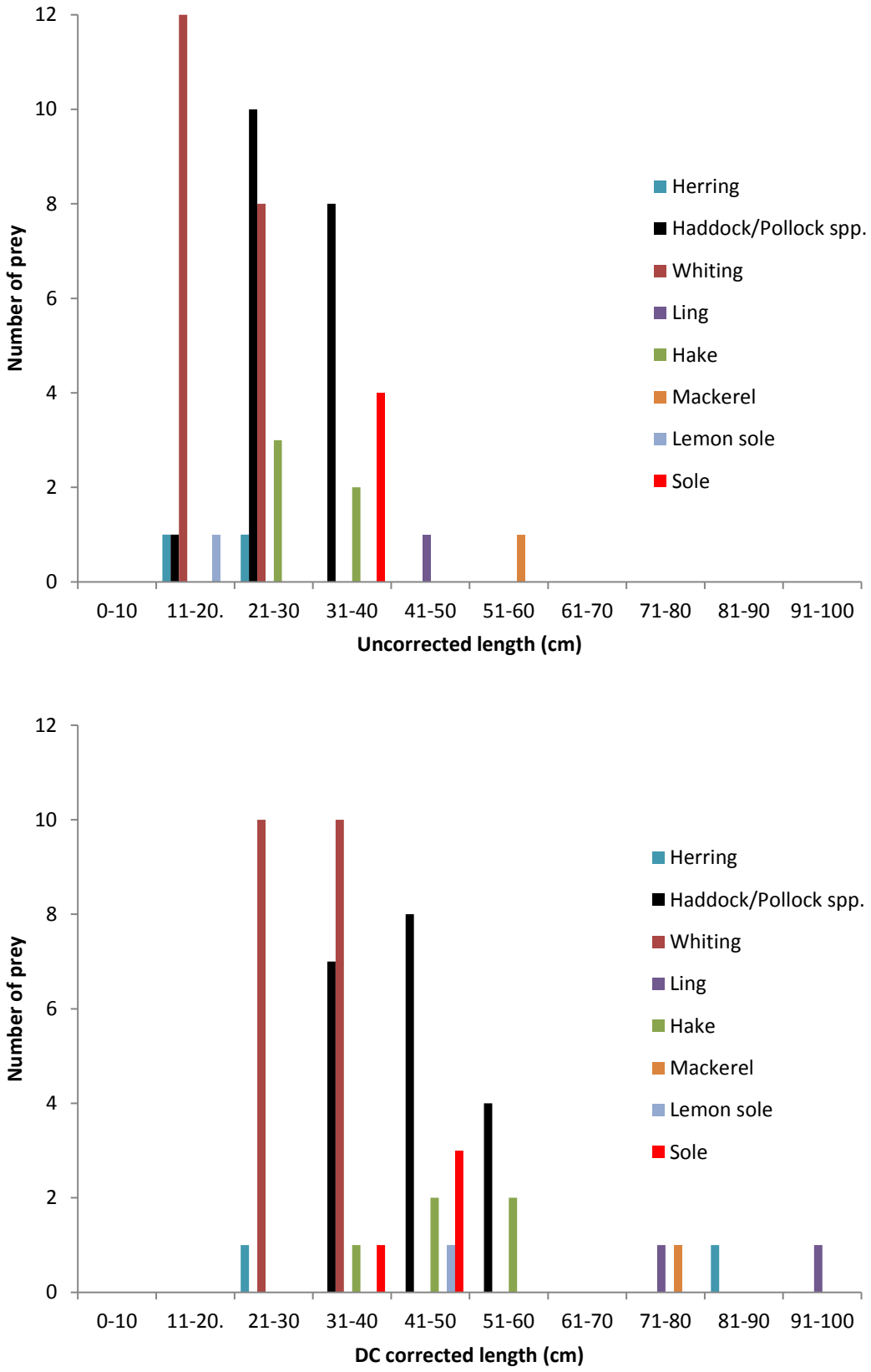


Figure 2.8: Length range distribution of commercially valuable prey species without the application of DC (upper frame) and with the application of DC (lower frame).

With the application of DC where available (549 prey items), weight significantly increases (Wilcoxon rank, $P<0.05$ in all cases where $n\geq5$). Similarly, the application of NCF to prey (59% of prey items) results in significant increased weights for the species they are applied to (Wilcoxon rank, $P<0.05$ in all cases where $n\geq5$). The uncorrected weights of all prey in the diet were compared to corrected weights where possible (and original weights when no DC or NCF were available). This results in weight increasing significantly for sandeels, dragonets, unknown gadoids, whiting, haddock/pollock spp., *Trisopterus* spp., hake, Labridae spp., sole (*Solea solea*), and *Loligo* spp. (Paired T-test, $P<0.03$ in all cases) after the application of DC. However, only sandeel and dragonet weight increased significantly (Paired T-test, $P=2.44x10^{8}$, $P=0.013$, respectively) after the application of NCF (Figure 2.9). These increases are mirrored in overall biomass contribution (Appendix III). The application of DC tends to over-represent the Gadidae family with other prey groups experiencing substantial decreases in weight contribution to the diet e.g. flatfish (Figure 2.9). Conversely, the application of NCF over-inflates sandeel contribution with other prey groups (except dragonets and squid) declining in diet contribution (Figure 2.9). This is likely due to many individuals from these prey groups having been identified from structures for which correction factors are not available (e.g. octopus, n=5), therefore they are under-represented in the diet when correcting for erosion.

When all correction factors are applied (where possible) and compared to uncorrected data using a mosaic plot (Figure 2.10), the weights of some species are more heavily influenced by correction factors than others (Pearson's Chi-square test, $\chi^2=17607$, $df=23$, $p<0.001$). While the total weight of prey increases substantially after applying all correction factors (see length of uncorrected versus corrected boxes in Figure 2.10), one would expect the weight of each species to similarly increase proportionally (see height of uncorrected versus corrected boxes). Instead correction factors tend to substantially increase weights of certain species e.g. sandeels, haddock/pollock, while grossly underestimating contribution of other prey species e.g. flatfish. In the mosaic plot the shading represents the number of residuals (deviations) from the null hypothesis (that no difference exists between the proportional uncorrected and corrected weights across species). The application of correction factors results in particular species dominating the diet (depicted in blue) in proportion to other prey which then tend to contribute proportionally less to the overall diet (depicted in red).

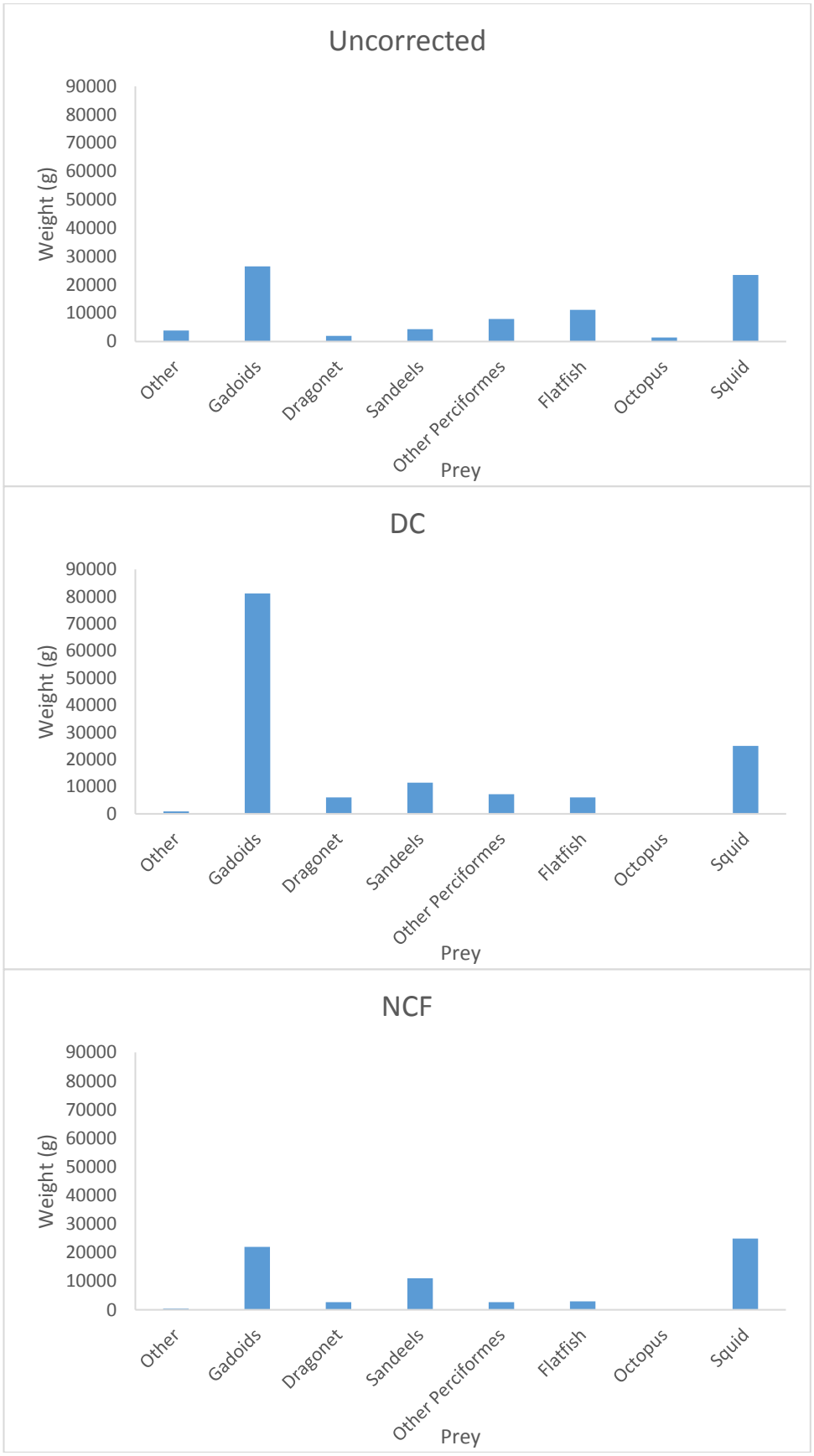


Figure 2.9: Weight contribution of prey when i) uncorrected for erosion, ii) DC corrected, and iii) NCF corrected. Other = lamprey, eels, and herring.

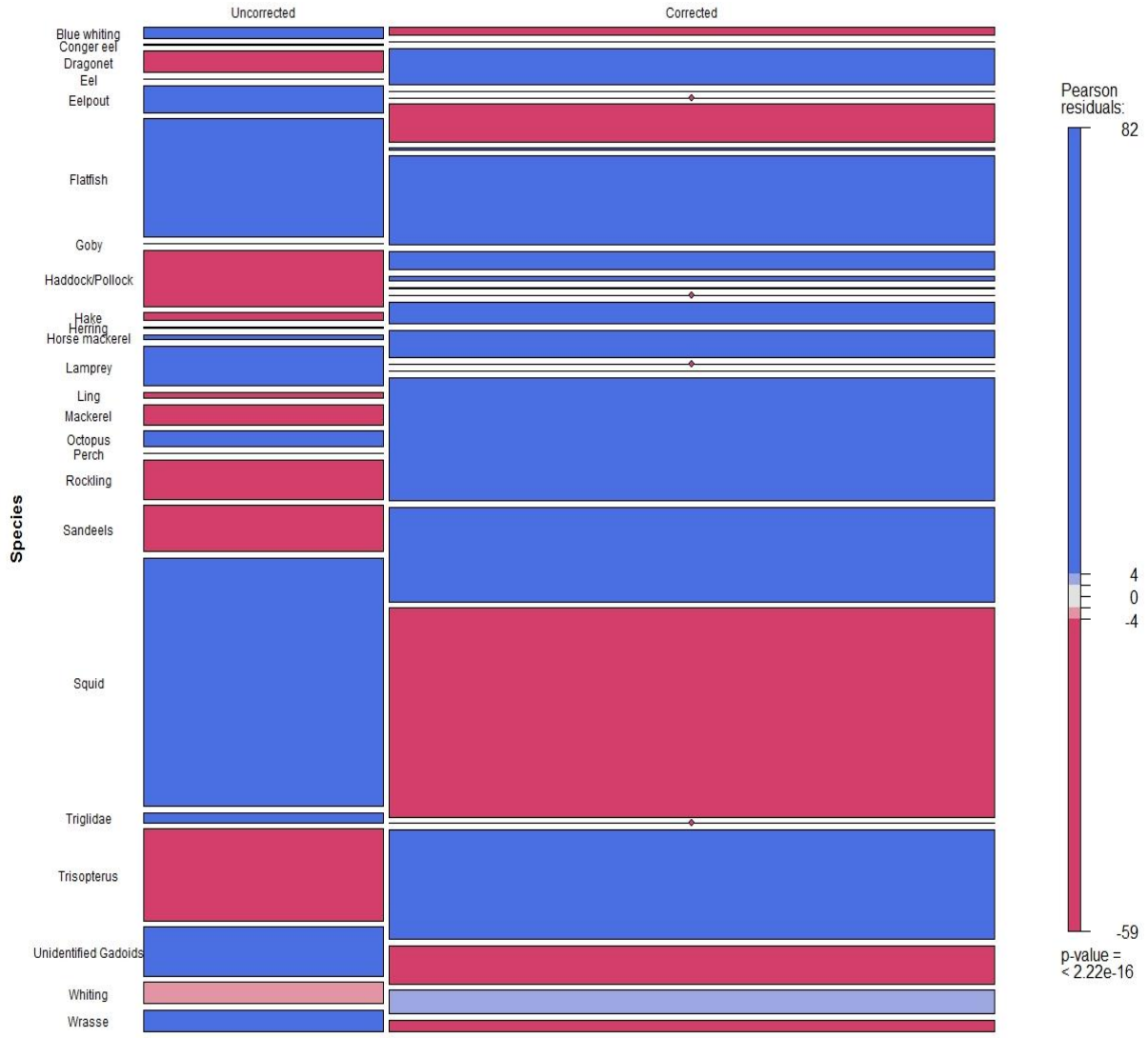


Figure 2.10: Mosaic plot showing uncorrected weights, and corrected weights for prey species within the grey seal diet. Colour denotes the number of Pearson's residuals associated with each species contribution to the diet by weight, where red indicates observed weights below the expected value, blue denotes observed weights above the expected value, and grey denotes weights have not altered significantly from the expected value.

Diet variability – effects of applying correction factors

Variations in grey seal diet was examined using uncorrected prey-specific biomass compared with prey-specific biomass after correction factors (both DC and NCF) were applied (Figure 2.11).

The application of correction factors did not alter the interpretation of the feeding strategy of grey seals or the overall importance of key prey species. Regardless of correcting for both partial and complete erosion, seals still display a generalised feeding strategy with key prey like sandeels, flatfish, dragonets, and *Trisopterus* spp. present in a large number of scats, suggesting they are consumed by the majority of the "population". Similarly, many other prey species occurred rarely in the diet (e.g. hake, Labridae spp.) irrespective of the application of correction factors. Furthermore, particular species such as ling, eelpout, rocklings, Triglidae spp., and Cephalopoda occurred infrequently, in low abundances within scats but constituted a large proportion of the diet due to their size, regardless of whether correction factors are applied. Only two species displayed a noticeable alteration in their positioning, with lamprey accounting for a slightly larger proportion of the diet and perch accounting for slightly less after the application of correction factors. Additionally, with the inclusion of correction factors, flatfish move fractionally closer to becoming rarer prey, however overall they still remain key prey within the diet.

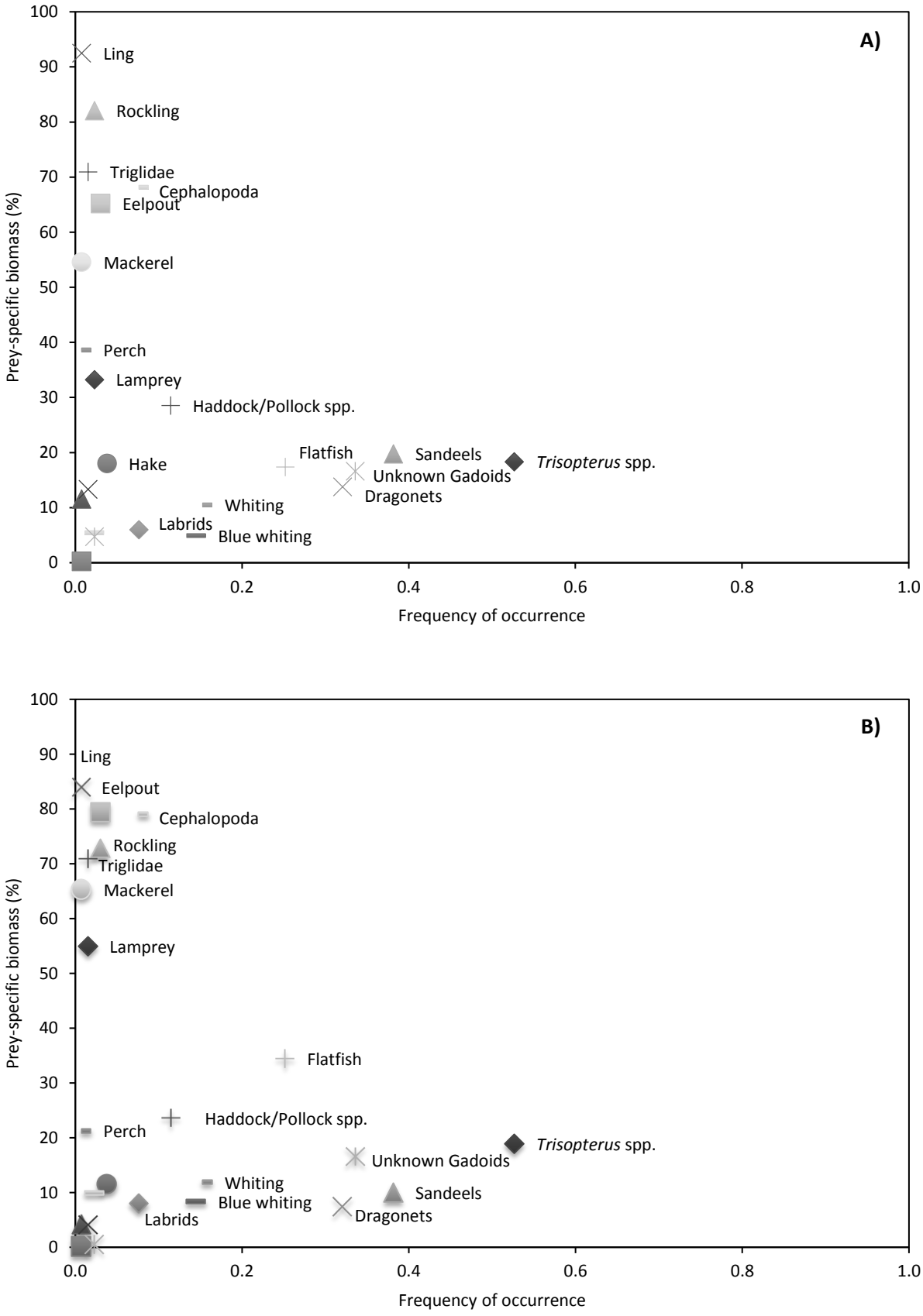


Figure 2.11: Costello-Amundsen plots displaying differences in prey biomass contributions using A) combined correction factors (DC & NCF), B) no correction factors.

2.4.4 Effect of misidentification of salmonids

Using the same samples, Gosch *et al*. (2014) previously identified 939 individual prey items. However, a subsequent review of samples highlighted 46 salmonids that were misidentified. The bone previously thought to be a salmon premaxilla, was later discovered to be the posterior end of the inter-opercular head bone found in gadoids. When reviewing each sample individually, the "salmonid" bone was present within the diet each time a gadoid had been identified. The bone occurred 70% of the time a *Trisopterus* species was identified, with the remaining 30% of occurrence coinciding with the identification of unidentified gadoids, whiting, blue whiting, and rocklings within the diet. The resulting abundance and frequency of occurrence for all other prey species did not alter when "salmonids" were reclassified and removed from the diet, however overall contributions to dietary indices of percentage abundance and percentage biomass did change.

Removing "salmonids" resulted in a 5.2% increase in the percentage abundance of all prey species within the diet. This effect was minimal with the greatest change occurring in the Gadidae family which increased from 37.2%N to 39.1%N. Prior to their removal "salmonid" contribution to the diet was 22%B (Gosch *et al*., 2014). Thus, their exclusion resulted in all other prey increasing in importance. However, this increase was not distributed evenly. Adjusted percentage biomass values show that gadoids and Cephalopoda were far greater contributors to the diet (32%B and 31%B) than previously reported, with a similar response noted for where NCF had been applied to salmonids (Figure 2.12).

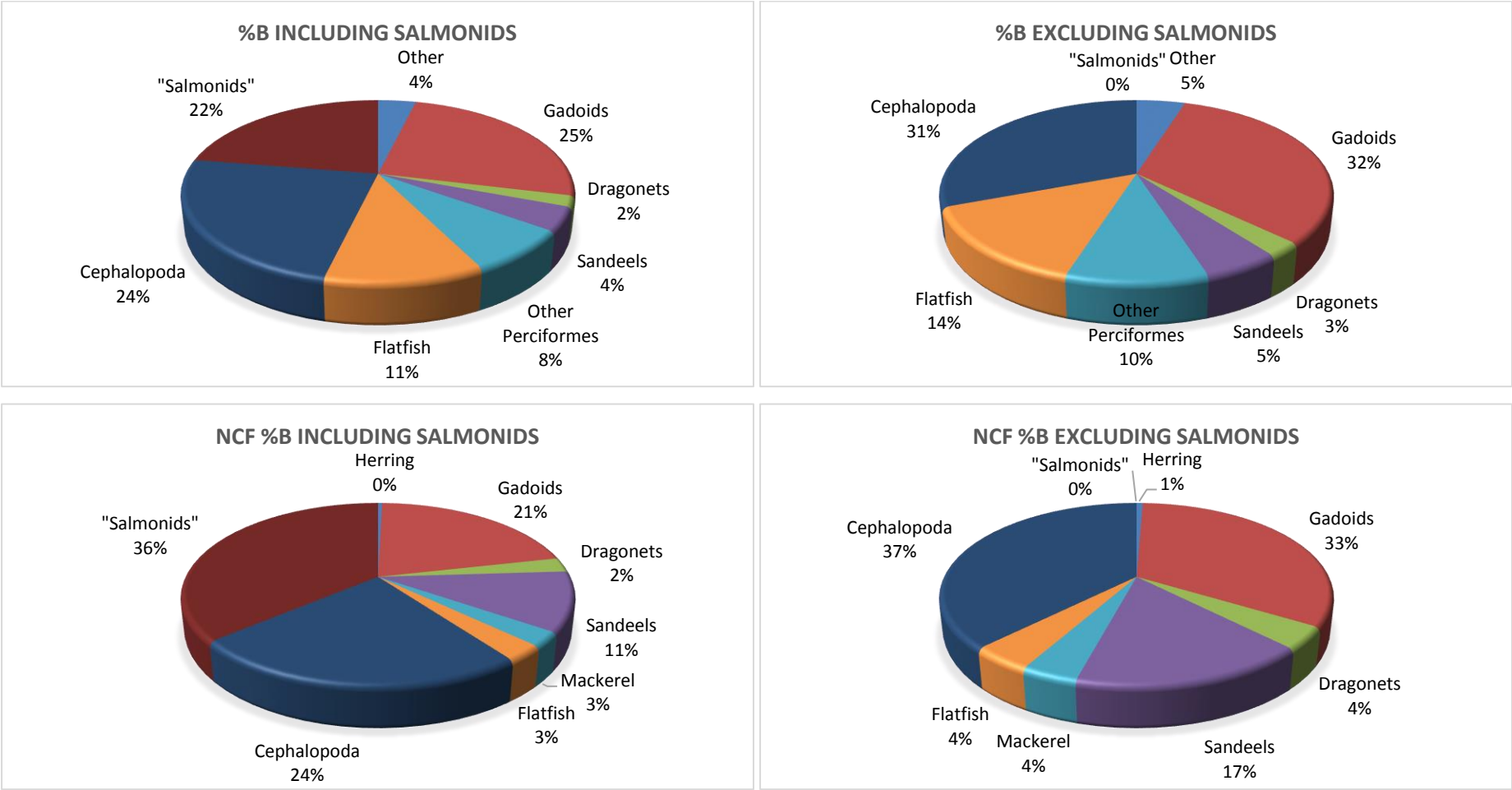


Figure 2.12: Differences in prey biomass contributions to grey seal diet when A) “salmonids” are included, B) “salmonids” are excluded, C) “salmonids” are included in NCF analysis, and D) “salmonids” are exluded in NCF analysis. Other = lamprey, eels, herring.

Diet variability – effects of misidentification of "salmonids"

Modified Costello-Amundsen plots were constructed to investigate whether seal diet altered extensively after the removal of misidentified "salmonids". Prey-specific abundance plots exhibited no difference in prey positioning apart from the "salmonid" data point not occurring. In terms of prey-specific biomass, the overall feeding strategy did not alter substantially, with grey seals still displaying a generalised feeding strategy, particularly in terms of *Trisopterus* spp., unknown gadoids, sandeels, dragonets and flatfish (Figure 2.13). The only alteration to these species after the removal of "salmonids" was a minimal shift further up along the x-axis. The key species within grey seal diet off southwest Ireland did not undergo any changes in selectivity or importance regardless of the inclusion or exclusion of misidentified "salmonids". However, with the removal of salmonid, lamprey accounted for a lesser proportion of the diet while eelpout, rocklings, Triglidae spp., and mackerel contribution to the diet of grey seals experienced an increase.

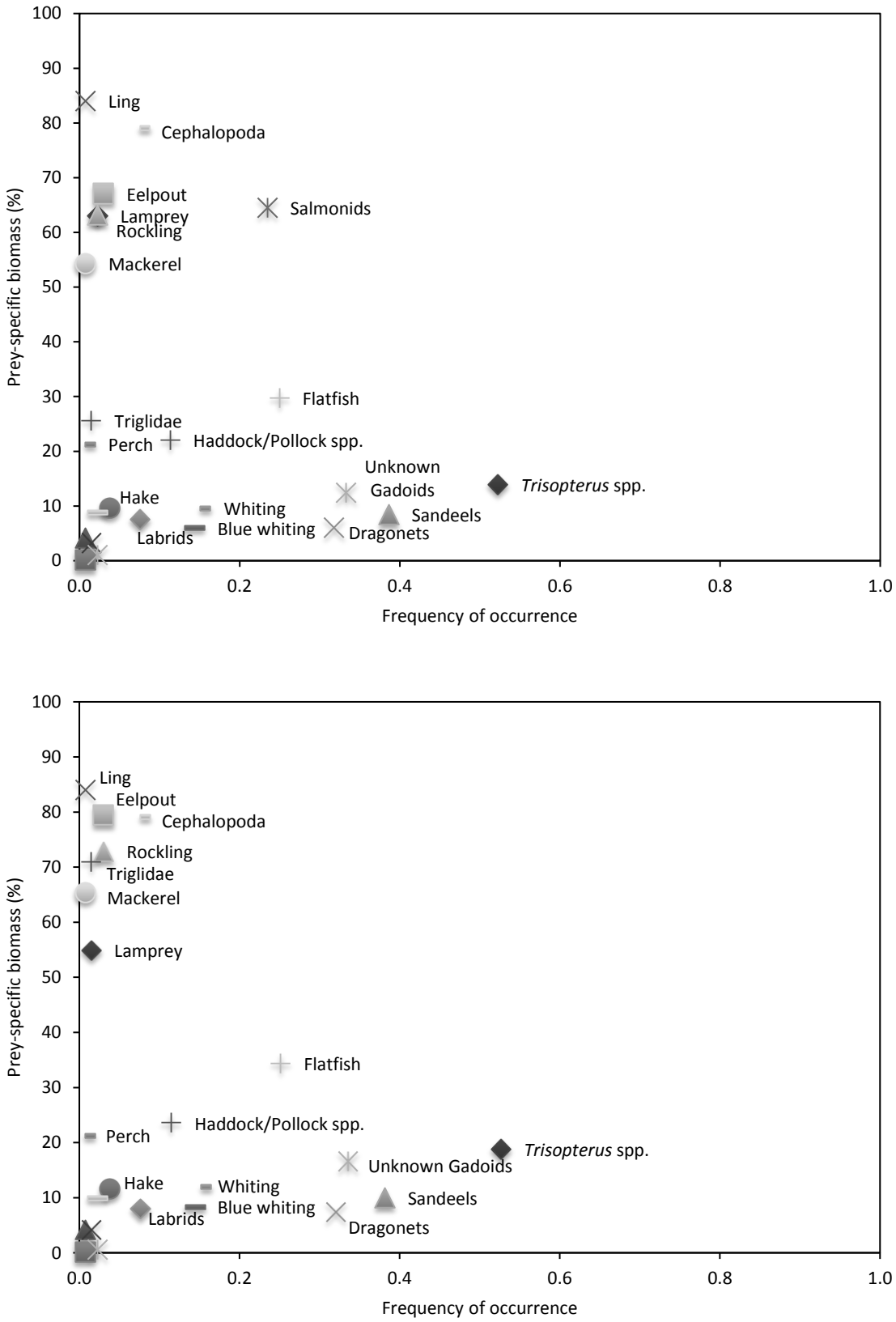


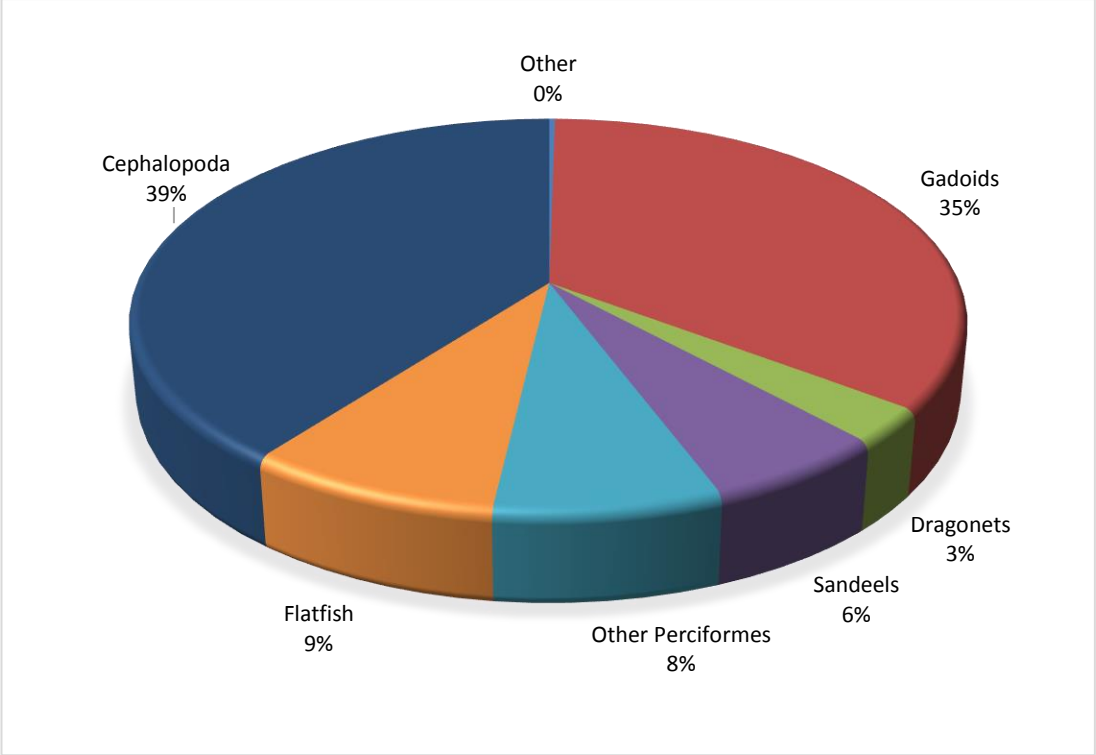
Figure 2.13: Costello-Amundsen prey-specific biomass feeding plots of grey seals off southwest Ireland; Including misidentified "salmonids" (upper frame), and re-analysed data excluding "salmonids" (lower frame). See Appendix III for unlabelled prey.

2.4.5 Effects of using average body sizes and general regression equations.

Within this study, the back calculation of prey was possible for 73% (n=655) of all prey items. 10% of all prey (unidentified fish and rays, n= 90 and n=2) were not assigned any lengths. The remaining prey items (n=146) were assigned average length/weights calculated from other individuals of the same species identified either within the same sample/month/year as the prey item for which size reconstruction was not possible. This enabled biomass contribution estimates for as many prey individuals as was possible, thereby potentially reducing uncertainty.

The percentage biomass was then re-analysed to exclude those prey items for which reconstruction of original size was not possible (Figure 2.14). Results did not greatly alter the diet composition with respect to key species from the Gadidae family, Cephalopoda, and flatfish, all still remaining the most important prey in terms of biomass contribution within the diet. However, after the exclusion of all prey for which size reconstruction was not possible, gadoids, Cephalopoda and sandeel biomass contribution all increased. Conversely, biomass values for other Perciformes (apart from sandeels and dragonets), flatfish, and other species (lamprey, eels, and herring) all decreased.

In instances when identification may only be possible to a genus/family level, general equations are employed. This occurred most frequently with respect to *Trisopterus* spp. and haddock/pollock spp. Applying regression equations for *T. minutus* where prey were identified as *T. minutus/luscus*, and unknown *Trisopterus* spp. resulted in average length decreasing from 14.9 cm (±0.3 SE) to 14.3 cm (±0.3 SE), and average weight decreasing from 44.0 g (±3.4 SE) to 39.9 g (±3.2 SE) – neither of which were significant (Paired T-test, $P>0.05$). This resulted in their overall biomass contribution to grey seal diet decreasing from 10.71% to 9.80%. Application of *P. pollachius* equations to haddock/pollock spp. resulted in length increasing from a mean length of 28.6 cm (±1.2 SE) to 32.5 cm (±1.6 SE), and average weight increasing from 240.0g (±29.3 SE) to 364.0 g (±55.5 SE). Neither of the increases where however significant (Paired T-test, $P>0.05$). The change in weight also resulted in an increase in biomass contribution from 6.52% to 9.57%.



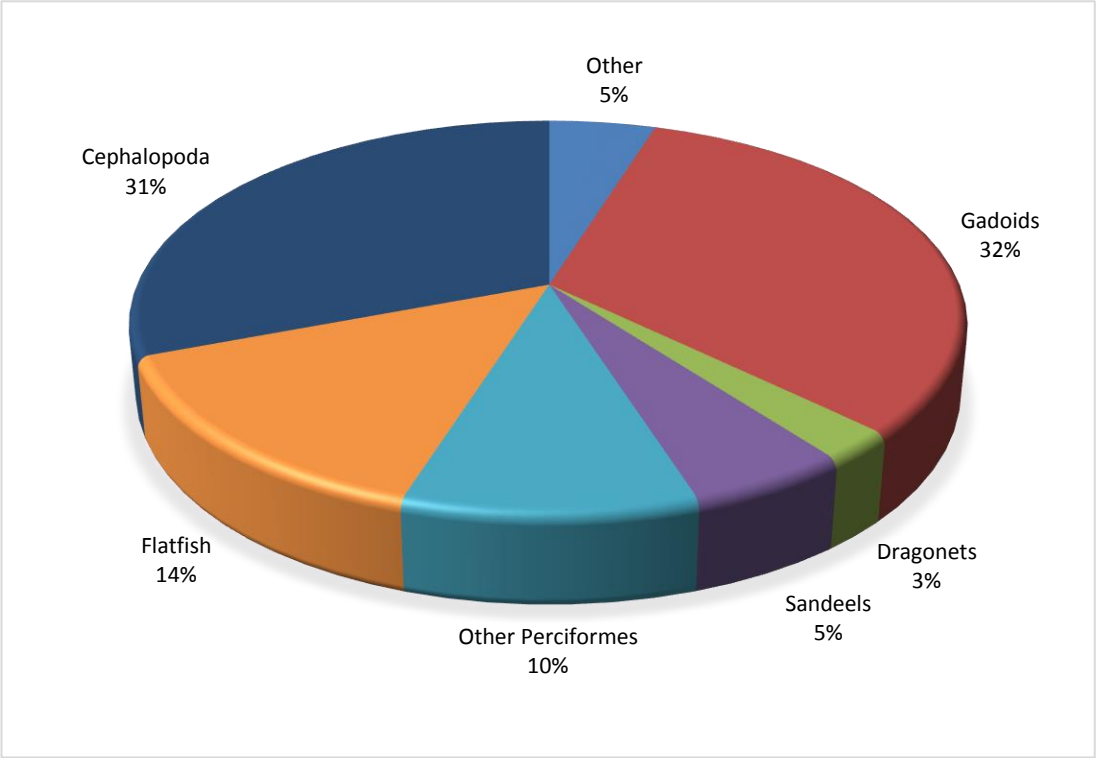


Figure 2.14: Differences in prey biomass contributions to grey seal diet when average prey sizes are excluded (upper frame) and when they are included (lower frame). Other = lamprey, eels, herring.

2.5 DISCUSSION

No one method for analysing pinniped diet can be universally recommended as each one has inherent limitations (Tollit *et al*., 2010). The approach adopted by the investigator depends on the question that is being addressed. This study examined the best approach to use when describing the diet of grey seals that haul out in southwest Ireland. When using otoliths/beaks alone, 578 prey items were identified. However, the inclusion of all diagnostic structures in addition to otoliths/beaks resulted in a 46% increase in the number of prey items identified. Four taxa were identified solely from non-otolith structures, and 315 prey items (35% of all prey items) were identified from non-otolith/beak structures. Not only does the identification of additional prey species and prey items alter dietary indices, by including other diagnostic structures, the picture of prey importance and diet variability of grey seal alters. With this new information, grey seals are now known to consume unidentified gadoids, sandeels, flatfish, and dragonets far more regularly, although particular prey species that occur rarely (e.g. Triglidae spp., lamprey, eelpout) now account for a larger proportion of the diet in terms of their weight contribution. As bones (non-otoliths) are generally more resistant to chemical abrasion (Pierce *et al*., 1993; Granadeiro & Silva, 2000), their inclusion in dietary studies is extremely important to accurately describe all prey species consumed by seals. Furthermore, species possessing fragile/small otoliths (e.g. clupeids and salmonids) may undergo complete erosion within the digestive tracts and therefore go undetected (Boyle *et al*., 1990; Tollit *et al*. 1997; Bowen, 2000; Grellier & Hammond, 2005), or can often be recorded as incidental prey due to low recovery rates in samples (e.g. Casper *et al*., 2006). Lundström *et al*. (2007) found that eelpout have a very low recovery rate, however, all eelpout in this study were identified from non-otolith structures. It is quite probable that eelpout predation by pinnipeds has been underestimated in studies using otoliths alone. This study suggests that the inclusion of all hard parts may offset some of the aforementioned biases associated with diet description from scat contents (as described in Browne *et al*., 2002; Laake *et al*., 2002).

There are, however, a number factors to consider when using a range of diagnostic structures for prey identification. Double counting of prey can potentially bias estimates (Joy *et al*., 2006), thus when estimating a minimum count for each prey species it is important to base the count on the skeletal structure which generates the

highest count within the sample (Tollit *et al*., 2010). Inter-specific variation in the resistance of non-otolith structures to the effects of erosion also has the potential to bias diet estimates towards those species with larger and/or more robust bones (Hansel *et al.*, 1988). While a certain degree of intra-specific variation exists, in general, dragonet preopercular bones are easily recognisable and frequently recovered from scat samples in good condition, potentially leading to this species being over-represented in pinniped diet estimations. However, many other species are recognisable from particular unique bones (Pierce *et al*., 1991a; Britton & Shepherd, 2005). For example, sandeels can be easily identified from their atlas vertebrae, premaxillae, and dentaries', flatfish urohyals are unique to each species, ling possess very distinctive post-temporal bones, and otic bullae can be used to detect the presence of clupeids within scat samples. Furthermore, it is also possible to identify many prey species from bone fragments (Hansel *et al*., 1988; Granadeiro & Silva, 2000). While these structures may not be as robust as dragonet preopercular bones and many gadoid premaxillae jaw bones, their recognition will ensure other prey species are not under-represented in the diet. It is therefore recommended that investigators familiarise themselves with an assortment of diagnostic structures from different species. Certain bones from particular prey species typically survive the digestive process, therefore it is important not to indefinitely introduce new bones to personal references collections as this will ultimately confuse the investigator. Prior to commencing dietary analysis of marine mammals, one recommendation would be to define which bones from common prey species categorically survive digestion best. Even though a high level of training is initially required (Cottrell & Trites, 2002) this will ensure recognition of species from bone fragments and avoid potential misidentification of prey.

As has been demonstrated in this study, the misidentification of a species from hard parts can result in large differences in quantifying contributors to the diet. The exclusion of salmonids noticeably altered the biomass contributions of all other prey species in the diet. In a previous study, "salmonids" accounted for one of the most important prey species within grey seal diet in southwest Ireland in terms of weight (Gosch *et al*., 2014). Following removal of misidentified salmonids, gadoids and cephalopods became the greatest biomass contributors to the diet, with the estimated weight contribution of both groups almost 1.5 times higher than previously identified. The misidentification and misrepresentation of biomass estimates for valuable

commercial species such as salmonids in pinniped diet studies can have serious implications, particularly in a region where the seal-fishery conflict is already a highly sensitive subject. To minimise this risk, the construction of a detailed reference collection of local fish species to aid in the familiarisation of diagnostic structures (Pierce *et al*., 1991a; Granadeiro & Silva, 2000) is recommended. Furthermore, when investigating the diet of pinnipeds where diagnostic structures are known to undergo various degrees of erosion, feeding trials and subsequent evaluation of eroded structures would undoubtedly be a valuable tool for their recognition in the diet, with perhaps the additional advantage of constructing regression equations and/or correction factors for common bones found within the diet (See Appendix IV for an example of such an attempt regarding salmonid bones).

While this study has demonstrated the merits of including all structures in pinniped diet analysis, the deficit of available regression equations for non-otolith structures resulted in the inability to reconstruct body size for 16% of prey items detected. By assigning average sizes to these items from previously reconstructed prey of the same species, it was assumed that the seals target fish of generally the same size within a species. While overall, biomass values did not alter substantially with the inclusion of average sizes, certain groups such as flatfish, Perciformes (apart from sandeels and dragonets) and other (lamprey, eels and herring), all exhibited increases in biomass contribution. This is likely due to many of these prey items having been identified from non-otolith structures. Therefore, species that are identified mainly from bones or for which no regression equations exist will automatically be markedly under-represented in the diet if no body size can be assigned to them. Although assigning average sizes introduces potential bias, as they are based on assumptions, their inclusion rather than exclusion is possibly a more accurate reflection of seal diet estimation. Further to this, the use of family/genus level regression equations, while common practice in diet studies, has the capacity to impact biomass estimates in relation to certain species. This study demonstrated that while *Trisopterus* species biomass did not significantly change when substituting *T. minutus* for unknown *Trisopterus* or *T. minutus/luscus* individuals, there was a noticeable increase in the biomass contribution of haddock/pollock (though not significant) once pollock regression equations were used instead of the generic haddock/pollock/saithe equation. Therefore, while general equations are undeniably useful for acquiring

biomass estimates, particularly when the occurrence of family/genus level identification is low, caution must be applied. In addition, widely distributed species have a tendency to display geographic variations in their relationship between body size and otolith size (Härkönen, 1986; Granadeiro & Silva, 2000) with body size also varying considerably between species within the same genus or family (Clarke, 1986).

Another acknowledged limitation of the traditional diet analysis method is the erosion of otoliths during the digestion process, thus affecting the reconstruction of the original prey size (Harvey 1989; Tollit *et al*., 1997; Bowen, 2000; Grellier & Hammond, 2006). Within this study, the application of digestion coefficients resulted in the Gadidae family substantially dominating the diet, while all other prey groups (except for sandeels and dragonets) experienced declines in biomass contribution, as has been similarly demonstrated in other studies (e.g. da Silvia & Neilson, 1985; Browne *et al*., 2002; Laake *et al*., 2002). Conversely, the application of numerical correction factors to account for complete erosion of otoliths, tended to underestimate the importance of gadoids and overinflate biomass contribution of less important prey such as sandeels, also demonstrated in other studies (e.g. Lundström *et al*., 2007; Tollit, unpublished, in Tollit *et al*., 2010). While fish of economic importance displayed significant increases in length after the application of digestion coefficients, other prey species exceeded their maximum recorded lengths according to Froese & Pauly (2016). Species-specific digestion coefficients can therefore overestimate certain prey sizes, particularly if applied to otoliths that may not be overly eroded. Using grade-specific digestive coefficients would be an alternative (e.g. Tollit *et al*., 1997; Grellier & Hammond, 2006), particularly when examining overlap in fish sizes targeted by seals and fisheries, however, the condition of each otolith first requires grading which introduces an element of subjectivity to prey reconstruction. The lack of correction factors for non-otolith structures is a fundamental limitation to using correction factors and an all structures approach in pinniped diet analysis. Prey items identified from non-otolith structures (e.g. Octopus and many Perciformes and flatfish) will be under-represented if correction factors are unfairly applied to only some of the prey recovered in the diet. The relative proportion of prey species for which correction factors can be applied therefore needs to be considered when reconstructing diet, together with intra- and inter-specific variation in the resistance of otoliths to the effects of erosion. Furthermore, various factors will influence the rate

of digestion with smaller meals, smaller prey and lower activity levels of the predator resulting in complete digestion and less recovery rates of otoliths (Harvey, 1989; Marcus *et al*., 1998). Given that many correction factors are based on calculations from feeding trials using captive seals kept in dry runs (e.g. Dellinger & Trillmich, 1988; Staniland, 2000) that are fed predominantly small meals containing single species (see Bowen, 2000), it is unlikely that this mirrors the true activity level, average meal size and meal content in wild seals (Cottrell *et al*., 1996; Casper *et al*., 2006).

Other observations to arise from this study relate to uncertainties regarding published regression equations, with caution advised when attempting to reconstruct prey size. Rocklings were larger than the maximum sizes for each species recorded by Froese & Pauly (2016), suggesting that the published regression equations by Härkönen (1986) may not be suitable for otoliths above a certain length. Similarly, the large variation in Cephalopoda body size amongst species means that applying genus level regression equations may overestimate the contribution of certain prey to the diet. Squid were found in low abundances in the diet however their contribution in terms of biomass was substantial, although beak sizes were often small. This suggests that regression equations by Clarke (1986) may be unsuitable for squid beaks below a certain length. While it is not always possible to reconstruct prey size, caution is also advised when assigning common sizes attained from Fishbase to prey individuals. Common lengths/weights may often be larger than what might be consumed by seals. For example, in this study common weights for two dab and three lamprey of 500 g and 1250 g, respectively, were obtained from Fishbase. However, it is unlikely that grey seals consumed an entire lamprey of this size.

When reconstructing pinniped diet using hard part analysis, it is important to be aware of the many possible biases that can influence prey estimates. The choice of which approach to take can have important implications regarding trophic interactions, particularly when considering seal-fisheries competition for resources. Overall, the application of digestion coefficients and numerical correction factors did not alter the interpretation of predator feeding strategy or prey selectivity and importance. Key species consumed by seals remained the same regardless of whether correction factors were applied, thus their use is of no benefit to the interpretation of grey seal foraging behaviour. However, correction factors did negatively bias the interpretation of diet

description more than it addressed underlying issues of otolith erosion. While digestion coefficients are beneficial when investigating overlap with commercial fish species sizes, their overall use in the diet is questionable due to the lack of availability for other species. If correction factors were available for all species and frequently recovered diagnostic structures, this would allow all prey proportions in the diet to be represented equally. Further work on constructing correction factors is clearly required. In order to avoid introducing gross biases in diet estimation and to maintain the same assumptions across the data, correction factors should not be applied to diet description data when a significant proportion of prey items cannot be corrected, thereby ensuring equal treatment of all prey within the diet.

This study also demonstrates that omitting prey identified from other structures leads to their gross under-representation in the diet. Repercussions may lead to key prey, such as sandeels, dragonets, and flatfish being misrepresented as rarely occurring in the diet. Furthermore, while the use of average sizes and genus/family level regression equations was shown to affect biomass estimates, it is deemed more beneficial to use them rather than to exclude prey altogether.

While the use of hard part analysis remains a low-cost and informative method of reconstructing diet, it does require a high level of training. The production of local reference collections and familiarisation with bone fragments will help avoid misidentification of prey. The use of molecular methods for prey identification such as immunoassays using polyclonal antisera, enzyme-linked immunosorbent assays (ELISA), fatty acid signature analysis, stable isotope analysis, and DNA techniques are now being employed with greater regularity in diet studies (e.g. Jarman *et al*., 2004; Parsons *et al*., 2005; Matejusová *et al*., 2008; Deagle *et al*., 2009). While each technique has its own set of advantages (see Tollit *et al*., 2010 for overview), many are hindered by protein degradation during digestion and lack detail on quantitative descriptions of prey species. However, by employing molecular techniques in tandem with hard part identification, the complementary methodology could substantially improve pinniped diet descriptions. This is turn will improve our understanding of the role of this top predator in the marine ecosystem.

CHAPTER 3

Seasonal and annual differences in the diet of grey seals from a colony of national importance off southwest Ireland



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3.1 ABSTRACT

The diet of grey seals has been analysed throughout parts of its range in the North Atlantic, although most studies are short term and often seasonally limited. Understanding how diet varies temporally and spatially contributes to our understanding of foraging strategies and habitat use. In this study, seasonal and annual variation in the diet of grey seals that occur off the southwest coast of Ireland was examined. Scat samples were collected from a colony of national importance over a period of four years and nine months. The general reliance of seals on particular prey species was assessed, together with seasonal and inter-annual trends. Sandeels and *Trisopterus* species were considered to be important prey species and apart from these forage fish, six other main prey groups were identified as being of importance to the diet of grey seals in this region. Significant temporal variation was also evident, with no consistency in prey occurrence apparent over time. Grey seal foraging behaviour is consistent with recent studies modelling prey preference in grey seals in Ireland, with seals consuming abundant lower trophic level species that are high in nutritional value. Prey switching was also evident, with higher abundance of commercial species diet coinciding with periods of low abundance of sandeels and *Trisopterus* species in the diet. Given the importance of these lower trophic level, and not commercially fished, species to the seals diet, and the wider ecosystem, any consideration of a commercial fisheries for these species should only be made after a thorough risk assessment be carried out, within the context of an ecosystems approach to fisheries management.

Keywords: sandeel, *Trisopterus*, commercial species, temporal dietary trends

3.2 INTRODUCTION

The presence of various climatic, physical and oceanographic features along Ireland's southwest coast, such as fronts and periodic upwelling events (Raine *et al*., 1990) supports important spawning grounds for numerous demersal and pelagic species (Marine Institute, 2015). Within 20km of the coast, the topography drops to 80-100m depth and extends as a relatively flat plateau as far as the shelf edge (OSPAR, 2000). Grey seals (*Halichoerus grypus*) are primarily demersal and benthic feeders (Pierce *et al*., 1990; McConnell *et al*., 1999; Brown *et al*., 2012; Gosch *et al*., 2014), and will generally dive to less than 150m, however deeper dives to the benthos of over 450m have been reported (Jessopp *et al*., 2013). The productive ecosystem, together with ease of access to foraging grounds, provides ideal foraging conditions for the local grey seal population using the southwest coast of Ireland. Islands such as the Blasket Island group in Co. Kerry support breeding and moulting colonies of national importance (Ó Cadhla *et al*., 2008, 2013).

While there have been many studies examining grey seal diet throughout their range in the North Atlantic (McConnell *et al*., 1984; Prime & Hammond, 1985, 1990; Bowen & Harrison, 1994; Hammond *et al*., 1994a, 1994b; Beck *et al*., 2007; Ridoux *et al*., 2007), to date, literature on seal diet in Ireland is very limited both spatially and temporally (BIM, 1997, 2001; Arnett & Whelan, 2001, 2002; Kiely *et al*., 2000; Gosch *et al*., 2014). Though it is widely acknowledged that certain gadoids and sandeels (*Ammodytes* spp.) are key prey within grey seal diet, the relative contributions of different species likely vary significantly across their range, even over relatively short distances. While sandeels are more important in the diet of grey seals around Orkney and other sites in north-eastern Scotland (Prime & Hammond, 1990; Hammond *et al*., 1994a), diet is dominated by gadoids around the Inner Hebrides (Hammond *et al*., 1994b), and salmonids are of importance in other areas around Scotland (Rae 1960; 1968; Pierce *et al*., 1991c; Carter *et al*., 2001). Such geographic variation in seal diet may be attributed to prey availability, seal foraging behaviour, or a combination of the two. Optimal foraging theory predicts that seals will target prey of high nutritional content while minimising the energetic costs this requires (Pyke, 1984). This does not necessarily imply that they will feed on whichever species is more abundant, but rather they may specialise on prey containing higher calorific values if these are readily

available (Pyke *et al*., 1977) and with a reduced handling time. Gosch *et al*. (2014) showed that the spring diet of grey seals off southwest Ireland is largely dominated by sandeels, while herring (*Clupea harengus*) contribution to the diet was negligible. Given the higher nutritional content of herring (Murray & Burt, 1977) and its prevalence in these waters (Gerritsen & Lordan, 2014; Marine Institute, 2015), one would expect herring to be found in far higher abundances than exhibited within the diet. Armstrong (1999) suggested that shoaling schools of herring off the seabed may be difficult for seals to catch. This suggests that seals off southwest Ireland may be feeding according to optimal foraging theory rather than consuming seasonally abundant prey, by balancing prey energy content with the energetic cost of obtaining it. Similar behaviour has been shown by predatory fish in the Celtic sea which select smaller prey of lower nutritional value rather than more abundant pelagic fish containing higher calorific values (Pinnegar *et al*., 2003). However, as grey seal diet is characterised by a wide variety of prey species, they are typically described as generalists, exploiting prey as it becomes locally and seasonally abundant (Benoit & Bowen, 1990; Hammond *et al*., 1994a; Bowen *et al*., 2006).

In order to assess grey seal diet in southwest Ireland, the potential or likely temporal variation in diet across the year must be considered. Seasonal changes in diet can however be challenging to detect. Variation in sampling effort due to the difficulty in accessing offshore island study sites during inclement weather, for example, can confound trends through differences in the number of samples collected across the year. Given the limited diet data available for grey seals in this geographic area, it is not evident if grey seals are selecting particular prey year round or if they switch to alternative prey according to seasonal availability, ease of capture or nutritional content. High occurrences of sandeels and low abundances of commercial species such as haddock (*Melanogrammus aeglefinus*) and pollock (*Pollachius pollachius*) have previously been identified in diet of grey seals in southwest Ireland in spring (Gosch *et al*., 2014) but it is not clear if this reflects the diet of grey seals in this region outside of spring. While Cronin *et al*. (2014) reported that in general, inshore Irish pollock fisheries experienced an increase in operational interactions with seals (i.e. seals removing fish from the nets) during the spring fishing season, the overall importance and contribution of haddock and pollock to the diet is not known. In order to understand the potential for competition for resources between fisheries and this

important predator, information on the relative contribution of valuable commercial species to the diet of grey seals is imperative, and whether this changes over time (between seasons and years).

The hypothesis that grey seals are generalists exploiting local, seasonally abundant fish assemblages was therefore investigated using a long term dataset of grey seal scat collected from a colony of national importance in the southwest of Ireland. Seasonal and inter-annual patterns in the diet, particularly key prey species, were also examined.

3.3 METHODS

3.3.1 Data collection

Scat samples from grey seals hauling out on Great Blasket, southwest Ireland (Figure 3.1) were collected monthly (where conditions allowed access to the site) over a period of just under five years, from February 2009 to November 2013. The site is the second largest grey seal breeding colony in Ireland, with an all-age population size of between 1,099 and 1,413 greys seals regularly hauling out on the broad sandy beach (Ó Cadhla *et al*., 2013) located on the northeast end of the island (10°30'53''W, 52°06'15''N). The site supports a mixed colony of sexes and age groups, and is easily accessible by boat during calm weather conditions. Regular trips were made to the site when weather conditions permitted with the aim to collect at least 20 samples per visit. Scat samples were collected at low tide, placed in separate polythene bags, labelled and stored frozen at -20°C.

3.3.2 Dietary analysis

The traditional dietary analysis method using hard part prey remains recovered from scat contents was applied for prey species identification, as described in Pierce *et al*. (1990), Pierce & Boyle (1991), and Chapter 2. In conjunction with using nested sieves, some samples were washed in a washing machine within mesh nylon bags with a mesh size of 0.5 mm, a length of 25.4 cm and a width of 15.24 cm, similar to the process used by Orr *et al*. (2003). Each sample was inserted into a separate bag, sealed using

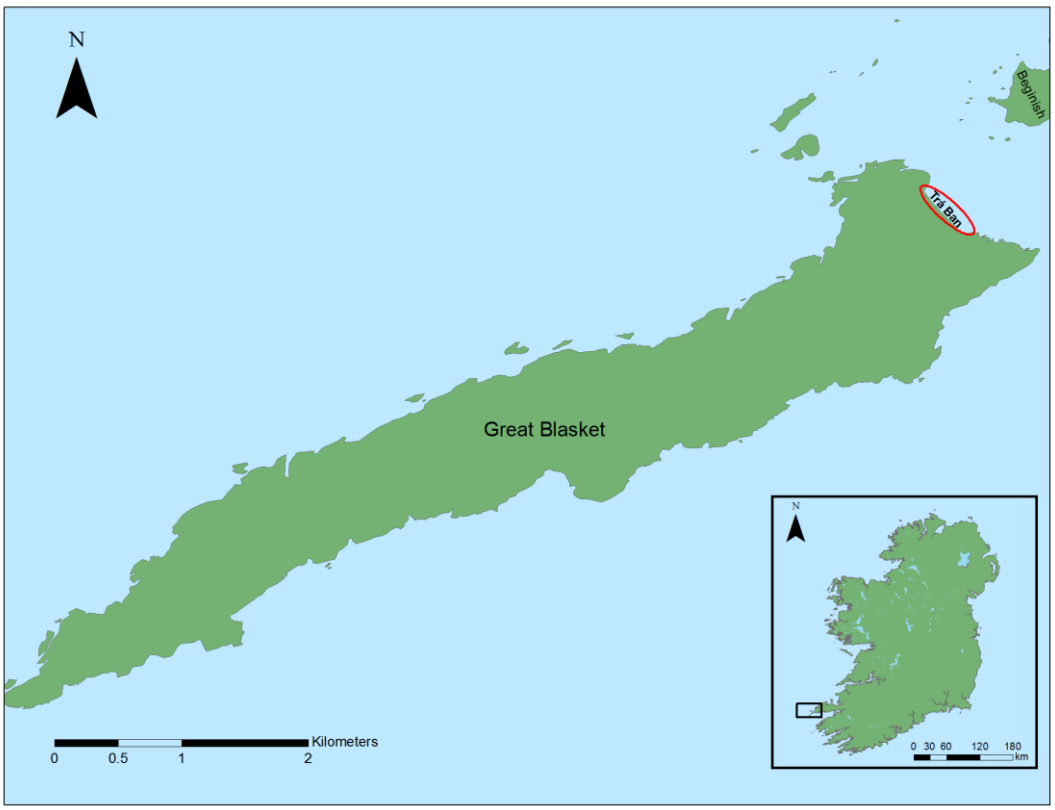


Figure 3.1: Map of Ireland denoting in red where samples were collected from the study site, An Trá Bán, on the Great Blasket Island, Co. Kerry.

rubber bands, and then inserted into another mesh bag of equal mesh size to account for any small otoliths that may have escaped the inner bag. A maximum of 15 samples were placed into a standard Whirlpool 2-speed/9 cycle washing machine at any one time and washed twice on a gentle cold water cycle using non-biological detergent. Upon removal, any waste scat material not broken down was removed by washing it through the 0.5mm and 0.25mm mesh sieves. This method was tested by Keaveney (2014) to ensure no further erosion of prey structures took place.

Subsequent to being sterilised and dried, all hard prey remains were identified to their lowest taxonomic level using published guides (e.g. Clarke, 1986; Härkönen, 1986; Watt *et al*., 1997; Tuset *et al*., 2008) and reference collections, with prey size then reconstructed using published regression equations when available (Appendix I). Those species that could not be differentiated due to the effects of erosion were either assigned to groups such as such as haddock/pollock species (*Melanogrammus aeglefinus/Pollachius pollachius/P. virens*), whiting/blue whiting (*Merlangius*

merlangus/Micromesistius poutassou) or identified to genus level e.g. *Trisopterus* species, family level e.g. unidentified Soleidae and unidentified Gadidae, order level e.g. unidentified Pleuronectiformes, or class level e.g. unidentified Cephalopoda (subclass: Coleoidea). When the back-calculation of prey size was not possible, the individual was assigned an average size from others of that species found within the same sample/month/season/year (see Chapter 2). This was also the case for unidentified Cephalopoda (those identified from eye lenses), with each individual assigned an average from others identified in the diet, thereby ensuring biomass estimates for this class were not under-represented in the diet. Small crustacean remains and diagnostic structures displaying a very high degree of erosion, such as sandeel otoliths greater than grade 3 as defined by Tollit *et al*. (1997), were considered secondarily ingested items and were excluded from further analyses (see McConnell *et al.,* 1984). Minimum prey counts per scat were quantified similar to the methods outlined in Chapter 2, with diet composition described in terms of prey percentage frequency of occurrence (%F), percentage number (%N) and percentage biomass (%B). As discussed in Chapter 2, correction factors were not applied in order to present an unbiased description of all species identified within the diet.

3.3.3 Species Accumulation plots

To determine whether the total sample size sufficiently captured species variability, prey species accumulation curves were constructed using PRIMER 6 statistical software (PRIMER 6, Plymouth Marine Laboratory) for all scat samples collected from the Great Blasket Island. Species accumulation curves were also produced for each season within all sampling years to determine whether sufficient samples had been collected to adequately reflect the range of species occurring in the diet within each season. To investigate whether grey seal diet was more diverse in one season compared with another, accumulation curves were also created for each season (all springs combined, summers combined etc.).

Accumulation curves are used to illustrate the increasing number of species identified in samples (*S*), as new samples are successively pooled to previously collected ones (Clarke & Gorley, 2006). An analytical form of a rarefaction curve (UGE) based on Ugland *et al*. (2003) was used for the collective number of samples. This is the

counterpart of the analytical form for the Sanders rarefaction curve given by Hurlbert (1971). Rarefaction curves generate the expected number of species within subsets of individuals repeatedly re-sampled at random from a single larger sample (Gotelli & Colwell, 2001). The UGE takes subsets of samples from a data matrix, gives exact fits to data and does not depend on an underlying distribution of individuals among species (Ugland *et al*., 2003). Essentially it derives a mean curve from the original *S* data to facilitate a comparison between the real accumulation curve with that of a smoother version (Clarke & Gorely, 2006). By producing species accumulation curves however, it is possible to determine whether the number of samples collected from the site is representative of species richness in the study system.

3.3.4 Statistical analysis

To determine whether either seasonal (intra-annual) and/or inter-annual patterns in diet occurred, certain prey species were amalgamated into broader groups such as Clupeidae, Lotidae (excluding ling, *Molva molva*), Bothidae, Pleuronectidae, Soleidae, and Cephalopoda to facilitate the analysis. Species abundances were square-root transformed to reduce the influence of numerically dominant species and were used to create a Bray-Curtis similarity matrix in order to quantify dissimilarities between prey. Prey species assemblages were then visualised using non-metric multidimensional scaling plots (nMDS) in PRIMER 6 (Clarke & Warwick, 2001). Using the PERMANOVA + package (Anderson *et al*., 2008), permutational multivariate analysis of variance was applied to test for differences in diet in seasons between years and between seasons within years. The SIMPER routine was then run to determine which species were responsible for the greatest similarities exhibited in the seals diet.

3.4 RESULTS

3.4.1 Sample collection

A total of 1066 scat samples were collected over five years (February 2009 – November 2013) from the main haul-out site used by grey seals on the Great Blasket Island, Co. Kerry. Of these, 494 samples were processed and found to contain 8697 prey individuals. 132 scat samples were previously analysed (Gosch *et al*., 2014), but subsequently reviewed and included in this study. Species accumulation curves suggested that sufficient samples had been collected for establishing a baseline for species diversity in the system (Appendix V). Combined seasonal accumulation curves (i.e. all springs, all summers etc.) also suggested enough samples were present to ensure the greatest contributors to the diet were accounted for. Adequate numbers of samples were also collected to effectively represent the main prey of seals in all separate seasons except autumn 2010, winter 2010 and summer 2011. A summary of the number of samples collected within each season/year combination is given in Table 3.1.

3.4.2 Seal diet composition

A total of 8697 individual prey representing at least 53 taxa were identified, with 77% of prey identified from otoliths and the remaining 23% identified using other hard parts. 95.7% of scats contained otoliths (11,083 otoliths in total). Prey remains that could not be identified to species or genus level (but assigned to groups gadoids, flatfish, Cephalopoda and other unidentified fish) accounted for 4.7% of all prey recovered. Dietary indices calculated for each prey type are presented in Table 3.2.

Combining all years, prey within the Gadidae family were consumed in the highest numbers and occurred in 86% of scats. *Trisopterus* species and sandeels were the most frequently occurring (Figure 3.2) and numerically dominant species (Figure 3.3) within the diet. Other important prey in terms of frequency of occurrence and abundance were flatfish (Pleuronectiformes), while blue whiting, dragonets (*Callionymus* spp.), haddock/pollock spp., whiting, and Cephalopoda (squid and unidentified cephalopods) occurred with regular frequency in the diet, but were typically found in smaller numbers (Table 3.2).

Crustacean remains such as carapaces or claws were frequently found in scats, however given their small size (<2 cm) and poor condition due to a high level or erosion, these were deemed to be secondarily ingested prey, and were omitted from the overall diet analysis.

Table 3.1: Total number of prey containing scats collected per season across all years

Season	2009	2010	2011	2012	2013	Total
Spring	83	49	18	21	20	191
Summer	20	32	5	20	20	97
Autumn	56	-	20	31	20	127
Winter	25	-	22	15	17	79
Total	184	81	65	87	77	494

3.4.3 Prey length, weight and biomass reconstruction

Out of 8697 individual prey, it was possible to reconstruct the sizes of 98.4% of prey items, which comprised 8396 fish and all 163 Cephalopoda (unidentified spp. n=82, squid spp. n=36, octopus spp=45). Prey items for which no regression equations exist (1.6% of all prey recovered) were excluded from further length, weight and biomass analysis. While this could introduce potential bias to prey species relative diet contribution, regression equations were available for all the major contributors to the diet (>0.4 %F and >0.1 %N) therefore those prey that were excluded were unlikely to impact diet contribution.

Overall, the majority of prey lengths occurred between 10 cm and 25 cm with fish prey varying in length from 0.25 cm (poor cod, *T. minutus*) to 94.1 cm (5-bearded rockling, *Ciliata mustela*). The mean size of fish prey in the diet was 14.8 cm (±0.1 SE) with 68% of all fish equal or less than this size. Squid spp. ranged in size from <0.1cm to 80.1 cm, displaying a mean mantle length of 11.8 cm (±3.6 SE), while octopus spp. ranged from 16.6cm to 159.9cm with a mean length of 8.6 cm (±0.5 SE). Out of all Cephalopoda in the diet, 63% exhibited sizes equal or less than 11.5cm (Appendix VI).

Table 3.2: Diet composition of grey seals off southwest Ireland, 2009 – 2013. %F= Percentage frequency of occurrence, %N= Percentage by number, %B = Percentage biomass.

Species	%F	%N	%B
AGNATHANS			
Lamprey *Petromyzon marinus*	1.8	0.1	-
CHONDRICHTHYES			
Ray *Raja* spp.	2.0	0.1	-
OSTEICHTHYES			
Eels Anguilliformes	0.4	<0.1	<0.01
Conger eel *Conger conger*	4.5	0.4	2.23
Herring *Clupea harengus*	3.4	0.5	0.87
Sprat *Sprattus sprattus*	5.9	0.4	0.02
Twait shad *Alosa fallax*	0.2	<0.1	0.02
Unidentified Clupeidae	1.0	0.1	0.06
Argentine *Argentina sphyraena*	0.2	<0.1	0.01
Cod *Gadus morhua*	1.4	0.1	0.55
Haddock *Melanogrammus aeglefinus*	7.7	0.7	3.60
Pollock/Saithe *Pollachius* spp.	10.5	1.0	6.25
Haddock/*Pollachius* spp.	6.3	0.7	4.12
Whiting *Merlangius merlangus*	18.8	2.2	4.81
Blue whiting *Micromesistius poutassou*	22.5	3.2	3.56
Whiting/Blue whiting	3.4	1.0	0.53
Norway pout *Trisopterus esmarkii*	3.8	0.3	0.04
Poor cod *Trisopterus minutus*	40.7	9.2	3.75
Bib *Trisopterus luscus*	15.0	1.4	2.39
Poor cod/Bib	14.2	2.7	1.90
Unidentified *Trisopterus* spp.	28.1	4.4	1.12
Silvery pout *Gadiculus argenteus*	1.4	0.1	0.01
Tadpole fish *Raniceps raninus*	0.2	<0.1	0.02
Greater forkbeard *Phycis blennoides*	0.4	<0.1	0.07
3-bearded rockling *Gaidropsarus vulgaris*	1.2	0.1	3.66
5-bearded rockling *Ciliata mustela*	3.0	0.2	4.33
Unidentified rocklings	0.8	<0.1	0.56
Ling *Molva molva*	5.7	0.4	2.43
Hake *Merluccius merluccius*	3.0	0.2	0.40
Unidentified Gadidae	21.7	2.1	3.22
Dragonet *Callionymus spp.*	22.5	2.2	1.59
Garfish *Belone belone*	4.3	0.3	1.63
Grey gurnard *Eutrigla gurnardus*	2.0	0.2	0.30
Unidentified Triglidae	0.4	<0.1	0.02
Shorthorn sculpin *Myoxocephalus scorpius*	0.2	<0.1	0.01
Unidentified sculpins	0.2	<0.1	0.01
Unidentified Cottidae	0.4	<0.1	0.07
Perch *Perca fluviatilis*	0.2	<0.1	0.01
Sea Breams Unidentified Sparidae	0.2	<0.1	<0.01
Cuckoo wrasse *Labrus mixtus*	2.4	0.1	0.35
Ballan wrasse *Labrus bergylta*	1.0	0.1	0.36

Species	%F	%N	%B
Unidentified Labridae	3.2	0.3	0.86
Eelpout *Zoarces viviparus*	0.8	0.1	-
Horse mackerel *Trachurus trachurus*	11.3	0.8	2.37
Greater sandeel *Hyperoplus lanceolatus*	10.3	2.7	2.26
Sandeels *Ammodytes spp.*	51.0	54.2	9.21
Tompot blenny *Parablennius gattorugine*	0.2	<0.1	-
Scaleless worm goby *Caragobius urolepis*	0.6	<0.1	0.01
Unidentified Gobiidae	0.4	<0.1	0.01
Mackerel *Scomber scomber*	3.4	0.2	0.63
Megrim *Lepidorhombus* spp.	14.8	1.3	3.22
Scaldfish *Arnoglossus* spp.	2.8	0.2	0.08
Unidentified Bothidae	0.2	<0.1	0.01
Plaice *Pleuronectes platessa*	4.0	0.3	0.77
Dab *Limanda limanda*	2.6	0.2	0.43
Flounder *Platichthys flesus*	1.6	0.1	0.23
Lemon sole *Microstomus kitt*	8.1	0.5	1.63
Long rough dab *Hippoglossoides platessoides*	2.0	0.1	0.30
Witch *Glyptocephalus cynoglossus*	0.6	<0.1	0.05
Unidentified Pleuronectidae	1.4	0.1	1.18
Solenette *Buglossidium luteum*	2.0	0.1	0.09
Sole *Solea solea*	2.2	0.1	0.89
Unidentified Soleidae	3.8	0.4	2.03
Unidentified flatfish	7.1	0.5	0.48
Unidentified fish	15.4	1.2	-
CEPHALOPODA			
Flying squid *Todaropsis eblanae*	0.2	<0.1	<0.01
Squid *Loligo* spp.	4.3	0.3	5.50
Squid Unidentified Ommastrephidae	2.6	0.1	0.19
Curled octopus *Eledone* spp.	2.8	0.2	0.87
Unidentified octopus	3.0	0.3	1.20
Unidentified Cephalopoda	11.9	0.9	10.67
Total Clupeidae	10.3	1.0	0.96
Total Haddock/*Pollachius* spp.	22.1	2.4	13.97
Total *Trisopterus* spp.	67.0	17.8	9.20
Total rocklings	4.9	0.3	8.54
Total Gadidae	86.0	29.9	47.31
Total Triglidae	2.4	0.2	0.31
Total Cottidae	0.8	<0.1	0.09
Total Labridae	6.7	0.5	1.56
Total Ammodytidae	54.5	56.9	11.47
Total Gobiidae	1.0	0.1	0.01
Total Bothidae	16.8	1.5	3.31
Total Pleuronectidae	16.8	1.4	4.59
Total Soleidae	7.9	0.7	3.01
Total flatfish	36.6	4.0	11.38
Total fish	100.0	98.1	81.57
Total Cephalopoda	20.6	1.9	18.43

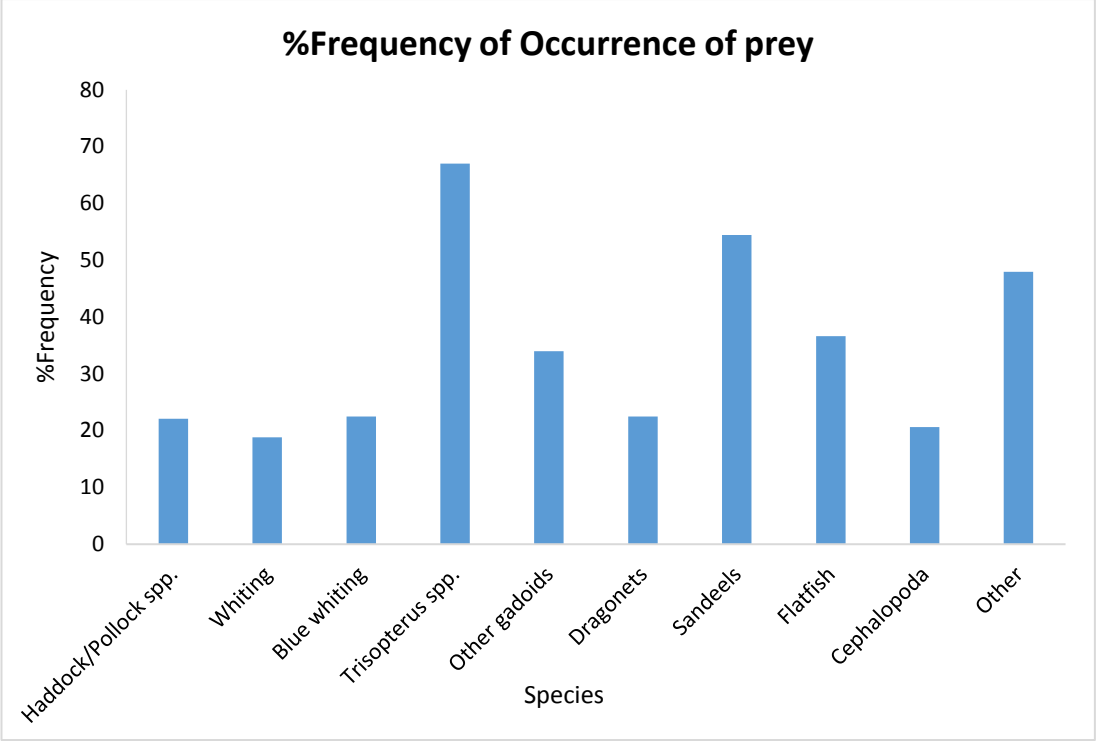


Figure 3.2: The percentage frequency of occurrence of all prey species contributing to the diet of grey seals (n=8697).

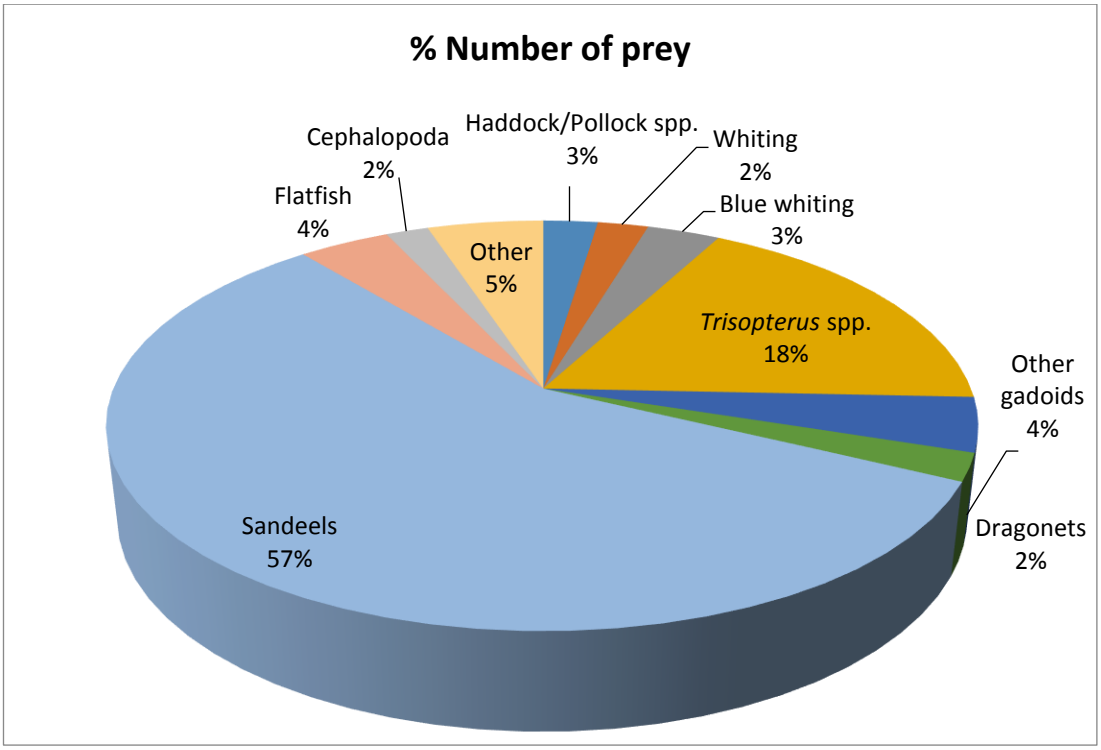


Figure 3.3: The percentage by number of all prey species contributing to the diet of grey seals (n=8697).

Mean weight of all prey species in the diet was 50.2 g (±2.7 SE), with fish prey displaying a mean weight of 41.7 g (±1.8 SE) and mean Cephalopoda weight being 485.7 g (±100.7 SE) (Appendix VI). Within this class, squid spp. exhibited a mean weight of 679.5 g (±335.0 SE), and octopus spp. had a mean weight of 197.2 g (±31.3 SE).

The overall percentage biomass contribution of each taxon was calculated after prey weight reconstruction (Table 3.2). The Gadidae family, collectively, were the most important biomass contributors to the overall diet, followed by Cephalopoda (unidentified cephalopods, 10.7%B; squid spp., 5.7%B; octopus spp., 2.1%B) and then haddock/pollock spp. Other important prey responsible for significant biomass contributions to the diet included sandeels, and all flatfish species combined (Figure 3.4). Within the flatfish group, both megrim (*Lepidorhombus* spp.) and lemon sole (*Microstomus kitt*) were the largest contributors of biomass (2%B, 2%B, respectively), while *Trisopterus* and rockling species each contributed 9 %B (Table 3.2). Whiting, blue whiting, and unidentified gadoids also contributed to the reconstructed biomass, but to a lesser extent (≤ 5%B).

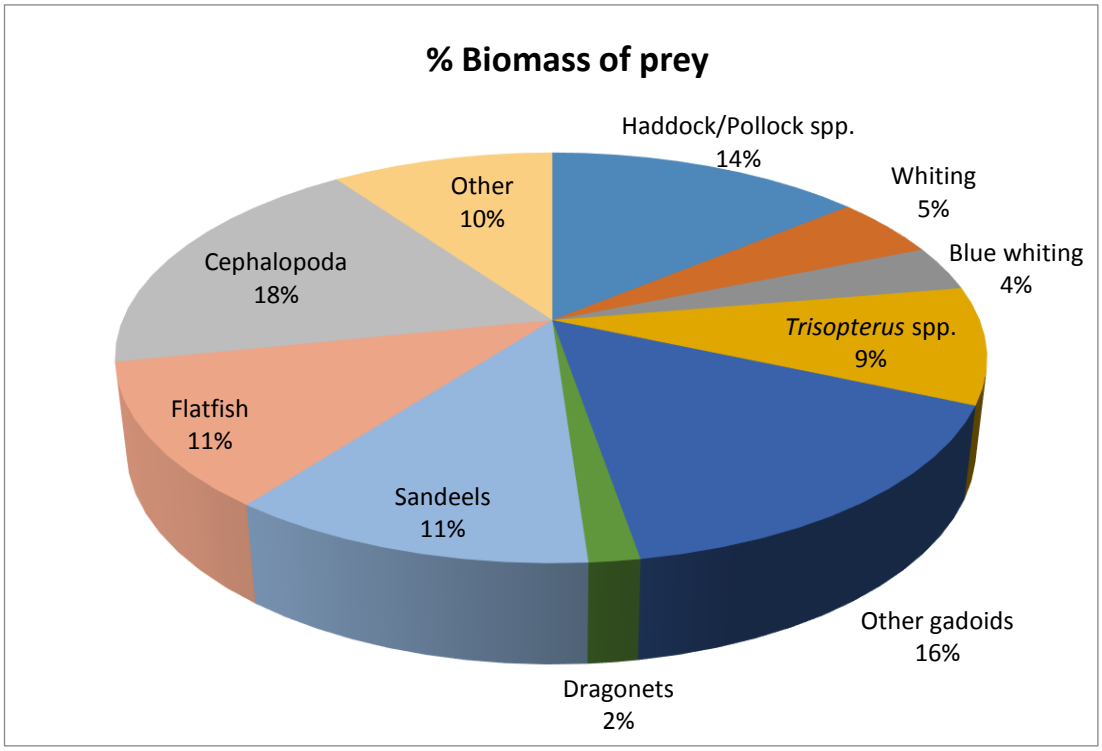


Figure 3.4: The percentage biomass of all prey species contributing to the diet of grey seals (n=8559).

3.4.4 Seasonal diet

To test the hypothesis that grey seals are generalists exploiting local, seasonally abundant fish assemblages, seasonal patterns in the diet were investigated. While nMDS plots (square-root transformed abundance data) showed large overlap in prey assemblages between seasons (Figure 3.5), significant differences in prey assemblages between seasons were apparent (PERMANOVA+ P=0.001, in all cases, Appendix VII).

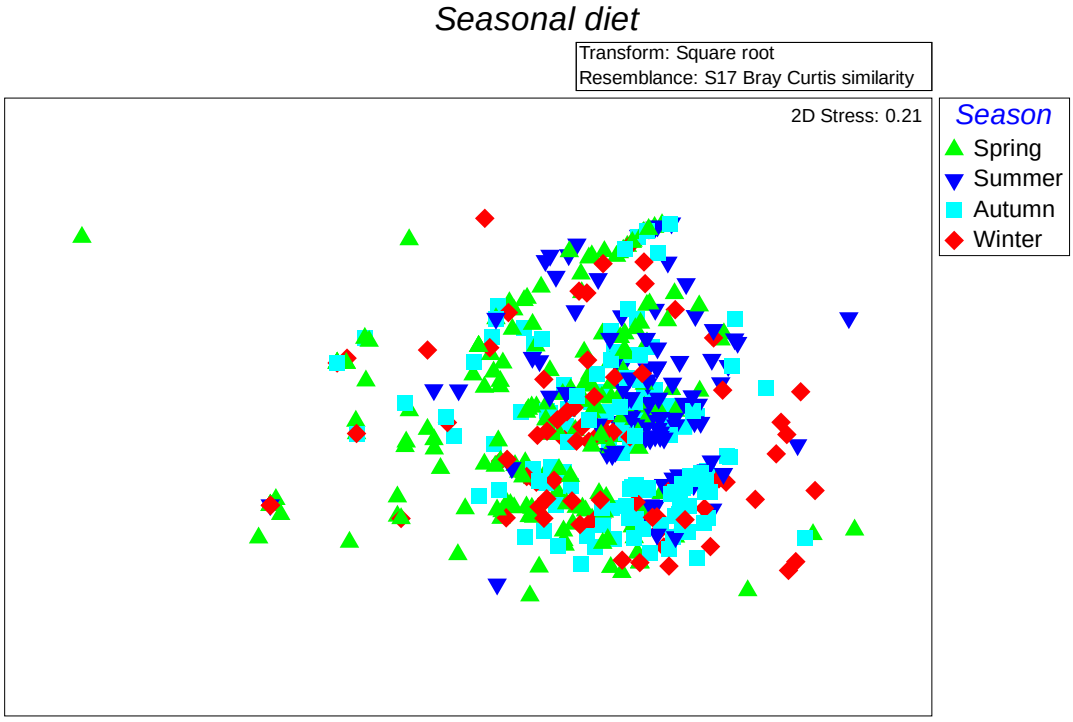


Figure 3.5: nMDS plot depicting general overlap of prey species assemblages between seasons across all sampling years. Each symbol represents an individual scat sample, with the distance between symbols representing (Bray-Curtis) similarity of prey assemblages (species and species abundance) between samples.

Sandeels were the most abundant prey group within the spring, summer and winter diet (73 %N, 56 %N, 50 %N, respectively), while the Gadidae family were numerically dominant in autumn (49 %N), with *Trisopterus* spp. accounting for the largest component within this family (33 %N). In terms of biomass, Cephalopoda were the largest contributors to the spring diet (40 %B). Amongst this class, larger squid spp. and unidentified cephalopod individuals accounted for the higher contributions to the diet by weight (17.3%B and 20.7%B, respectively). During summer, autumn and

winter, the Gadidate family were of greater importance (50 %B, 52%B, 63 %B, respectively). Amongst the Gadidae family, haddock/pollock spp. were the primary biomass contributors in summer and winter (15% B & 27 %B, respectively), while *Trisopterus* spp. were of greater importance to autumn diet (15 %B). *Trisopterus* spp. were also the most frequently occurring taxa in most seasons (58 %F spring, 81 %F autumn, 62 %F winter), except for summer when sandeel frequency was higher (75 %F). While seals relied heavily on sandeels and *Trisopterus* species year round, SIMPER analysis highlighted the variation in relative abundances of both taxa as being responsible for some of the greatest dissimilarities in diet between all seasons. Large variations in sandeel relative abundances were primarily responsible for the largest seasonal differences, except when comparing autumn and winter seasons when *Trisopterus* species accounted for the greatest seasonal dissimilarities (Table 3.3). Other species of importance to the diet and predominantly responsible for seasonal dissimilarities comprised dragonets within spring (29 %F, 2 %N, 2 %B), and blue whiting in the summer diet (46 %F, 8 %N, 13 %B). Flatfish (particularly megrim) were important within autumn months (46 %F, 6 %N, 15 %B) and haddock/pollock species were sizable contributors to winter diet (42 %F, 7 %N, 27 %B). Both Cephalopoda and whiting consistently occurred in the diet throughout the year with whiting contribution of greater importance during summer months (21 %F, 4 %N, 6 %B). Cephalopoda were consumed in slightly higher abundances during the winter (unidentified cephalopods, n=16; squid spp., n=8; octopus spp., n=12) although these were comprised mainly of small individuals.

Table 3.3: Species accounting for the greatest dissimilarities between seasons, expressed as square-root transformed abundance data. Avg. Abund = Average Abundance; Contrib% = the percentage contribution to Bray-Curtis dissimilarity.

Species	**Avg. Abund**	**Avg. Abund**	**Contrib%**
	Spring	*Summer*	
Sandeels	1.65	1.93	27.33
Trisopterus spp.	0.93	1.31	14.27
Blue whiting	0.16	0.77	9.18
Dragonets	0.34	0.19	4.83
	Summer	*Autumn*	
Sandeels	1.93	1.12	20.54
Trisopterus spp.	1.31	1.78	15.94
Blue whiting	0.77	0.32	9.29
Whiting	0.33	0.31	5.07
	Autumn	*Winter*	
Trisopterus spp.	1.78	1.10	17.02
Sandeels	1.12	1.02	16.55
Haddock/Pollock spp.	0.22	0.58	7.05
Bothidae spp.	0.39	0.14	5.03
	Winter	*Spring*	
Sandeels	1.02	1.65	21.14
Trisopterus spp.	1.10	0.93	14.33
Haddock/Pollock spp.	0.58	0.17	7.66
Cephalopoda	0.32	0.29	5.58

3.4.5 Inter-annual diet

To investigate whether seasonal differences in diet were consistent from year to year, inter-annual patterns in diet were visualised using nMDS plots (based on square-root transformed abundance data), and tested using PERMANOVA (Figure 3.6). While species diversity (the prey species contributing to diet) was largely the same across years, particularly during summer and winter, the relative contribution of each species tended to differ, with significant inter-annual differences in assemblages (PERMANOVA, $P<0.05$) within most seasons across years (Appendix VIII). Seal diet in 2009 was highlighted as being significantly different to all other years ($P<0.05$). Summer diet differed significantly between 2010 and 2011 ($P=0.034$), while spring and winter seal diet in 2011 was significantly different to 2012 ($P<0.05$). Apart from autumn diet, 2012 varied significantly when compared to seal diet in 2013 ($P<0.03$).

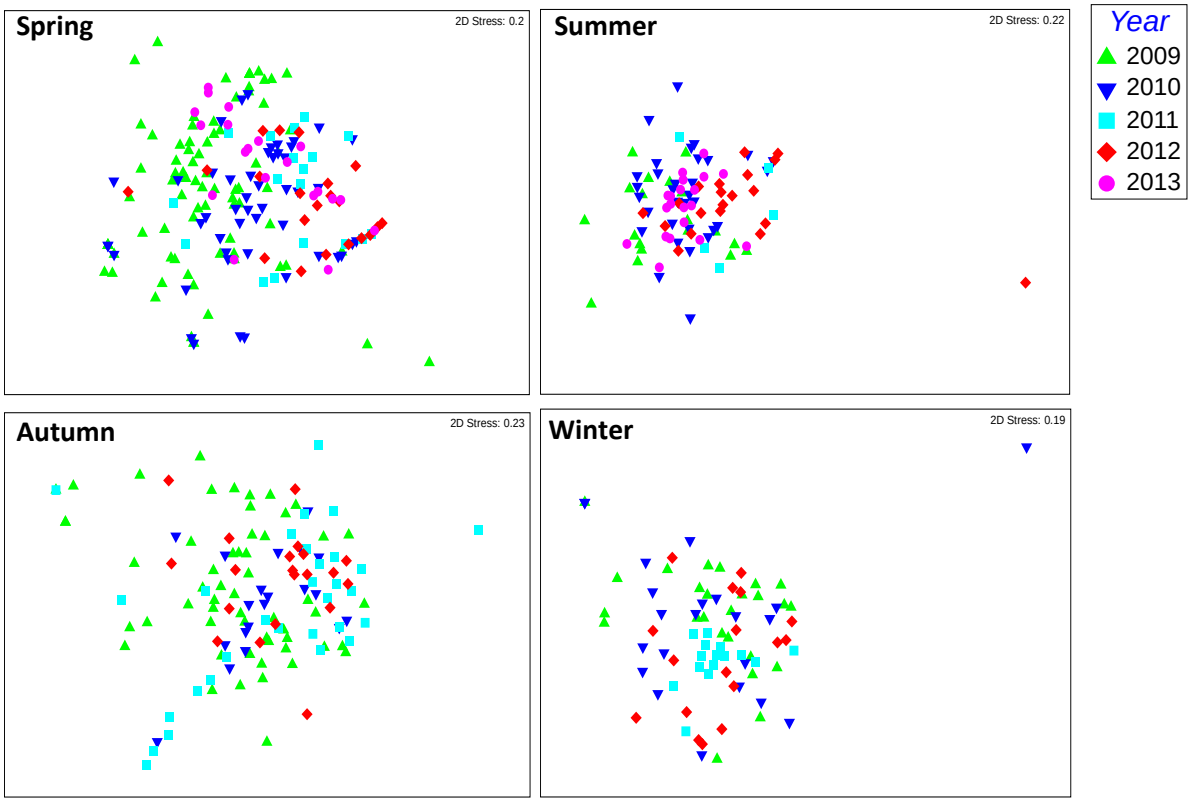


Figure 3.6: nMDS plots of seal diet depicting general seasonal overlap of prey species assemblages within samples between years. Each symbol represents an individual scat sample, with the distance between symbols representing (Bray-Curtis) similarity of prey assemblages (species and species abundance) between samples.

SIMPER analysis identified relative abundances of sandeels and *Trisopterus* spp. in the diet as being responsible for the largest differences exhibited between years. Inter-annual variation in the relative abundances of haddock/pollock spp., whiting, blue whiting, dragonet, flatfish, and Cephalopoda was also evident, and contributed to the dissimilarities displayed in the diet between years. Absolute abundance for these species in the diet tended to increase when sandeel and *Trisopterus* spp. abundances exhibited a decrease (see Figure 3.7). Indeed, the highest abundances of dragonets and Cephalopoda occurred in summer 2011, also coinciding with the lowest abundances of *Trisopterus* spp. within the diet. While this is based on the mean number of individual species per sample, with large variations in species average abundances, these patterns of prey switching are nevertheless still apparent.

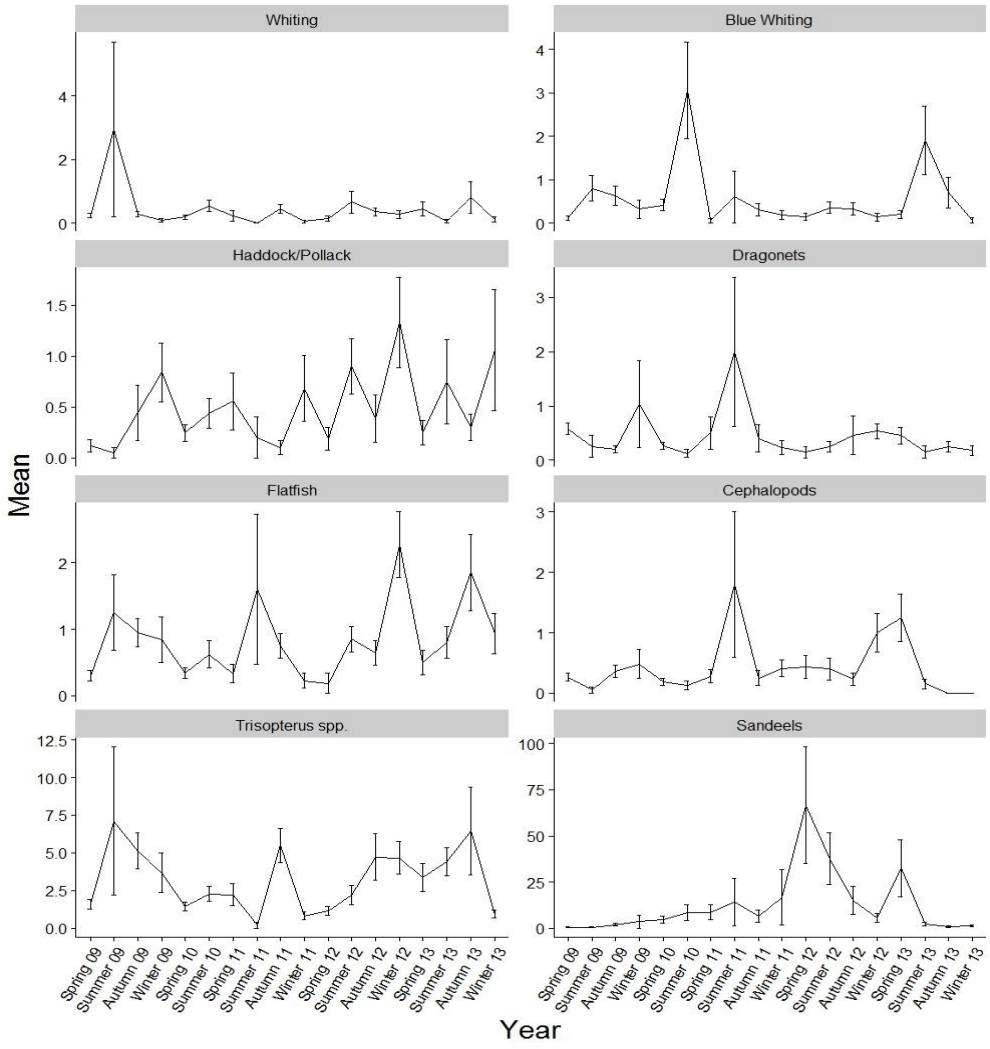


Figure 3.7: The average abundance per scat of the main prey species identified within grey seal diet, plotted over time.

3.5 DISCUSSION

Grey seal diet from the Great Blasket Island, was analysed to examine seasonal and inter-annual variation in the diet. While over one hundred demersal and benthic species occur within the Celtic Sea, only 25 of the most abundant species account for 99% of the total estimated biomass within this region (ICES, 2016). Some of the most abundant of these fish species consist of *Trisopterus* species, haddock, whiting, blue whiting, and megrim (Marine Institute, 2012; ICES, 2016) with the long-finned squid (*Loligo forbesi*) being one of the most common Cephalopoda species along the shelf edge (ICES, 2016). Results showed grey seal diet in southwest Ireland clearly reflects the higher abundance of these particular species. Although squid (*Loligo* spp.) were

identified in low numbers (n=22), there were relatively high abundances of unidentified Cephalopoda species within diet (n=82). It is therefore plausible that grey seals in this region are taking advantage of the local abundance of long-finned squid, and that this species may account for the occurrences of unidentified Cephalopoda in the diet. While the diet consisted of a very wide variety of prey species, this study identified 8 main groups that occurred consistently in generally higher numbers and frequency within the diet. Such reliance of grey seals on key species across a wide range of taxa is also described in diet studies across the grey seals' distribution range in the North Atlantic (McConnell *et al*., 1984; Prime & Hammond, 1990; Pierce *et al*. 1990; Hammond *et al*., 1994a; Bowen & Harrison 1994; Ridoux *et al*., 2007).

Key contributors to the diet of grey seals in southwest Ireland across all dietary indices consisted of sandeels, *Trisopterus* species, haddock/pollock species, whiting, blue whiting, dragonets, flatfish (particularly megrim) and Cephalopoda. However, in terms of biomass, conger eels (*Conger conger*), Lotidae (rocklings & ling), and horse mackerel (*Trachurus trachurus*) were also important contributors to the diet. It should however be noted that reconstructed length sizes for 5-bearded rocklings (*Ciliata mustela*) were all above their maximum size of 25 cm (Froese & Pauly, 2016) for all but one fish, suggesting that published regression equations for size reconstruction may not always be suitable for structures above/below a certain size, as discussed in Chapter 2. Similarly, 57% of *Loligo* spp. were under 1 cm in length, while five individuals weighed more than 1 kg and one *Loligo* spp. individual weighed nearly 11 kg. A deficit in published regression equations for most cephalopod species means that using a regression equation from a similar species may substantially over/underestimate size, given the large variety in body sizes that exists between cephalopod families and genera (Clarke, 1986). The small squid individuals identified in this study may have originated from the Atlantic bobtail squid (*Sepiola atlantica*), which display a mantle length of approximately 21 mm (Reid & Jereb, 2005), and these are therefore underestimated in length as a result of applying a generic regression equation. Whether these squid were secondary items from carnivorous fish is difficult to determine as beaks remained in good condition within scat samples and thus may also have been opportunistically consumed by the seals in the water column. While cephalopods are undoubtedly important dietary components for grey seals, further work regarding issues surrounding available regression equations is clearly needed.

It is evident that grey seals are consuming species which are presumably locally abundant in this region. A key finding is the importance of sandeels as prey for grey seals in southwest Ireland. This is similar to results reported from other dietary studies (Pierce *et al*., 1990; Hammond *et al*., 1994a; Bowen & Harrison, 1994; McConnell *et al*., 1999; Trzcinski *et al*., 2006). Seals fed mainly on the inshore sandeel species *Ammodytes marinus* although the larger offshore species *Hyperoplus lanceolatus* accounted for 3% by number in the diet. Though small in size, when consumed in large quantities sandeels were substantial contributors to the diet in terms of biomass (11%) and were the third highest biomass contributors after Cephalopoda and haddock/pollock species. *Trisopterus* species were also important components of grey seal diet and have traditionally played a key role in the diet of seals elsewhere (Pierce *et al*., 1990). Poor cod (*T. minutus*) was the dominant species of the *Trisopterus* genus in terms of all diet indices. This fish is typically found throughout coastal waters at depths of 15 – 200m (Marine Institute, 2012), well within the typical diving range of seals tracked from southwest Ireland (Jessopp *et al*. 2013).

Absolute and relative abundances of key contributors to the diet varied both seasonally and inter-annually. Similar to other studies, sandeels were more prevalent in spring and summer (Hammond *et al*., 1994a; Hauksson & Bogason, 1997), and absolute abundance increased substantially from 2009, with a considerable spike after winter 2011 until autumn 2012. *Trisopterus* species featured consistently across the entire sampling period with a marked decrease in absolute abundance only evident during summer/winter 2011 and winter 2013. This coincided with a marked increase of Cephalopoda and dragonets in the diet during summer 2011, while abundance of haddock/pollock species increased noticeably in winter 2011 and reached their highest in the diet during winter 2013. It should however be noted that the lowest numbers of scat samples were collected during summer 2011 (n=5), likely influencing the diet description for that period.

In general, *Trisopterus* species abundance in the diet decreased in winter, as did sandeels which spend much of their time buried in the sediment during this season (Reay, 1970). In contrast, the occurrence of other gadoids increased during winter, particularly haddock/pollock species which were of substantial importance to the diet in terms of biomass. While abundances of haddock/pollock species were generally at a minimum during the spring season and at their highest during winter, overall they

varied in importance both seasonally and between years. Summer abundances of haddock/pollock species experienced an increase in both 2012 and 2013. Average lengths in the diet were 38 cm (when corrected for partial erosion) which coincides with fish of between 2-3 years, of which 80-99% of females will be mature (Marine Institute, 2012). Haddock spawn during late spring, early summer and peak spawning for pollock occurs in March to April (Cohen *et al*., 1990). It is therefore possible that grey seals may have been feeding on late spawning fish in summer 2012 and 2013. Prey assemblages will differ over time due to variations in distribution which are symptomatic of a changing biological community governed by natural forces such as the availability of food resources, spawning stock biomass, recruitment, spawning and timing of migration.

While prey varied significantly between seasons, yearly differences in diet appeared stronger. Apart from changes in inter-annual prey species abundance and distribution, the differing energy requirements of grey seals during their annual life cycle may also be responsible for the observed seasonal variations in the diet. Grey seals are capital breeders and therefore undergo periods of intense fasting during the female lactation period and the breeding and moulting season (Beck *et al*., 2007). As this species is sexually size dimorphic, they also exhibit strong variations in their foraging habitat (Breed *et al*., 2006). Male seals display a lower basal metabolic rate and must acquire greater energy stores between breeding season, however they can afford to consume lower quality prey compared to females (Beck *et al*., 2003). Furthermore, differences in prey preference has been shown to exist between juvenile and adult grey seals (e.g. Lundström *et al*., 2010) with juveniles tending to be less selective and exhibiting a broader niche breath (Beck *et al.,* 2007). Such age and sex-specific differences in dietary requirements, foraging strategies and annual life cycles would almost certainly account for some of the variation observed in the diet over the course of a year. Even so, it is evident that certain prey species are almost always present within the diet.

Forage fish such as sandeels and *Trisopterus* are important prey of many predators including seals, harbour porpoise (*Phocoena phocoena*), piscivorous fish and various seabirds (Furness & Tasker, 2000; Santos & Pierce, 2003; Trenkel *et al*., 2005). While it is not possible to categorically state that seals show a preference for sandeels and *Trisopterus* species, due to a lack of data on prey availability in this region, it does appear that seals in southwest Ireland are taking advantage of these higher energy prey

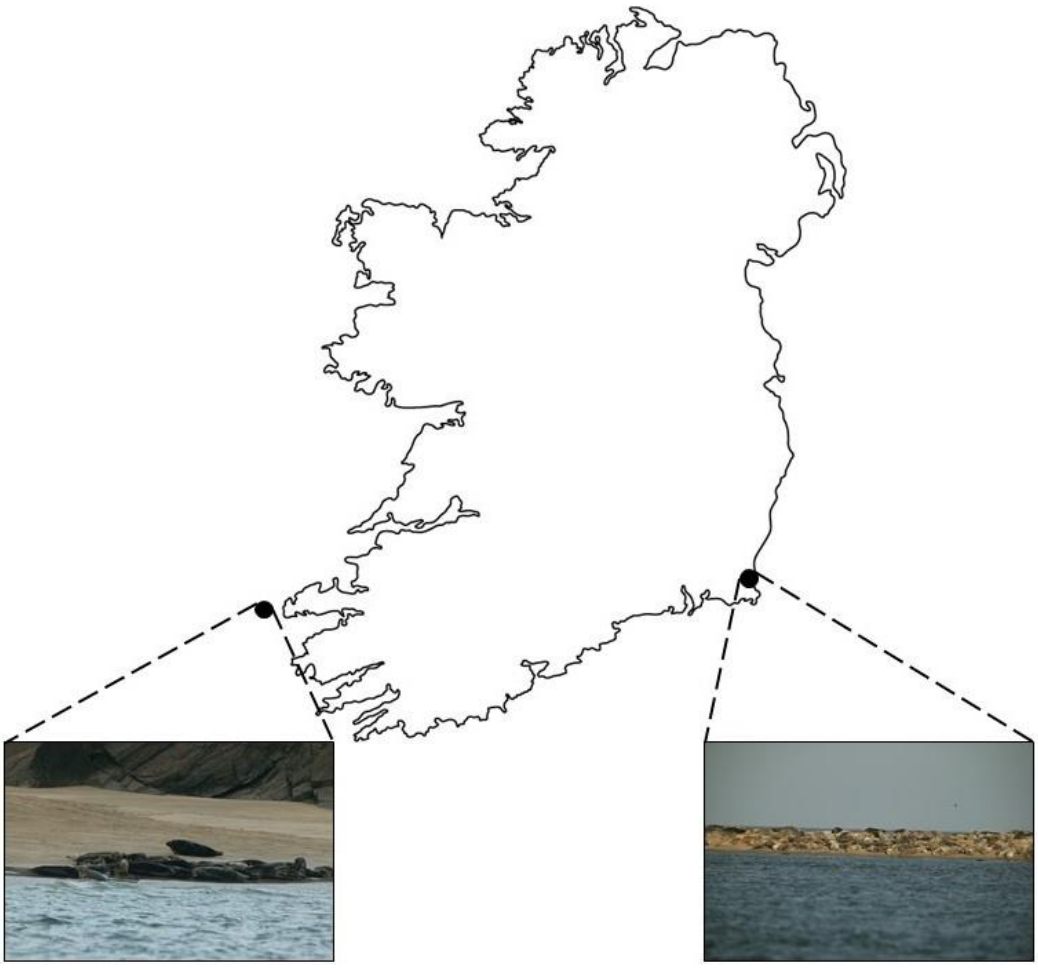
(Murray & Burt, 1977; Wilson *et al*., 2002). This may be due to ease of handling, or as He (1993) suggests, that with increased body size comes the potential for increased swimming speed. Given that the average lengths of sandeels and *Trisopterus* species in the diet were 13.5 cm and 11.5 cm, respectively, it is plausible that these smaller prey are also easier to catch relative to larger faster schooling species such as mackerel (*Scomber scomber*) and herring (Armstrong, 1999) that are even higher in nutritional content (Murray & Burt, 1977). Optimal foraging theory suggests that predators will want to exploit prey that deliver either (or both) high returns and low costs. Models derived from this theory imply encounter rates of such high value prey will decrease relative to low value prey under intense exploitation by predators (Lyman, 2003). Alternatively, prey may exhibit "behavioural depression" (Charnov *et al*., 1976) where they will actively avoid areas targeted by predators or, may undergo "microhabitat depression" (Charnov *et al*., 1976) entailing a relocation to areas outside predator range when feeding, resting or reproducing. A reduction in the availability of prey containing high nutritional content, through exploitation by a fishery could result in a top-down cascade effect, with encounter rates decreasing should these species become "depressed". Given their importance as forage fish and the lack of information on the status of these stocks, the recommendation from ICES and The Marine Institute of Irelands Fisheries Ecosystems Advisory Services is that fisheries should not be allowed to develop for sandeel and *Trisopterus* species (Marine Institute, 2015). Local and small-scale effects of such fisheries could have a negative impact on the local population of grey seals, as well as many other predators, including seabirds and odontocetes off southwest Ireland. Fishery induced changes in size structure and abundance of sandeel stocks, and its subsequent effect on the distribution and abundance of seals and other top predators such as seabirds, have been documented in the North Sea (e.g. Furness, 2002; Sharples *et al*., 2009). Intensive removal of sandeels through fisheries has already been linked to declines in seabird breeding success (Rindorf *et al*., 2000). A reduction in their availability may see a decline in the general health of the seals given the high nutritional content of sandeels (Hislop *et al*., 1991).

To conclude, this study has demonstrated the importance of 8 main prey groups to the diet of grey seals off southwest Ireland, with sandeels and *Trisopterus* species found in higher abundances compared with all other taxa, possibly due to their higher nutritional value (Meynier *et al*., 2008). The diet exhibits both seasonal and inter-

annual variability in prey abundance with seals alternating between prey groups, presumably depending on whichever are locally and seasonally available. By exploiting a generalist feeding strategy, seals have the ability to adapt to poor fish recruitment years by taking whichever prey species may be more abundant at the time. Low sandeel and *Trisopterus* abundances within the diet coincided with substantial increases in blue whiting occurrence in the diet during summer 2010, while haddock/pollock species displayed marked increases during winter 2013. While most prey within the diet consists of small non-commercial species, an overlap between species targeted by both seals and fisheries is apparent. However, in general seals appear to select smaller sized prey than targeted by fisheries, also demonstrated in Chapter 5 and other studies (Houle *et al*., 2016). It is evident from this study that commercial species are generally found in higher abundances in seal diet when sandeel and *Trisopterus* abundance is extremely low. It is therefore imperative that sandeel and *Trisopterus* fisheries in this region do not develop, or if they do, that they adhere to an ecosystems approach to fisheries management (Marine Institute, 2015).

CHAPTER 4

Regional variation within the diet of grey seals from colonies along the southeast and southwest coast of Ireland



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This chapter is in preparation for submission to the Journal of *Marine Mammal Science.*

4.1 ABSTRACT

Regional variations in the diet of grey seals were examined from two study sites along the coast of Ireland, with samples collected over the same sampling period. Scats were collected from Wexford harbour, southeast Ireland and from Great Blasket Island, southwest Ireland between autumn 2011 and winter 2013. Significant differences in prey assemblages between sites were apparent with relative abundances of species common to both sites, such as sandeels and *Trisopterus* spp., exhibited strong variation between regions. Sandeels and Gadidae (particularly haddock/pollock spp.) were the most important prey items in terms of weight in scat samples from the southwest coast. Gadidae were also substantial contributors to the diet of seals at the southeast site however, whiting was the most important component within this family by weight, while flatfish and Cephalopoda were also key prey in this location. Particular species such as blue whiting and horse mackerel were completely absent from the diet of seals that use the southeast coast haul out site. Similarly, certain species like weever fish and butter fish were noticeably absent from diet samples collected from the southwest coast. Relatively high numbers of rays (Rajidae spp.) were recovered from the southeast coast diet, a species that inhabit sandy/coarse sediments in the Irish Sea. Regional variations in diet may be attributed to the different habitats surrounding the study sites, with the higher proportions of pelagic species found in the southwest coast diet possibly due to the proximity of the continental shelf edge and deeper water.

Keywords: regional diet variation, trophic interactions, foraging habitat,

4.2 INTRODUCTION

A fundamental question in ecology is the role animals play in their environment (Carter *et al*., 2016). Marine mammals in particular, as a result of their size and abundance, can exert an important influence within their ecosystem. Being top consumers, they have the potential to impact the structure and functioning of marine ecosystems through their trophic interactions (Hammill *et al*., 2007). To better understand the role of apex predators in their local environment, it is necessary to obtain information on foraging behaviour and habitat use (Jessopp *et al*., 2013). While biologging technology has facilitated the collection of increasingly fine scale data on predator location and dive observations (Carter *et al*., 2016), it does not provide information on the type and quantity of prey species consumed by predators. Tools such as Ecopath with Ecosim (EwE) enable marine ecosystems to be modelled and can elucidate trophic interactions by estimating how much biomass predators may be removing from a specific region (Heymans *et al*., 2016). However, in order to apply these models, baseline data on predator diet is initially required. To quantify trophic interactions, predator diet estimation traditionally uses prey remains obtained from faecal or stomach samples (Tollit *et al*., 2010). There are however practical difficulties associated with obtaining such data. The dynamic nature of the marine ecosystem means that the structure of prey communities will vary over seasons, years, and regions (Hindell *et al*., 2003). Differing oceanographic conditions and subsequent differences in habitat type may also result in prey assemblage or prey abundance variation within predator diet between regions (Lundström *et al*., 2010). Understanding the extent of this variation is an important factor when evaluating the potential impact seal populations may have on the ecosystem, particularly in areas where fish stocks are already over exploited. Management decisions that apply to one region may not be relevant for other areas when dealing with wider geographic scales. This is because intra-specific differences between populations may arise due to variations in environmental conditions that can affect local food supply and consequently foraging habitats (Thompson *et al*., 1996). Region specific diet data is therefore crucial when investigating trophic interactions and predator habitat use, particularly when using diet data to input into consumption models such as EwE.

The grey seal (*Halichoerus grypus*) is an apex predator within Irish waters. Irish grey seals constitute a single population (although they are part of a larger metapopulation i.e. UK and France), with several large colonies existing along the coast of Ireland (Boskovic *et al*., 1996). While grey seals can remain at sea for extended periods (Cronin *et al*., 2012), they generally return to particular haul out sites to rest. This tendency suggests that seal diet composition will be related to the prey availability and abundance surrounding the haul out region (Smout *et al*., 2014). However, as generalists, grey seals will forage on seasonally and locally abundant prey (Hauksson, 1984; Murie & Lavigne, 1992; Grellier & Hammond, 2006). For this reason, it is likely that the diet of grey seals will vary over both spatial and temporal scales. Improved knowledge on trophic interactions and the extent of prey biomass removal by this predator is particularly important given the perceived threat to Irish fisheries posed by an increasing grey seal population (5,509-7,083 in 2007 to 7,284-9,365 in 2013) in Ireland (Ó Cadhla *et al*., 2008; Ó Cadhla *et al*., 2013; Cronin *et al*., 2014; Cosgrove *et al*., 2015).

Studies to date on the diet of grey seals that haul out along the coast of Ireland are limited in effort and restricted in geographical range (BIM 1997; 2001; Kiely *et al*., 2000, McKibbon, 2000; Philpott, 2001; Gosch *et al*., 2014). However, regional variations in diet are apparent; Cephalopoda occurred in 50% of grey seal digestive tracts in the northwest (BIM 1997; 2001), yet contributed little by way of occurrence in the southwest (Gosch *et al*., 2014). Similarly, along the northwest coast, whiting were the most important prey species while sandeels are not considered important prey (BIM 1997; 2001), yet Gosch *et al*. (2014) demonstrated that sandeels are currently an important component of grey seal diet in the southwest, with minimal contribution of whiting. More recent data presented in Chapter 3 from scat samples collected in southwest Ireland corroborates earlier findings from this region highlighting the importance of sandeels to grey seal diet.

Limited studies of grey seal diet from the Irish and eastern Celtic Sea (based primarily on assessment of stomach contents) suggests the diet is characterised by the co-dominance of flatfish and gadoids, with flatfish dominance lessening as sampling moves from the east coast towards the south coast (Philpott, 2001; Kiely *et al*., 2000). Such differences in prey assemblages over both broad scales and relatively short distances have been similarly confirmed in other areas of the species distribution

(Benoit & Bowen, 1990; Hammond & Prime, 1990; Hammond *et al*., 1992; Hammond *et al*, 1994a; 1994b; Lundström *et al*., 2007; Hammill *et al*., 2007).

The spatially patchy studies on Irish grey seal diet heretofore are generally over 15 years old and cover short time scales. The limited studies were not conducted simultaneously and differences in findings could be attributed to temporal and/or spatial variation in diet and as it is established that grey seal diet varies temporally (see Chapter 3, Hammond & Prime, 1990; Bowen *et al*., 1993; Beck *et al*., 2007) as well as spatially (Benoit & Bowen, 1990; Prime & Hammond, 1990; Hammond *et al*., 1994a). In order to determine whether regional differences in grey seal diet does occur within Irish waters, it is necessary to compare diet samples collected during the same time frame from two different haul out sites in a simultaneous study. However, investigations into geographic differences in seal diet can be confounded by irregular sample collection. This is typically due to variations in grey seal availability as a result of life history traits. Particular periods of the year may see seals spending relatively large portions of time at sea (Beck *et al*., 2003). Furthermore, Bowen *et al*. (1993) notes that during the breeding season and moult period, low proportions of prey remains may be recoverable due to seals undergoing a fasting period. To counter these effects, it is necessary to obtain dietary samples over an extended period of time and use study sites that support higher numbers of seals so as to provide ample opportunity for scat collection. By attaining up to date knowledge on seal diet composition over longer time scales and geographical areas, this information can be used assessing the impact of grey seals on Irish fisheries, as well as providing baseline data for ecological modelling tools.

While Chapter 3 demonstrated how grey seals from a colony of national importance in southwest Ireland exhibited strong seasonal and inter-annual variations in diet, this Chapter focuses on regional differences in grey seal diet, by comparing prey assemblages from two important breeding and moulting sites; the Great Blasket Island in the southwest, and Wexford harbour in the southeast of Ireland, with scat samples collected over the same sampling period. The aim of the study is:

(i) to establish whether significant variations in regional diet of grey seals in Ireland occurs

(ii) whether the same core prey species are relied on within both regions.

4.3 METHODS

4.3.1 Study sites and sample collection

Scats were collected from the southeast and southwest coasts of Ireland. Scat sampling on the southeast coast of Ireland was carried out from September 2011 – August 2013 at Raven Point grey seal haul-out site, Wexford Harbour (Figure 4.1). A total of 77 scat samples were collected between September 2011 to September 2012 by an MSc. Student (Luck, 2013). Grey seals in this region haul out on two separate sandbars (52°20'20.28''N, 6°21'26.10''W and 52°19'42.71''N, 6°22'38.29''W) which become partially submerged during high tide (Figure 4.2A). Seal numbers range from less than 50 during winter months to approximately 500 in summer months (*per. obs.*), with the site supporting mixed ages and genders. The haul out sites at Raven Point were accessed by boat when weather permitted at or just after low tide, with collected scat samples placed in labelled polythene bags and stored frozen at -20°C for further processing. Samples were collected on a bimonthly basis for the first 12 months and on a monthly basis thereafter.

Scat samples were also collected at the Great Blasket Island, southwest Ireland (Figure 4.1 & 4.2B) as outlined in Chapter 3. For comparative purposes, only samples collected during the same period as the southeast coast site were used in this study.

4.3.2 Diet analysis

Waste material was separated from prey hard structures using nested sieves (mesh size of 0.25 mm, 1 mm, 2 mm, and 5 mm) following Pierce & Boyle (1991), and also by placing scats in nylon mesh bags and running them through two washing machine cycles, similar to Orr *et al.* (2003). All hard prey remains were sterilized in 70% ethanol for 24 hours, left to dry for a further 24-48 hours and then stored in labelled test tubes. Cephalopoda beaks were kept in 70% ethanol until identification. Crustacean remains were excluded from dietary analysis as, due to their small size and poor condition they were deemed to be secondarily ingested prey (McConnell *et al*., 1984; Arnett & Whelan, 2001; Browne *et al*., 2002).

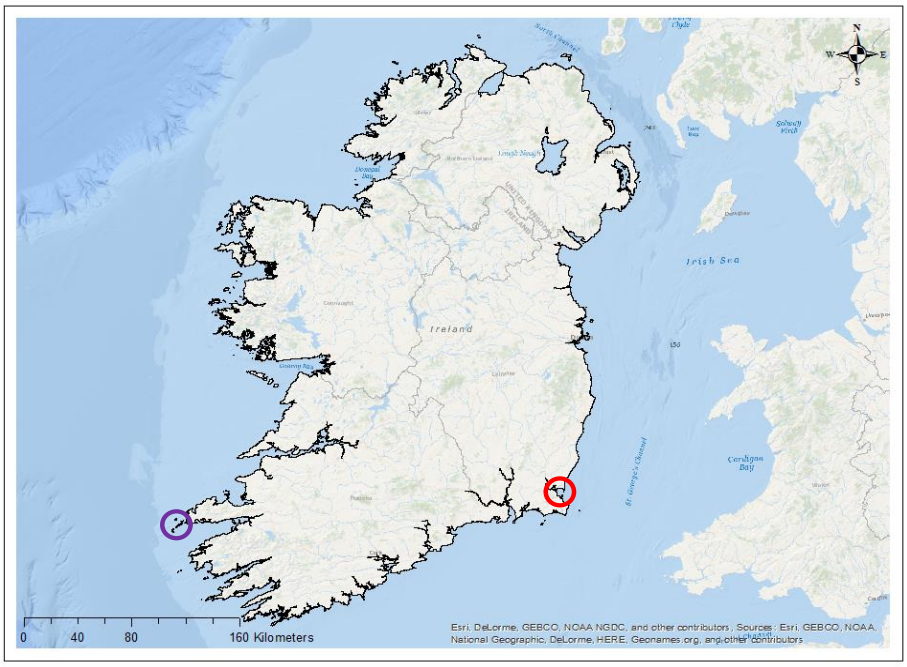


Figure 4.1: Map of Ireland denoting in red where the Wexford harbour (southeast) study site is located, and in purple where Great Blasket (southwest) study site is situated.



Figure 4.2: A) Wexford harbour denoting in red where scat samples were collected from the two main haul out sandbars used by grey seals, and B) The Great Blasket Island denoting in red where sample were collected from An Trá Bán. Source: Google Earth (2016).

Following recommendations outlined in Chapter 2, the "all structures" method was employed (e.g. Cottrell *et al*., 1996; Tollit *et al*., 2003) to improve the probability of prey detection. All prey were identified to their lowest taxonomic level where possible, with minimum numbers of prey per scat determined following the methods detailed in Chapters 2 and 3. Prey size reconstruction was achieved using published regression equations when available (Appendix I) or, averages were assigned from other individuals of that species/genus/class (e.g. unidentified Cephalopoda) which were identified in either the same sample/month/year so that the biomass contribution of all prey in the diet could be represented as accurately as possible. Correction factors were not applied for this same reason, as discussed in Chapter 2. Unfortunately, it was not always possible to acquire original prey sizes, as in the case of unidentified fish spp.

Based on Gravendeel *et al.* (2002) dermal denticles of rays (Rajidae) detected within the diet were deemed to originate from thornback rays (*Raja clavata*). However, given the morphological similarities between these and spotted rays (*R. montagui*), they are termed *Raja* spp., as positive identification of *R. clavata* cannot be guaranteed. Abundances of rays within this study were conservatively estimated with the presence of denticles assumed to represent only one *Raja* spp. per sample. While reconstruction of original size cannot be determined from denticles, given the generally high occurrences of *Raja* spp. and their high energy values (Le Boeuf *et al*., 1993), their inclusion within biomass estimates allows for a more unbiased representation of prey biomass contribution. Therefore, an average length was assigned to each individual identified within the diet. Browne *et al*. (2002) stated that all Rajidae consumed by harbour seals (*Phoca vitulina*) appeared to be juveniles, and a conservative estimate of ray biomass to grey seal diet was based on this. An average length of 29.5cm was based on exclusion of mature *R. clavata* specimens (>47cm; McCully *et al*., 2012; Froese & Pauly, 2016) from Irish groundfish survey data (Marine Institute, 2012). This was deemed to be an appropriate conservative size estimate for *Raja* spp. within this study and prey weight based on this length was then obtained from Froese & Pauly (2016).

4.3.3 Statistical analysis

Only seasons for which adequate sample sizes were available per site, based on seasonal accumulation curve results, were compared. Similar prey types were grouped

into larger categories to facilitate comparisons e.g. Pleuronectiformes (flatfish), Lotidae (rocklings and ling, *Molva molva*), Cephalopoda. Analysis was similar to that in Chapters 2 and 3, with square-root transformed species abundances used to generate a Bray-Curtis similarity matrix. Similarity between samples was visualised using non-metric multidimensional scaling plots (nMDS) in Primer 6 (Clarke & Warwick, 2001) and prey assemblage differences between locations tested using permutational multivariate analysis of variance using the PERMANOVA+ package (Anderson *et al*., 2008). The SIMPER routine was applied to the relative abundances of all prey species from both sampling locations to determine which species, if any, were responsible for seasonal differences between sites.

4.3.4 Diet variability

Variability within the diet of grey seals at both the southeast and southwest coast site was examined, using methodology outlined in Chapter 2, and compared using a modified Costello-Amundsen feeding plot (Costello, 1990; Amundsen *et al*., 1996). The prey-specific abundance and biomass were compared from both sites, plotted against the frequency of occurrence on a two-dimensional graph (See Chapter 2). This was done to facilitate a visual examination of any variability in feeding strategy, selectivity, and prey importance which may be occurring between sites.

Prey-specific abundance is expressed by:

$$P_i = (\sum S_i / \sum S_{ti}) \times 100$$

P_i represents the prey-specific abundance/biomass of prey *i*, S_i signifies the total contribution of prey *i* to the scat content, and S_{ti} denotes the total abundance/biomass of all prey within all samples containing prey *i*.

Frequency of occurrence as a fraction is expressed as:

$$F*i* = N*i*/N$$

Where N*i* is the sum of all samples containing prey *i* and N is the total number of scat samples containing all prey within the diet.

4.4 RESULTS

4.4.1 Sample collection

Southeast site:

Of the 305 seal scats collected from the southeast site, 149 samples were found to contain prey remains (Table 4.1). 77 of these were processed by a MSc student (Luck, 2013) for a separate study and were subsequently re-analysed for the purpose of this study. The species accumulation curve for all southeast samples showed that sufficient samples had been collected to adequately represent the prey species contributing to seal diet at this site. Within seasons, accumulation curves began to level off after 15 samples suggesting that the major contributors to the diet had been detected by this point.

A total of 2375 individual prey items, representing a minimum of 49 taxa were identified from southeast scat samples (Table 4.2). Within these samples 2734 otoliths were recovered (81.9% of scats) with 73% of individuals identified from these and the remaining prey identified using other diagnostic structures. 6.2 % of prey items could not be identified to a genus/species level and were assigned to broader taxonomic groups e.g. unidentified gadoids, flatfish, Cephalopoda, and unidentified fish.

Southwest site:

A total of 206 scats containing prey were collected from the Great Blasket site (Table 4.1). Accumulation curves previously derived for southwest samples in Chapter 3 confirmed that sufficient numbers of scats were collected within each season to provide a baseline for prey diversity in that system.

A total of 5488 prey items were identified within the southwest coast diet, over double that found at the southeast site. However, these represented a minimum of 47 prey taxa, which is similar to the southeast site. 1.7% of all prey in the diet were assigned to broader categories such as unidentified gadoids etc. The contribution of all prey within the diet of both sites in terms of their percentage frequency of occurrence (%F), percentage by number (%N) and percentage biomass (%B) is shown in Table 4.2.

Table 4.1: Total number of prey containing samples collected per site within each season across years.

Season	***Southeast***				***Southwest***			
	2011	**2012**	**2013**	**N**	**2011**	**2012**	**2013**	**N**
Spring	-	19	29	48	-	21	20	41
Summer	-	21	8	29	-	20	20	40
Autumn	8	22	7	37	20	31	20	71
Winter	14	5	16	35	22	15	17	54
Total	22	67	60	149	42	87	77	206

Table 4.2: Diet composition of grey seals off southeast Ireland, 2011 – 2013. %F= Percentage frequency of occurrence, %N= Percentage by number, %B = Percentage biomass.

Species	*Southeast*			*Southwest*		
	%F	**%N**	**%B**	**%F**	**%N**	**%B**
AGNATHANS						
Lamprey *Petromyzon marinus*	0.7	<0.1	-	1.0	<0.1	-
CHONDRICHTHYES						
Ray *Raja* spp.	42.3	2.7	4.37	0.5	<0.1	0.04
OSTEICHTHYES						
Eels Anguilliformes	1.3	0.1	<0.01	0.5	<0.1	<0.01
Conger eel *Conger conger*	2.0	0.1	0.65	3.9	0.2	1.45
Herring *Clupea harengus*	2.7	0.6	0.87	2.9	0.1	0.16
Sprat *Sprattus sprattus*	4.0	0.3	0.04	10.2	0.4	0.03
Twait shad *Alosa fallax*	-	-	-	0.5	<0.1	0.05
Unidentified Clupeidae	2.0	0.1	0.11	1.9	0.1	0.09
Cod *Gadus morhua*	6.7	0.7	1.47	1.5	0.1	0.45
Haddock *Melanogrammus aeglefinus*	4.0	0.6	1.83	10.7	0.6	4.99
Pollock/Saithe *Pollachius* spp.	9.4	1.3	5.66	15.5	1.1	8.77
Haddock/*Pollachius* spp.	6.7	1.3	4.05	5.8	0.5	4.08
Whiting *Merlangius merlangus*	49.7	10.1	12.42	21.4	1.3	6.85
Blue whiting *Micromesistius poutassou*	-	-	-	24.8	1.6	3.80
Norway pout *Trisopterus esmarkii*	-	-	-	4.4	0.2	0.03
Poor cod *Trisopterus minutus*	24.2	9.2	5.13	56.8	9.2	5.30
Bib *Trisopterus luscus*	3.4	0.3	0.80	14.6	0.8	1.67
Poor cod/Bib	6.0	0.6	0.53	9.7	0.7	0.40
Unidentified *Trisopterus* spp.	32.2	6.6	2.85	19.4	2.2	0.53
Silvery pout *Gadiculus argenteus*	-	-	-	1.5	0.1	0.01
Greater forkbeard *Phycis blennoides*	0.7	0.1	0.01	1.0	0.1	0.16
3-bearded rockling *Gaidropsarus vulgaris*	2.0	0.6	0.22	1.0	0.1	4.41
4-bearded rocking *Rhinonemus cimbrius*	0.7	0.1	0.01	-	-	-
5-bearded rockling *Ciliata mustela*	-	-	-	2.4	0.1	3.50
Northern rockling *Ciliata septentrionalis*	4.7	0.4	0.41	-	-	-
Unidentified rocklings	4.7	1.8	1.00	1.5	0.1	0.64
Ling *Molva molva*	0.7	<0.1	0.70	9.2	0.4	3.61
Hake *Merluccius merluccius*	0.7	<0.1	0.05	1.9	0.1	0.22
Unidentified Gadidae	23.5	2.5	1.93	12.1	0.7	2.48
Dragonet *Callionymus spp.*	49.7	12.9	4.85	20.9	1.1	0.87
Garfish *Belone Belone*	-	-	-	6.3	0.3	2.30
Grey gurnard *Eutrigla gurnardus*	8.1	1.0	2.26	4.9	0.3	0.66
Unidentified Triglidae	1.3	0.7	0.54	-	-	-
Shorthorn sculpin *Myoxocephalus scorpius*	1.3	0.1	0.25	-	-	-
Longspined bullhead *Taurulus bubalis*	2.0	0.2	0.10	-	-	-
Unidentified sculpins	3.4	0.4	0.36	0.5	<0.1	0.16
Horse mackerel *Trachurus trachurus*	-	-	-	14.1	0.7	3.16
Pogge *Agonus cataphractus*	0.7	0.1	0.03	-	-	-
Sea Breams Unidentified Sparidae	0.7	<0.1	<0.01	-	-	-
Cuckoo wrasse *Labrus mixtus*	-	-	-	1.0	<0.1	0.01
Ballan wrasse *Labrus bergylta*	1.3	0.3	2.31	1.5	0.1	0.52
Unidentified Labridae	2.0	0.1	0.26	2.4	0.1	0.20

Eelpout *Zoarces viviparus*	0.7	<0.1	0.01	-	-	-
Butterfish *Pholis gunnellus*	7.4	0.9	0.20	-	-	-
Greater weever *Trachinus draco*	4.0	5.6	1.79	-	-	-
Greater sandeel *Hyperoplus lanceolatus*	7.4	3.5	1.05	16.0	3.2	4.06
Sandeels *Ammodytes spp.*	21.5	10.1	1.01	55.8	68.7	15.02
Tompot blenny *Parablennius gattorugine*	-	-	-	0.5	<0.1	-
Black goby *Gobius niger*	3.4	0.5	0.02	-	-	-
Painted goby *Pomatoschistus pictus*	0.7	<0.1	<0.01	-	-	-
Unidentified Gobiidae	0.4	<0.1	0.01	0.5	<0.1	0.01
Mackerel *Scomber scomber*	0.7	<0.1	0.02	5.8	0.2	0.38
Megrim *Lepidorhombus* spp.	2.0	0.2	0.66	18.4	0.9	3.02
Scaldfish *Arnoglossus* spp.	-	-	-	5.3	0.2	0.13
Unidentified Bothidae	2.0	0.2	0.61	0.5	<0.1	0.02
Plaice *Pleuronectes platessa*	22.1	2.6	5.70	6.3	0.2	0.91
Dab *Limanda limanda*	13.4	3.1	1.82	3.9	0.2	0.68
Flounder *Platichthys flesus*	8.1	1.6	1.13	2.9	0.1	0.24
Plaice/Flounder	5.4	1.1	1.63	-	-	-
Dab/Flounder	1.3	0.1	0.22	-	-	-
Lemon sole *Microstomus kitt*	5.4	0.4	0.98	10.7	0.5	1.68
Long rough dab *Hippoglossoides platessoides*	4.7	0.3	0.19	1.5	0.1	0.40
Dab/Long rough dab	2.7	0.6	0.76	-	-	-
Witch *Glyptocephalus cynoglossus*	0.7	<0.1	0.06	0.5	<0.1	0.10
Unidentified Pleuronectidae	9.4	2.3	6.22	1.9	0.1	1.71
Solenette *Buglossidium luteum*	9.4	0.8	0.30	1.9	0.1	0.09
Sole *Solea solea*	14.8	1.1	4.20	2.4	0.1	0.82
Unidentified Soleidae	7.4	0.8	2.23	6.3	0.5	3.49
Unidentified flatfish	14.1	2.2	0.86	6.3	0.3	0.46
Unidentified fish	3.4	0.2	-	3.9	0.1	-
CEPHALOPODA						
Squid *Loligo* spp.	8.1	0.7	1.76	5.8	0.2	0.01
Squid Unidentified Ommastrephidae	5.4	0.6	0.22	3.9	0.1	0.01
Curled octopus *Eledone* spp.	9.4	1.2	3.52	3.4	0.2	1.03
Unidentified octopus	4.7	1.1	2.51	5.8	0.3	1.86
Unidentified Cephalopoda	16.8	1.3	2.51	10.7	0.6	2.22
Total Clupeidae	8.7	1.1	1.01	15.0	0.6	0.33
Total Haddock/*Pollachius* spp.	16.1	3.2	11.53	28.6	2.1	17.85
Total *Trisopterus* spp.	53.0	16.7	9.31	71.8	13.0	7.93
Total rocklings	11.4	2.7	1.64	4.9	0.3	8.55
Total Gadidae	85.2	36.2	39.08	84.5	19.5	51.92
Total Triglidae	9.4	1.7	2.80	4.9	0.3	0.66
Total Cottidae	6.0	0.7	0.70	1.5	0.1	0.17
Total Labridae	3.4	0.5	2.57	4.9	0.2	0.73
Total Ammodytidae	26.2	13.6	2.06	60.7	71.8	19.08
Total Gobiidae	6.7	1.1	0.04	0.5	<0.1	0.01
Total Bothidae	3.4	0.4	1.27	21.8	1.1	3.17
Total Soleidae	26.8	2.8	5.98	10.2	0.6	4.40
Total Pleuronectidae	45.0	12.1	18.71	21.8	1.2	5.73
Total flatfish	61.7	17.5	26.81	43.2	3.2	13.76
Total fish	99.3	95.1	86.99	100.0	98.5	94.87
Total Cephalopoda	34.9	4.9	13.01	23.3	1.5	5.13

4.4.2 Regional/seasonal diet variation

Similarities in prey species assemblages across sites were examined for each season using nMDS plots based on square-root transformed abundance data (Figure 4.3). A small amount of overlap in prey assemblages between sites was apparent, particularly in spring 2013, but PERMANOVA+ analysis confirmed significant differences in prey assemblages between the southeast and southwest sites (P=0.001) in all four seasons (Table 4.3).

Table 4.3: PEMANOVA+ results highlighting the effects of regional differences in diet, using square-root transformed abundance data.

Groups	n	*t* statistic	P
Summer 2012	41	2.902	0.001
Autumn 2012	53	2.1837	0.001
Winter 2012/2013	31	2.0182	0.001
Spring 2013	49	2.2578	0.001

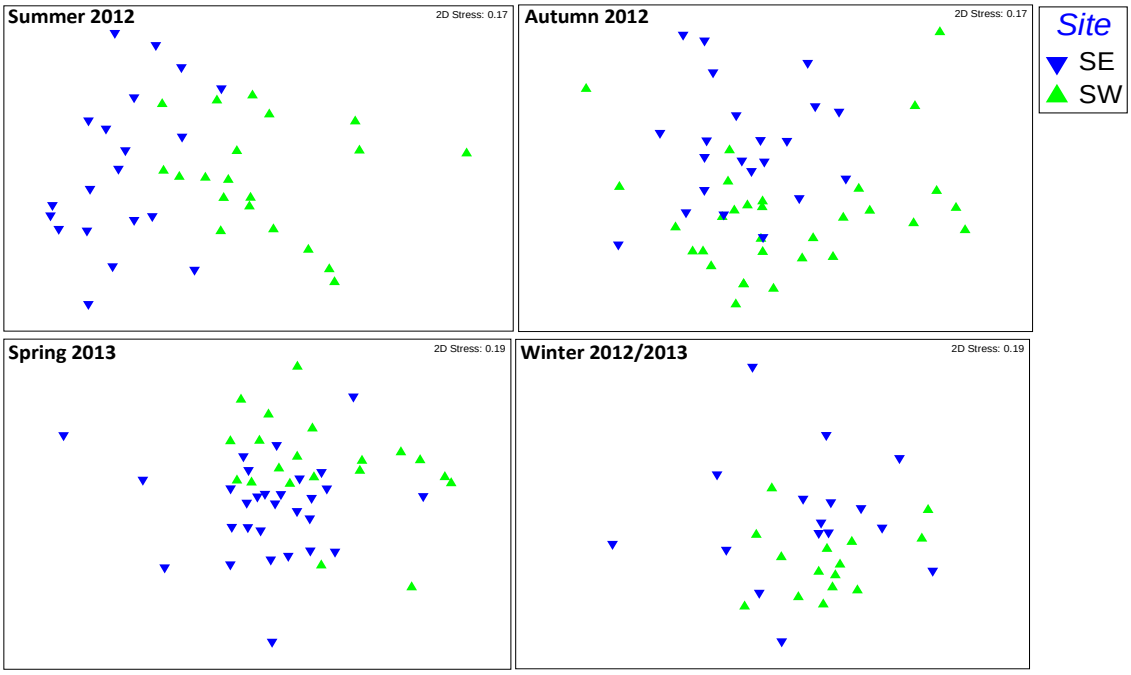


Figure 4.3: nMDS plots of seal diet depicting regional similarities in seasonal/yearly prey species assemblages between sites. Where SE = Southeast Ireland, and SW = Southwest Ireland.

Southeast site:

Within the southeast coast site, the Gadidae family was the dominant component of the diet of grey seals across all indices, followed by flatfish (Pleuronectiformes) of which Pleuronectidae were by far the most important (45%F, 12%N, 19%B). Aside from these, *Trisopterus* spp., dragonets (*Callionymus* spp.), and whiting (*Merlangius merlangus*) were the most frequently occurring prey within the diet, found in ≥50% of all samples (Figure 4.4), while rays also occurred relatively frequently (42 %F). Numerically, *Trisopterus* spp., sandeels (*Ammodytes* spp.), dragonets and whiting were recovered in much higher abundances than other prey (>10% N) (Figure 4.5). Cephalopoda (particularly octopus spp.), whiting, haddock/pollock spp., and *Trisopterus* spp. were the largest biomass contributors to the diet, after the Gadidae family combined and Pleuronectiformes (Figure 4.6A).

Southwest site:

Similar to the southeast coast, the Gadidae family were the largest contributors to the diet of grey seals at the southwest site in terms of frequency of occurrence and biomass, but not in terms of percentage number. Instead, sandeels dominated the diet in terms of abundance (72%N) followed by the Gadidae family. *Trisopterus* spp. were the most frequently occurring species in the diet followed by sandeels (Figure 4.4) and were recovered in relatively high abundances (13%N) compared to other prey in the diet (Figure 4.5). While flatfish were found in far smaller numbers compared to the southeast site, they still occurred in 43% of all samples. In terms of biomass, sandeels were the largest prey taxa contributors to the southwest coast diet, followed closely by haddock/pollock spp. and then flatfish (Figure 4.6B).

Overall SIMPER analysis highlighted seasonal variations in the relative abundances of sandeels, *Trisopterus* spp., haddock/pollock spp., flatfish, dragonets, whiting and Cephalopoda as being responsible for the greatest dissimilarities displayed in diet between regions.

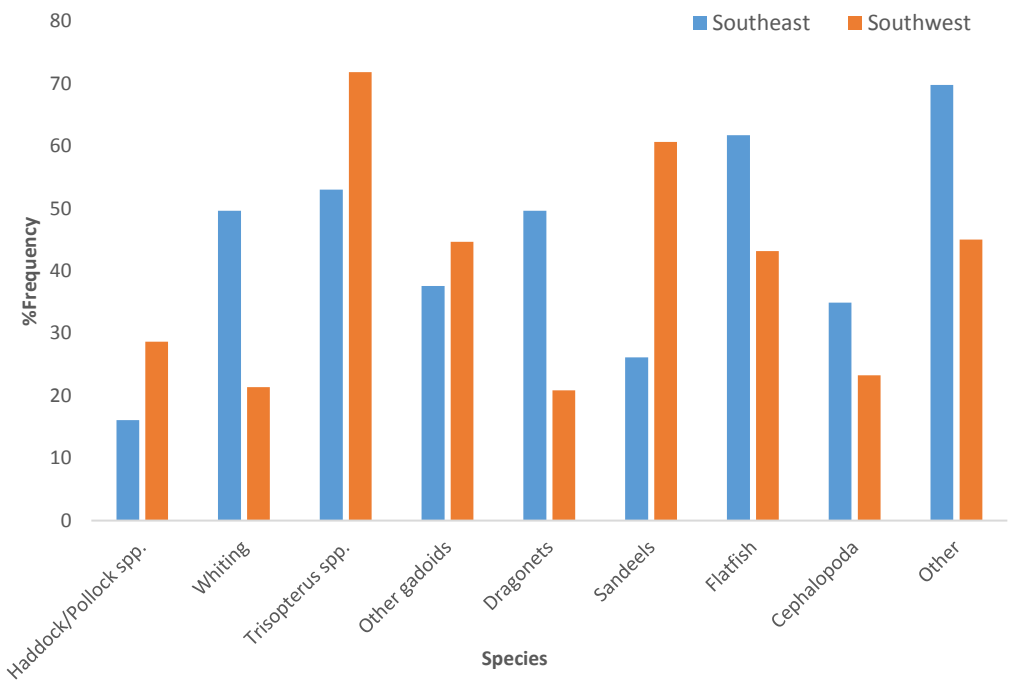


Figure 4.4: The percentage frequency of occurrence of all prey types contributing to the diet of grey seals in southeast Ireland (n=2375), and southwest Ireland (n=5488).

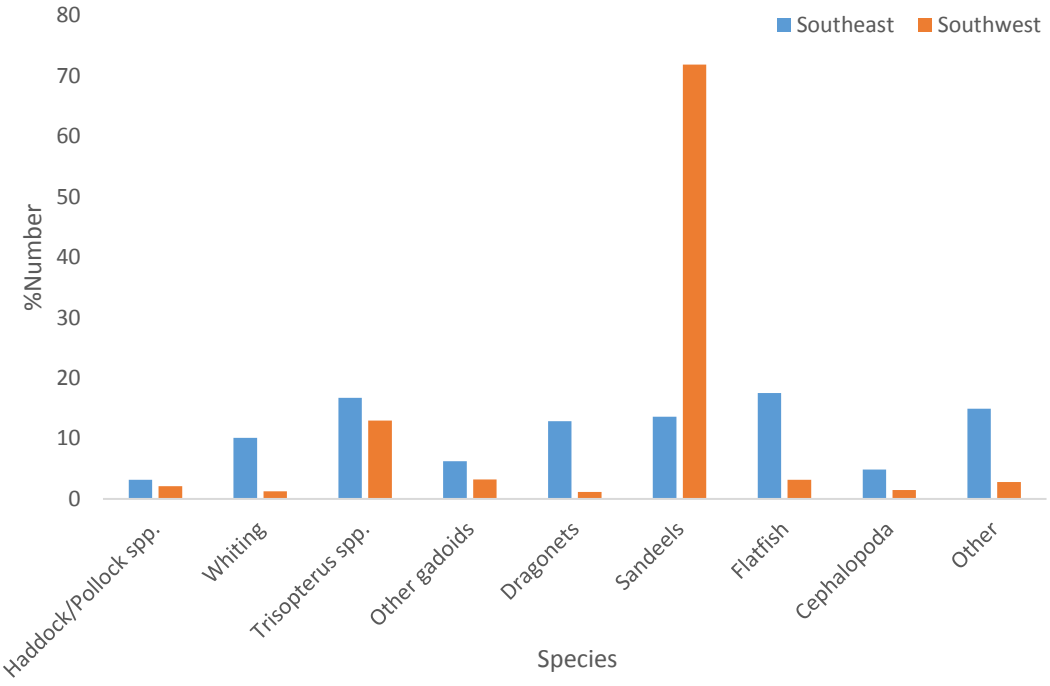


Figure 4.5: The percentage by number of all prey types contributing to the diet of grey seals in southeast Ireland (n=2375), and southwest Ireland (n=5488).

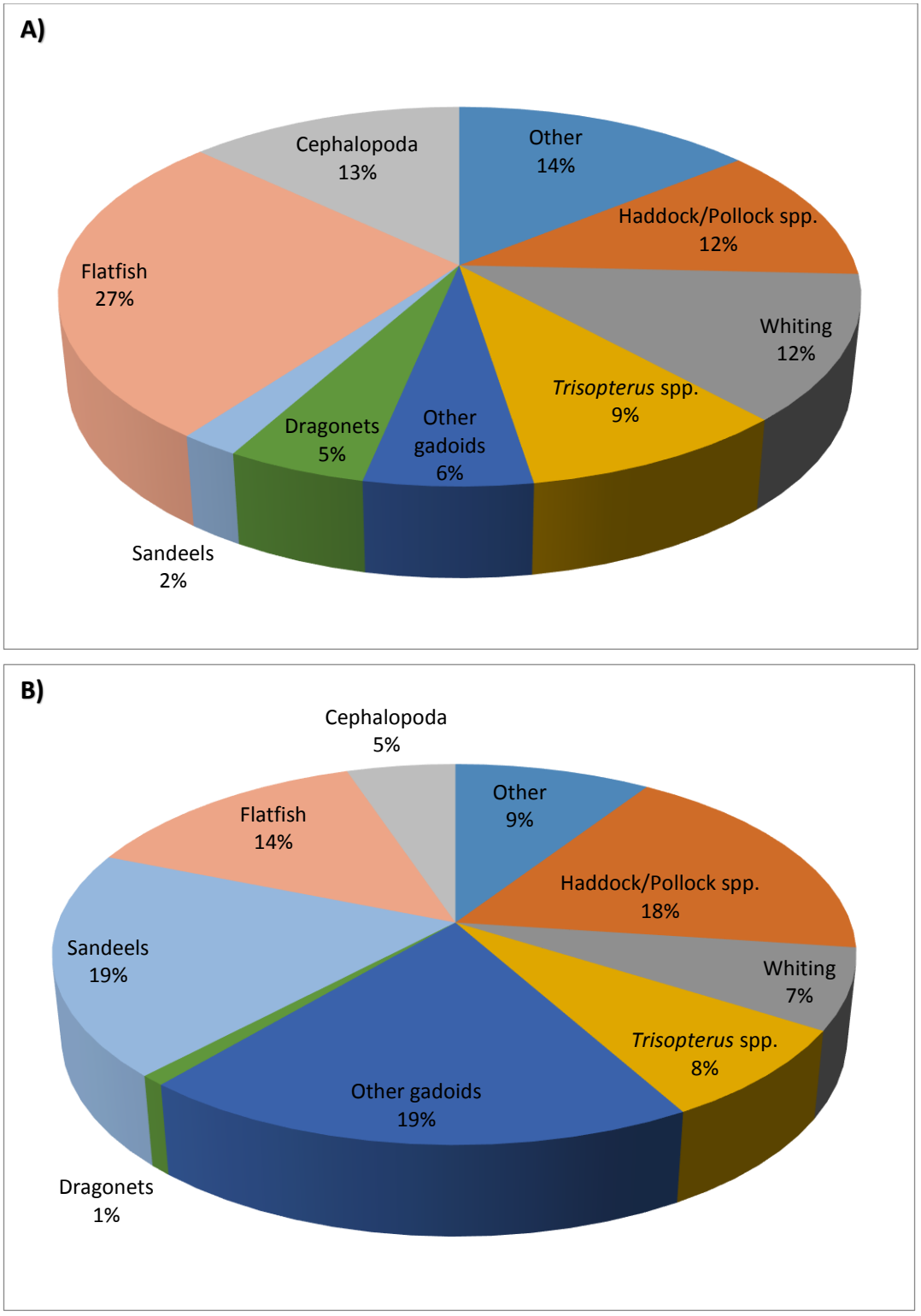


Figure 4.6: The percentage biomass of prey species contribution to the diet (A) southeast Ireland and (B) southwest Ireland.

Grey seals using the southwest site also preyed on pelagic species such as blue whiting (*Micromesistius poutassou*), horse mackerel (*Trachurus trachurus*), and garfish (*Belone belone*) which were noticeably absent in the diet of seals using the southeast site. In fact, a total of ten species found in the diet at this site were completely absent from the southeast coast site (Figure 4.7). Similarly, eleven species in total were completely absent from the southwest coast diet, with seals at the southeast coast site preying on species such as weever fish (*Trachinus draco*) and butterfish (*Pholis gunnellus*).

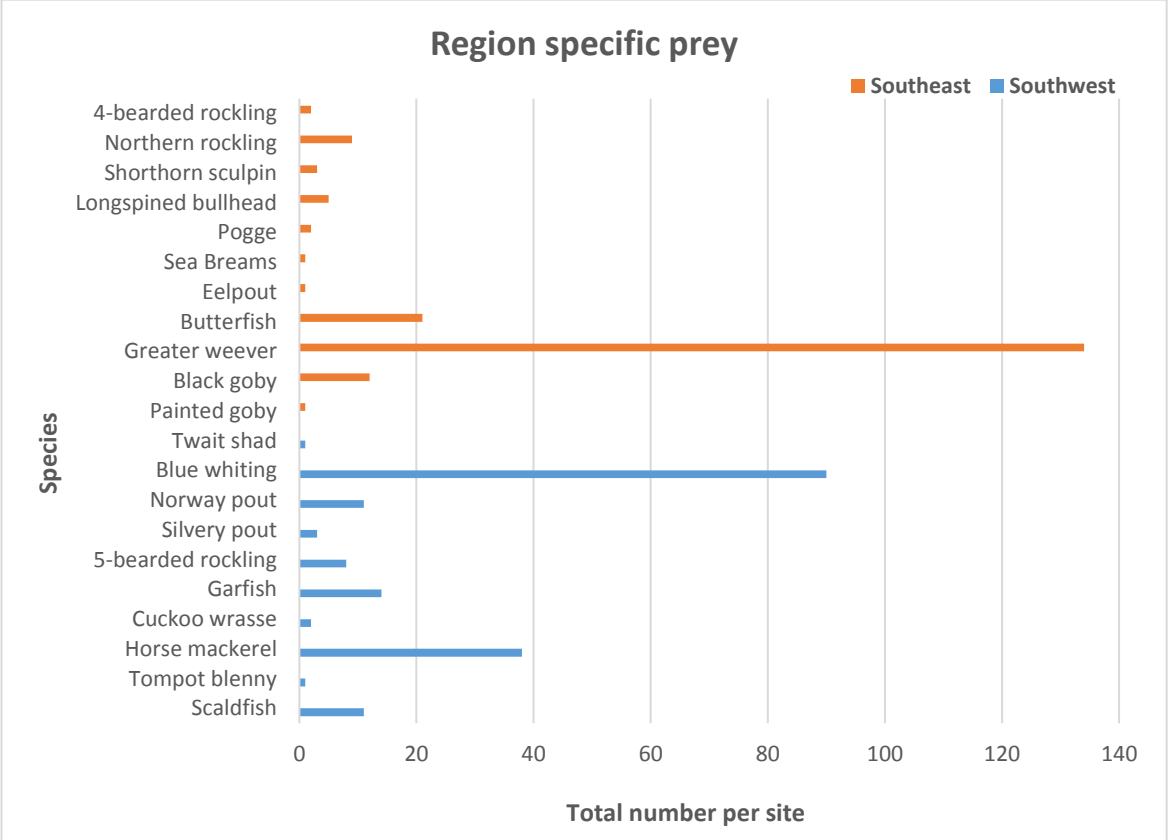


Figure 4.7: The absolute numbers of prey species which occurred only in the southeast or southwest coast seal diet.

4.4.3 Diet variability

Variability within grey seal diet from both sites were examined using a modified version of the Costello-Amundsen plot. Both southeast and southwest coast seal populations largely display an overall generalised feeding strategy, with the important

prey groups identified from dietary indices generally located towards the bottom of the vertical axis e.g. Cephalopoda, rays, whiting and dragonets for southeast seals (Figure 4.8A) and haddock/pollock spp. and flatfish for southwest coast seals (Figure 4.8B). While most prey (see Table 4.2) occurred rarely in scat samples collected at both regions (lower left side of plot), in terms of prey-specific abundance, sandeels are present within nearly all samples from the southwest coast and consequently account for a considerable proportion of the diet. Overall, seals at both sites are generally exploiting many resources simultaneously. In the southwest, *Trisopterus* spp. occur in very high frequencies within samples, although they account for a small proportion of the diet, with flatfish exhibiting a similar tendency in southeast coast samples, however they represent a higher proportion of the diet at this site. However, in terms of prey-specific biomass, some prey such as wrasse (Labridae spp.) and weever fish in the southeast (Figure 4.8C) and rocklings in the southwest (Figure 4.8D), occur rarely in samples but account for a larger proportion of the diet.

4.4.4 Prey length and weight

Original sizes were attainable for 2369 prey items (99.7% of all prey identified) recovered from southeast coast samples. Prey lengths ranged from <1 cm (Unidentified squid spp.) to 64 cm (Conger eel, *Conger conger*). Mean prey length at this site was 15.0 cm (±0.1 SE) with 61% of all prey in the diet equal or less than this (Figure 4.9). Prey weights ranged from <1g (unidentified Gadidae) to 2064.6g (*Loligo* spp.). Mean weight of all southeast prey was 52.4g (±2.0 SE) with 74% of all prey in the diet equal to or less than this (Figure 4.10).

Lengths and weights from 5477 southwest coast prey individuals (99.8% of all prey) were reconstructed. Mean length of prey at this site (14.1 cm (±0.9 SE)) was similar to southeast site, 71% of prey were equal to or less than this (Figure 4.9). Mean weight of southwest coast prey was much lower than southeast coast prey at 35.3 g (±2.3 SE) with 85% of all prey below this weight (Figure 4.10).

Median prey weight for the southeast coast site was 21.2g, whilst prey exhibited a median weight of 7.4g at the southwest coast site. This difference can perhaps be attributed to southwest coast diet being largely dominated by smaller species such as sandeels, while the weight of prey at the southeast site is skewed towards larger prey such as rays.

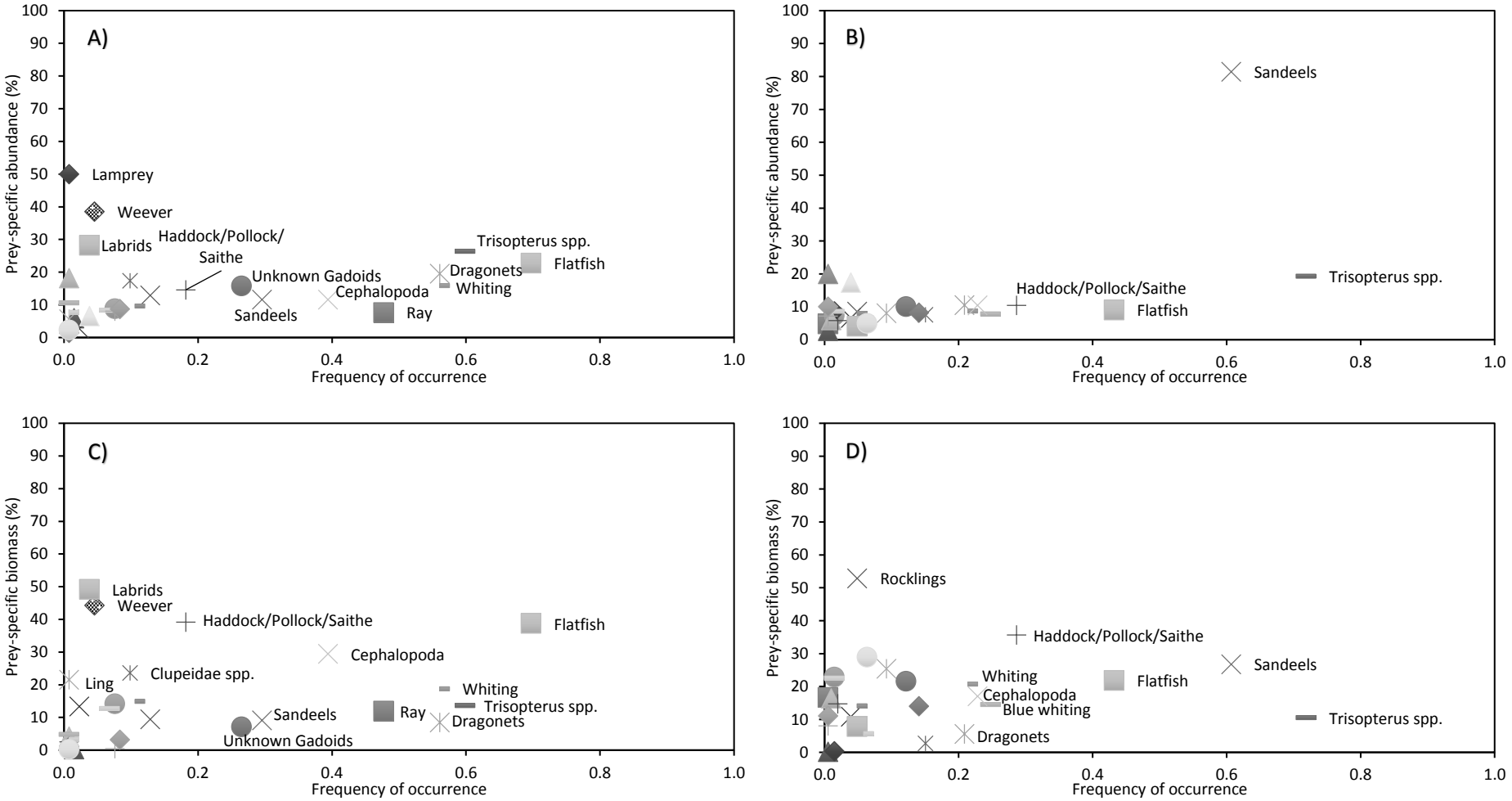


Figure 4.8: Costello-Amundsen plot of grey seal prey species off southeast and southwest Ireland in terms of A) southeast species-specific abundance, B) southwest species-specific abundance, C) southeast species-specific biomass, and D) southwest species-specific biomass. See Table 4.2 for unlabelled prey.

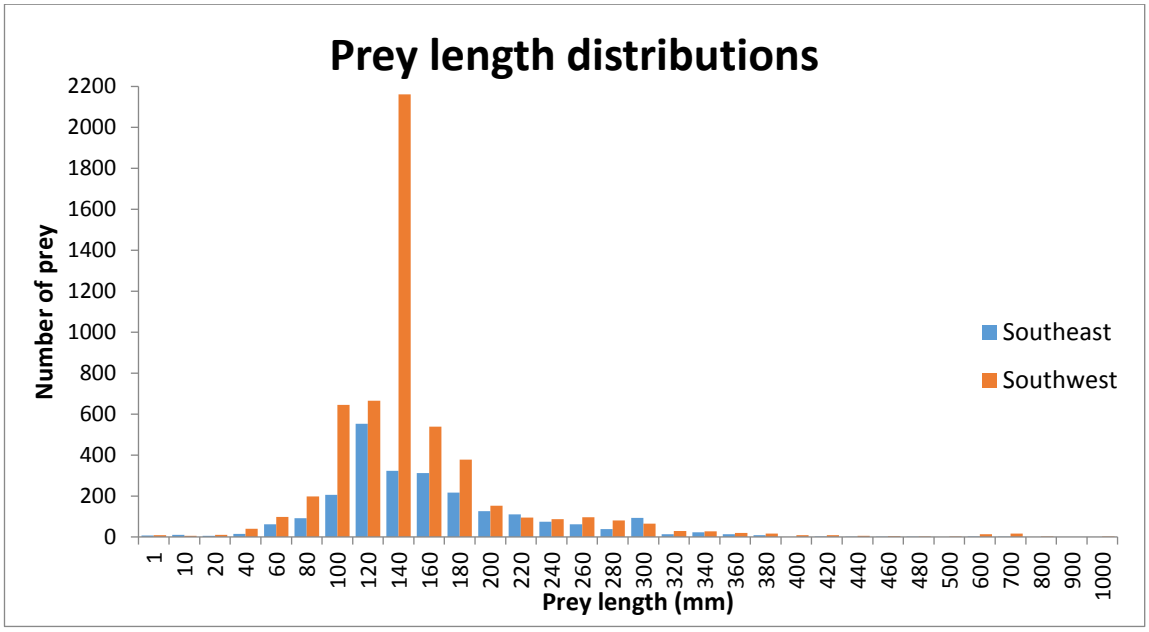


Figure 4.9: Prey length distributions for prey identified in southeast and southwest coast sites.

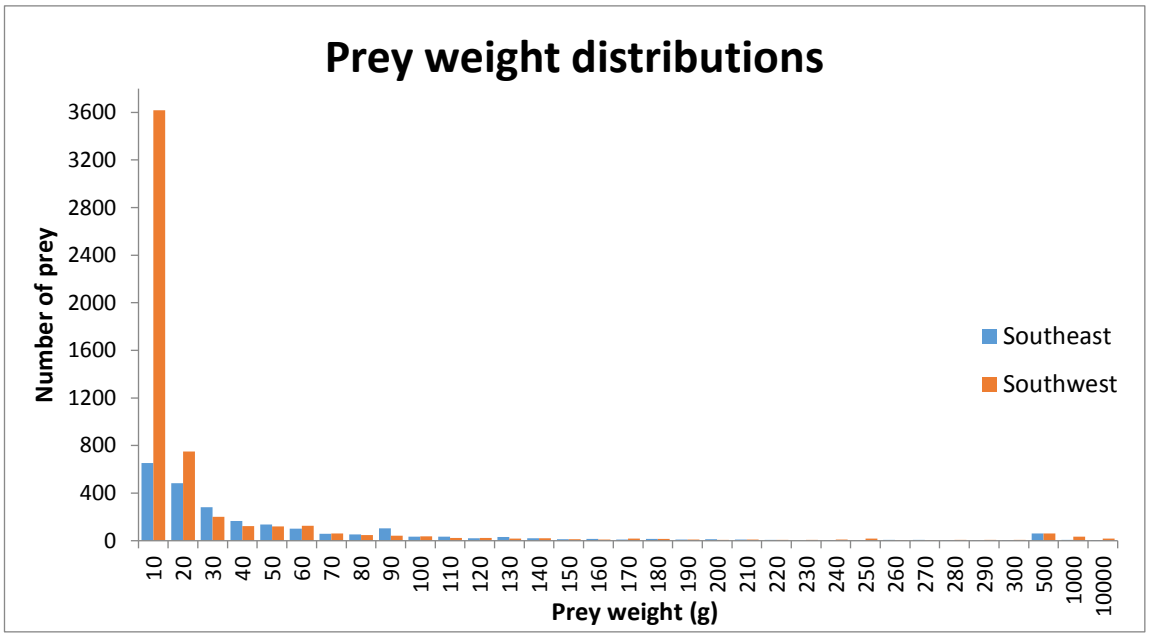


Figure 4.10: Prey weight distributions for prey identified in southeast and southwest coast sites.

4.5 DISCUSSION

This study has demonstrated that while no one prey taxon dominates grey seal diet, depending on the geographic region, variations in prey assemblages and prey importance are apparent. Grey seals utilising both haul out sites display a generalist feeding strategy, as demonstrated by the Costello-Amundsen feeding plot, with certain prey, such as weever fish and rays at the southeast site and blue whiting and horse mackerel at the southwest site, occurring rarely across all scat samples but found in high frequencies/numbers within a limited number of samples. Despite the common occurrence of some key prey (e.g. *Trisopterus* species, sandeels, flatfish and Cephalopoda), their relative contribution to the diet tends to change regionally. Most noticeably is the importance of sandeels in particular, and other pelagic species to the diet of seals utilising the southwest site. Seals that haul out on the southeast coast however, consume far more flatfish and Cephalopoda (particularly octopus spp.). Furthermore, considerably higher numbers/occurrences of whiting and rays were found at the southeast site with species such as weever fish only present in seal diet within this region. Conversely, pelagic species such as blue whiting, horse mackerel and garfish which account for between 2-4% of the diet each by weight at the southwest coast site, are completely absent from the diet of seals hauling out at the southeast coast site.

The differences in the diet of grey seals between regions is likely to be reflective of the habitat type surrounding the study sites. Telemetry data from grey seals tagged at the Great Blasket Island, southwest Ireland during 2009 and 2010 (Cronin *et al*., 2012) and from grey seals tagged in Wexford harbour, southeast Ireland during 2013 and 2014 (Cronin *et al*., 2016; Huon *et al*., in prep) show spatial usage by seals in each region. When these are compared to substrate maps from the European Marine Observation Data Network (EMODnet, 2016), it is possible to broadly compare the seal foraging areas/areas of high usage with that of the underlying substrate. Sediment type around the southeast coast site and pushing into the Irish sea mainly comprises shallow sands and coarse/mixed sediments. The high numbers/frequency of occurrence in the diet of fish species which occur on or bury themselves in this type of sediment such as dragonets, whiting, flatfish, *Raja* spp., and greater weever fish suggest that the preferred foraging grounds of grey seals in this region is reflective of

the surrounding habitat type. Species exclusive to the diet of seals utilising the southeast coast site such as pogge (*Agonus cataphractus*) are described as rarely occurring where stones are present, instead preferring sandy substrate such as is located directly outside Wexford harbour, while the 4-bearded rockling (*Rhinonemus cimbrius*) is typically found on muddy sand that is located between areas of hard substrate, also found to the southeast of the study site. Small pockets of photic rock or biogenic reef exist further along the north coast of Wexford harbour and along the coast just south of the harbour. Although not found in high numbers in the diet, it is likely that species such as conger eel (*Conger conger*) and wrasse that inhabit reefs were consumed as a result of foraging trips to these areas. Furthermore, water depth north of the study site in the Irish Sea, varies from less than 50 m to a maximum exceeding 275 m in the deepest part of the North Channel (Howarth, 2005). Within scat samples collected from this site, the curled octopus (*Eledone* spp.) was the principle cephalopod species. Curled octopus are found inshore at depths of typically less than 100 m (ICES, 1998) which could make these cryptic prey more accessible to grey seals foraging in this region.

The same pattern of prey assemblages reflecting habitat type appears to be true for prey identified within the diet of southwest coast grey seals. The area immediately surrounding the Great Blasket Island is largely dominated by rock and/or biogenic reef which turns to sand and then mud further to the west. North of the study site also contains pockets of mixed to coarse sediment. Prey assemblages within the diet of seals that haul out at the southwest coast site were largely made up of demersal species however many pelagic species that did not occur in the diet of seals using the southeast coast site were also identified. The higher frequencies of haddock/pollock species and higher quantities of wrasse found in the diet in this region is symptomatic of foraging over rocky peaks or reefs. Given that diet in the southwest is largely dominated by sandeels which are found over sandy or muddy bottoms, the substrate type surrounding the southwest coast of Ireland would facilitate their occurrence. Pelagic species that were only present in the diet at this site and found in relatively high frequencies, such as blue whiting, horse mackerel and garfish are presumably more readily available in this region given its proximity to the shelf edge (approximately 300 km from the Great Blasket Island) and deeper water, preferred by pelagic species. *Loligo* spp. was the most frequently occurring cephalopod species within diet samples

from this site. *L. forbesi* is the most common squid species found in Irish waters with the highest abundances found at between 150-250 m, near the shelf break (Lordan *et al.*, 2001; ICES, 2016). It is possible that grey seals that haul out on the Great Blasket Island are foraging near the shelf edge and are exploiting these abundant squid species along with pelagic prey. Seals tagged at the southwest study site have been shown to forage to the edge to the shelf (Jessopp *et al*., 2013). While scat samples are thought to only represent the previous few days' worth of meals (Tollit *et al*., 2010), telemetry studies by Cronin *et al*. (2012) demonstrated how grey seals can travel up to 511 km with foraging trips lasting several days. Thus, habitat type appears to be reflecting prey choice and availability and is therefore an important factor governing regional variations in diet.

In general, prey lengths were similar at both sites with the prevalence of sandeels at the southwest site driving the finding of smaller, lighter but more numerous prey compared to the diet of seals that haul out at the southeast coast site. Some overlap between prey size ranges and minimal landing sizes for commercial species were apparent at both sites suggesting potential competition between grey seals and fisheries in both these regions. As discussed in Chapter 3, caution is advised when applying generic squid regression equations to small squid beaks, as these may underestimate the original size of the prey consumed.

Grey seals using the southeast site have been shown to forage largely within the Irish Sea (Cronin *et al*., 2014) and consume commercial species such as plaice, whiting and ray, all of which were substantial contributors to grey seal diet in this region. Rays are difficult to detect within traditional pinniped diet analysis due to the absence of otoliths and bones (Bowen & Harrison, 1994), but denticles can be recovered and identified to species level (Gravendeel *et al*., 2002). Unfortunately, quantification is not possible therefore all rays in this study were conservatively estimated at 1 fish per scat when denticles were present. Even so, rays were detected in 62 scats, providing a minimum biomass estimate of 4.4%. It is likely that this figure underestimates the contribution of rays to the diet as, apart from conservative quantification estimates, weights for this taxa were attained from sizes assigned from juvenile fish. Given that rays can grow to over one meter in length, it is plausible that similar to harbour seals and Antarctic fur seals, grey seals mainly consume juveniles (Browne *et al*., 2002; Ciaputa & Siciński, 2006). Data from annual Irish groundfish surveys provide a common length of 54 cm

along the coast of Ireland (Marine Institute, 2012). Should grey seals be consuming these naturally abundant prey at 54cm this would provide an estimate of 29.8% biomass contribution to the southeast coast diet (for thornback rays), making them the second most important prey after Gadidae. Skates and rays have been found in the diet of other pinnipeds (Le Boeuf *et al*., 1993; Ciaputa & Siciński, 2006; Deagle *et al*., 2009), however presence within grey seal diet has typically been minimal (Mansfield & Beck, 1977; Bowen & Harrison, 1994; Browne *et al.*, 2002; Bowen *et al*., 2006; Benoît *et al*., 2011; Gosch *et al*., 2014). Therefore, this is the first such study to identify rays in such high numbers in grey seal diet. Given their high nutritional value (Le Boeuf *et al*., 1993), and availability (Marine Institute, 2014), rays may be an important component of grey seals that haul out along the southeast coast of Ireland. While stock status for *R. clavata* remains favourable and consequently competition between grey seals and fisheries over this species should be minimal, management plans for rays should take into consideration predation by higher predators such as seals.

Overall, the findings of this study are broadly similar to previous studies investigating grey seal diet. The diet of seals that haul out on the southwest coast of Ireland primarily consists of gadoids and sandeels, which would be in agreement with diet descriptions from the northwest Atlantic (Bowen & Harrison, 1994) and the northeast Atlantic (Hammond & Prime, 1990; BIM, 1997). However, unlike studies from other regions which have demonstrated relatively high occurrence of cod within the diet (Benoit & Bowen, 1990; Pierce *et al*. 1990; Beck *et al*., 2007; Harvey *et al*., 2012), grey seals that haul out in southwest Ireland rarely feed on cod, with minimal contribution by weight to diet. This is also true for grey seals utilising the southeast coast haul out site, with gadoid species such as whiting far more important to the diet. Furthermore, flatfish and Cephalopoda, rather than sandeels, are major contributors to the diet of seals in this region. In other regions where sandeel occurrence in the diet is low, previous studies have also demonstrated how prey groups such as flatfish, clupeids or Cephalopoda emerge as major components to grey seal diet (e.g. Benoit & Bowen, 1990; McKibbon, 2000; Lundström *et al*., 2007; Ridoux *et al*., 2007). Similarly, McKibbon (2000) showed how flatfish were dominant in the diet of grey seals on the east coast of Ireland, with reliance shifting towards gadoid species as sampling moved further south. Indeed, within a single population, large geographic variation in grey seal diet is not uncommon, with Hammond & Prime (1990) demonstrating how flatfish

accounted for 50% of the diet by weight in Donna Nook (North Sea) while in other regions of the UK they represented less than 10% of the diet by weight.

To conclude, grey seals that use haul out sites in southeast and southwest Ireland display significant regional variation in prey assemblage diversity within the diet. Furthermore, while certain species are consumed by both populations, the relative proportions of prey species within the diet tends to differ between regions. As generalists, grey seals at both sites feed on a wide variety of prey with no one species dominating the diet. However, in both regions particular prey species were found in higher abundances/frequencies within a small number of scat samples and these tended to differ depending on the location. While it is not possible to infer from this study whether certain seals were specialising on particular prey (e.g. weever fish), this could be achieved by repeated scat sample collection from the same individual (identified using genetic techniques) combined with telemetry studies assessing the preferred foraging location of the predator. Prey selection appears to be related to surrounding habitat type and associated species availability with seals in the southeast coast likely foraging over sandy/coarse sediment, while seals that haul out on the southwest coast consume more prey that inhabit reefs or pelagic waters. A certain amount of overlap between prey sizes of commercial species targeted by fisheries occurs at both sites, however for the most part grey seals consume low quantities of commercial species and tend to select smaller prey. Unfortunately, there is insufficient available data on fish abundance and distribution trends for species occurring in Irish waters. Therefore, it is not possible to determine whether the geographic variation exhibited by grey seals in Ireland is as a direct result of greater prey species availability in each region. However, the continued analysis of grey seal diet would facilitate the need for up to date region specific information, so as to better understand the role grey seals play in their ecosystem. Furthermore, this study has demonstrated that if using baseline diet data to model consumption estimates and biomass removal, it is imperative that the data be region specific. If not then there is a risk of drawing the wrong conclusions given that within the Irish grey seal population, diet can vary substantially between regions.

CHAPTER 5

Caught in the act? Little evidence for the depredation of fish catches by by-caught seals.



M. Gosch, M. Jessopp, R. Cosgrove, E. Rogan, and M. Cronin

This chapter incorporates reviewer comments and is re-submitted to *ICES Journal of Marine Science*.

5.1 ABSTRACT

Each year, Irish set-net fisheries experience catch losses attributed to seals, and at the same time, seal by-catch is known to occur in these fisheries. It is not known why seals become entangled in fishing gear, but by-catch during depredation at nets may be a contributory factor. This study aimed to evaluate whether by-caught juvenile and sub-adult grey seals were depredating nets. Digestive tracts from by-caught seals were recovered from trammel- and tangle- net fisheries off Irelands south and west coasts. Non-metric multidimensional scaling plots showed significant differences between stomach contents and corresponding catch composition at both sites. Although depredation was recorded by both fisheries, especially in cod, pollock, and ling, these prey were recovered infrequently in digestive tracts. Reconstructed fish lengths from seal digestive tracts were below the sizes caught by the fisheries in all cases except for four fish with one pollock showing clear signs of having been depredated. The prey lengths were also consistent with the size of fish identified from seal scat analysis, which reflects population-level diet. The lack of fish species caught in nets found in seal stomachs suggests that by-caught juvenile seals in this study were not depredating fish in the nets. Juveniles likely became entangled unintentionally as they came into contact with nets when they swam past. Results suggest that some other cohort of the seal population is primarily responsible for the high levels of depredated monkfish and pollock recorded (67 % and 58% of the entire catch, respectively). The by-catch of juvenile seals has important implications for the management of the fisheries, as grey seals are a protected species under the Habitats Directive. Potential future mitigation measures are addressed in relation to these findings.

Keywords: grey seal, seal-fisheries interactions, depredation, mitigation.

5.2 INTRODUCTION

Seal-fishery interactions at nets have been well documented worldwide (e.g. Northridge, 1991; Holma *et al*., 2014; Machado *et al*., 2016). Typically, two interactions can occur; biological interactions where seals and fisheries compete for shared prey resources; and operational interactions. The latter can result in a number of outcomes: the unintentional mortality of seals through entanglement (by-catch); and seal-induced catch loss through removal or damage to the fish catch (depredation) and/or fishing gear (e.g. Northridge & Hofman, 1999; Read, 2008; Hamer & Goldsworthy, 2006; Rafferty *et al*., 2012; Cronin *et al*., 2014; González *et al*., 2015; Cosgrove *et al*., 2013; 2015; 2016). Incidental capture in static fishing gear is one of the greatest anthropogenic threats to marine megafauna, including marine mammals (Lewison *et al*., 2004; Read *et al*., 2006; Brown *et al*., 2015), while depredation and seal damage to fishing gear has been increasing worldwide (Arnould *et al*., 2003; Goetz *et al*., 2008; Varjopuro, 2011; Rafferty *et al*., 2012).

Grey seals (*Halichoerus grypus*) are top predators in the North East Atlantic, distributed from Northern Russia south to the coast of France where they feed on a large variety of prey species (Bowen & Harrison, 1994; Hammond *et al*., 1994a; 1994b; Ridoux *et al*., 2007; Gosch *et al*., 2014). Telemetry studies have shown that whilst grey seals undertake wide-ranging foraging trips, (e.g. McConnell *et al*., 1992; Thompson *et al*., 1996; Cronin *et al*., 2013) they mainly have a coastal distribution, often bringing them into contact with inshore static fishing gear (including gill-nets, tangle-nets and trammel-nets). Depredation appears to have increased in inshore waters around Ireland leading to a growing conflict between seals and fisheries (Cronin *et al*., 2010; 2013; Cosgrove *et al*., 2015).

Grey seals are protected under the EU Habitats Directive and listed as an Annex II & V species (92/43/EEC). Studies by Cosgrove *et al*. (2013; 2016) provided the first quantitative information on seal by-catch in static-net fisheries in Irish waters and found that by-catch rates were high in a large meshed tangle-net fishery with the majority of animals caught being juvenile (< 2 years) grey seals, as has been recorded in other by-catch studies (BIM, 1997; Bjørge *et al*., 2002; Bäcklin *et al*., 2011; Kauhala *et al*., 2015). These authors all concluded that the risk of seal by-catch in this gear type was high, representing a potential threat to seal conservation. While all individuals

within a population are not of equal importance, young females are future reproducers and their over-representation as by-catch may affect future numbers of mature females (Kauhala *et al*., 2015). Though grey seal abundance in Ireland has experienced a steady increase in recent decades (Ó Cadhla *et al*., 2013), the relatively high rates of by-catch in certain fisheries presents both ethical and conservation problems. Furthermore, there exists within the fishing industry a perception that the removal of seals, through entanglement in fishing gear, may indirectly address the issue of depredation. Yet, despite regular incidents of by-catch reported in some fisheries (Cosgrove *et al*., 2016), rates of seal depredation in Ireland remain high (Cronin *et al*., 2014; Cosgrove *et al*., 2015).

Damage to fish catch by seals typically involves either bites out of the belly, thereby removing parts such as viscera or flesh and leaving behind the main body of the fish, or the entire removal of the body with only the head and sometimes partial spine remaining in the net (Northridge *et al*., 2013). Furthermore, the handling of by-caught seals and subsequent damage to the fishing gear can prove costly. Recent research suggests that the economic impact of seal depredation in Ireland has substantially increased in set-net fisheries since the 1990's (Cosgrove *et al*., 2015). The problem is quite a significant one for small scale coastal fishermen, with between 10-59% of damaged catch in Ireland estimated to be attributed to seal damage (Cosgrove *et al*., 2015). The economic impact as a result of catch depredation by seals is highest in set gill-nets targeting pollock (*Pollachius* spp.), hake (*Merluccius merluccius*) and cod (*Gadus morhua*); and tangle- or trammel-nets, targeting crawfish (*Palinurus elephas*), angler/monkfish (*Lophius* spp.) and turbot (*Scophthalmus maximus*) (Cronin *et al*., 2014). In certain areas in Ireland, depredation by seals has rendered some fisheries such as the monkfish fishery untenable (Cronin *et al.,* 2014).

Despite the growing problem of depredation, many questions remain unanswered such as whether depredating seals specifically target nets to obtain prey or, as generalists do they opportunistically remove fish as they pass by? Though adult grey seals are regularly observed close to fishing gear (Fjälling *et al*., 2007; Lehtonen & Suuronen, 2010; Königson *et al*., 2013; Oksanen *et al*., 2014) and in the vicinity of marker buoys when hauling commences (Cosgrove *et al*., 2015), juveniles rather than adults constitute the majority of by-caught seals in inshore fisheries. Whilst it is likely that the lack of experience around nets by juveniles may lead to a higher probability of by-

catch, it is not clear if they are targeting and depredating fish in the nets when they are caught. In order to reduce seal depredation levels within the Irish tangle-net fisheries sector, data on what demographic of the population is primarily responsible for much of the problem is firstly required (Kauhala *et al*., 2015). Such information may then facilitate the implementation of effective targeted mitigation measures.

This study investigates whether by-caught seals recovered from two set-net fisheries in Ireland were depredating nets prior to being entangled, or whether some other cohort of the grey seal population is responsible for observed depredation. We tested a number of hypotheses; 1) the 'indiscriminate' hypothesis: if by-caught juvenile seals were indiscriminately depredating nets, fish of similar species composition would occur within both the nets and the digestive tracts of seals; 2) the 'targeted' hypothesis: if by-caught juvenile seals were targeting specific fish in nets, depredated species would be disproportionately represented in the digestive tracts of seals; 3) the 'opportunistic' hypothesis: if by-caught juvenile seals were taking fish opportunistically from nets, the length of fish in digestive tracts would be of similar size to those caught in nets; 4) the "non-depredation" hypothesis: contents of digestive tracts will be unrelated to net contents in terms of composition and size, indicating that juvenile seals became entangled as a result of other factors such as not perceiving nets in the water rather than during depredation events.

5.3 METHODS

By-caught seals were obtained from two fisheries operating along the west and south coasts of Ireland (Figure 5.1). Seals were recovered from the nets of a 16 m inshore fishing boat operating along the west of Ireland between June 2011 and July 2012. The vessel used a combination of 270 & 320 mm tangle nets when targeting crawfish and rays (*Raja* spp.). Other commercial fish species that were not specifically targeted but were landed in this fishery included pollock, cod, ling (*Molva molva*) and brill (*Scophthalmus rhombus*). Seals were also by-caught in a trammel net fishery within 19 km of the south coast of Ireland, between November 2012 and April 2014. This 14 m vessel used mesh sizes of between 270 – 360 mm when targeting monkfish, spider crabs (*Maja squinado*) and rays. The fishery also landed pollock, haddock

(*Melanogrammus aeglefinus*), cod and ling, although these species were not specifically targeted. By-caught seals were categorised as either juveniles or sub-adults based on total length and weight. Seals were determined to be juvenile when exhibiting weights of less than 60 kg and total lengths of less than 160 cm. "Sub-adults" had total lengths of between 160 cm to 185 cm and weights of less than 150 kg. These were based on length and weight descriptions for eastern Atlantic grey seals according to Bonner (2004).

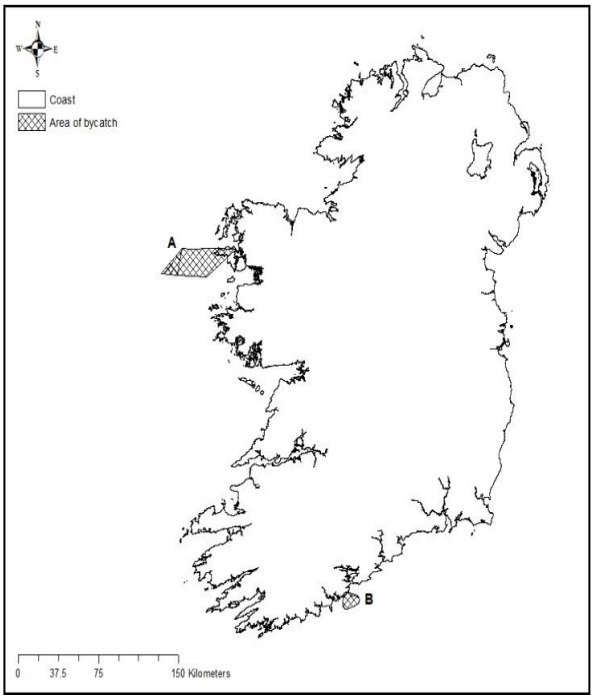


Figure 5.1: Map of Ireland depicting sampling sites. A = West coast, B = South coast.

5.3.1 Data collection

A dedicated observer was assigned to the west coast vessel during normal commercial fishing operations, totalling 27 days over a 13 month period. Following a detailed data collection protocol, all landed catch was quantified and measured. A catalogue of pictures depicting seal damage was collected and any fish displaying signs of damage were recorded. Seal damage was characterised by the removal of all or part of the fish belly (V-shaped bite), removal of all or part of the entire body, and removal of skin or rake marks to the body. Observers were not on board during fishing operations on the south coast, so seal by-catch was retained by the operator and collected at port on 16 separate occasions spanning a 17 month period. Corresponding data on the numbers

of landed catch and depredated fish from each by-catch event was provided by the vessel operator, who took detailed records of catch composition, depredation, and by-catch following instructions provided to ensure consistency with west coast. Fish length data were not recorded for the south coast fishery.

All by-caught seals were photographed, sexed, measured (length, neck, behind flipper and mid-line girths) and a broad range of tissue samples were taken for follow up studies. Stomach removal was performed *in situ* aboard the west coast vessel, and in the laboratory on seals collected from the south coast fishery. The digestive tract was ligated at the oesophagus just below the throat and directly below the duodenum, thereby preventing loss of liquid food material, before being removed. The posterior end of the intestinal tract was ligated directly above the anus in the case of all south coast by-caught seals before being stored frozen at approximately -20°C.

Frozen stomachs were thawed for analysis and all stomachs were then weighed to determine their full capacity weight, before being fully opened along the natural curvature of the organ. The contents were washed through a nest of sieves, with a maximum mesh size of 5 mm and a minimum mesh size of 0.5 mm, to remove soft waste. Any flesh recovered within the stomach was recorded and whole prey was weighed, measured and identified. All other hard prey remains such as otoliths, bones, cephalopod beaks and crustacean carapaces/claws were sterilised in 70% ethanol for 24 hours, dried for 48 hours and stored in dry, labelled polythene bags for later identification. Empty stomachs were then reweighed, to estimate the weight of prey contents consumed.

5.3.2 Data analysis

Following the "all structure" approach (Tollit *et al*., 2003), prey remains (including but not limited to otoliths, premaxillae, maxillae, dentaries', vertebrae, post-temporals, urohyals, cephalopod beaks) were identified to their lowest taxonomic level, where possible, using a reference collection and published guides (e.g. Clarke, 1986; Härkönen, 1986; Watt *et al*., 1997; Tuset *et al*., 2008). Diagnostic structures were measured using a Zeiss 200S binocular dissecting microscope at x40 magnification fitted with an eye-piece graticule when prey items were less than 1 cm and digitals callipers (accuracy ± 0.01 mm) for prey greater than 1 cm. The minimum number of

prey per stomach was determined by counting the highest number of species-specific diagnostic structures identified per stomach i.e. left/right otoliths/premaxillae/maxillae/dentaries', upper/lower cephalopod beaks. Vertebrae were also used to quantify prey occurrence and divided into types (i.e. atlas, caudal, abdominal etc.). If two or more anterior caudal vertebrae from the same species were found within a stomach, the minimum number of individual fish was determined by differentiating vertebrae through size, variations in colour and state of erosion. Prey length and weight was reconstructed using published regression equations (see Gosch *et al*., 2014). While many dietary studies apply correction factors to account for partial and complete erosion, most are based on prey remains recovered within faecal material (e.g. Tollit *et al*., 1997; Grellier & Hammond, 2006) that have gone through the whole digestive process. All prey diagnostic structures in this study were identified from stomach contents. The otoliths of all commercial fish species found within the stomachs all exhibited low digestion grades (≤1; see Tollit *et al*., 1997). Given that the majority of diagnostic structures remain intact within the digestive tracts with otoliths exhibiting a good state of preservation (Pierce *et al*., 1991a) and correction factors are only available for otoliths of certain species, such correction factors may lead to these species being over-estimated in the diet. Therefore, correction factors were not applied in this analysis so that all prey species within the diet were represented equally. Any otoliths displaying degrees of erosion greater than grade 3 as defined by Tollit et al. (1997), highly eroded vertebrae, and small crustacean remains (<2 cm) recovered from stomachs were deemed to be secondarily ingested items (see McConnell *et al.*, 1984) and were thus excluded from subsequent analyses. Diet composition was expressed using standard dietary indices of percentage Number, Frequency, and Biomass (%N, %F, %B, respectively) as described in Gosch *et al*. (2014), with any empty stomachs excluded from the analysis.

The breakdown of each fishery catch composition was calculated in terms of the percentage contribution by number of each species, from all nets containing by-catch. Corresponding information on depredation for each species were also examined from both sites, represented by the percentage number of depredated fish in nets. As landed catch was small, often containing only a few fish within each net, all nets containing by-caught seals at each site were compared to by-caught stomach contents rather than each seal-net pair.

5.3.3 Net versus stomach content analyses

To test the hypothesis that if by-caught juvenile seals were indiscriminately depredating nets, fish of similar species composition would occur within both the nets and the digestive tracts of seals, we compared net and stomach contents. Any empty nets or stomachs were omitted from the analysis. Prey species abundances were transformed using Presence/Absence (PA) transformation to account for species where quantification by number was not possible (e.g. *Raja* spp.), and Square-Root (SR) transformation to allow less abundant but potentially larger prey species to contribute to similarity/dissimilarity between nets and stomach contents while accounting for relative abundance of species. Transformed prey species abundance data were used to create a Bray-Curtis similarity matrix, and multivariate patterns of species occurrence in net versus stomach composition were visualised using two-dimensional non-metric multidimensional scaling (nMDS) plots (Clarke and Warwick, 2001). Permutational multivariate analysis of variance (PEMANOVA+) was used to test for differences between net and stomach contents (Anderson *et al*., 2008) using PRIMER 6 statistical software (PRIMER 6, Plymouth Marine Laboratory). The SIMPER routine was then used to determine which species contributed the greatest similarity/dissimilarity between stomach and net contents. A subset of the data focusing only on species of commercial value that would ordinarily be caught and landed by the fishery (see Appendix XI) was further analysed to investigate whether the occurrence of commercial species in digestive tracts is representative of net contents.

To test the hypothesis that depredated fish would be over-represented in the digestive tracts of by-caught seals, we compared the contribution of depredated species (pollock, cod, ling, monkfish) in digestive tracts to the occurrence of these species in the general diet of grey seals in Ireland from scat analysis. Scats were collected over a 5 year period (2009-2013) from the southwest coast of Ireland, and contribution to diet calculated in terms of % Frequency, % Number and % Biomass. Finally, the length-frequency distributions of any landed fish species common to both west coast nets (with & without by-catch) and all seal stomachs were compared in order to assess whether by-caught seal prey size preference was correlated with fish size caught by this fishery. These sizes were then compared to fish lengths identified from scat

analysis (Chapters 3 & 4) in order to ascertain whether by-caught seal prey sizes differed from fish sizes taken by the wider population (i.e. natural foraging, although this may include some contribution from depredation).

5.4 RESULTS

Twenty-two by-caught grey seals were obtained from the south coast fishery which targeted monkfish, spider crabs and rays. Of these, 12 were juvenile males ranging from 115 cm to 151 cm in length; two were sub-adult males with lengths of 168 cm and 182 cm, with the remaining eight juvenile females measuring between 121 cm to 147 cm. A further 22 grey seals were by-caught in the west coast tangle net fishery which targeted crawfish and rays. These comprised of 11 juvenile females ranging in length from 103 cm to 155 cm, 2 sub-adult males (160 cm and 185 cm), and 9 juvenile males displaying lengths between 129 cm – 157 cm.

5.4.1 By-caught seal diet composition versus net contents

Of the 44 seal stomachs collected, two contained no prey remains; one stomach from each sampling location. The remaining 42 stomachs contained prey weights (i.e. full stomach weight minus empty stomach weight) ranging from between 10 g to 1750 g. Among these stomachs, the mean reconstructed weight of prey items was 153.2 g (±243.2, SD) with individual reconstructed prey weight ranging between 0.1 g to 1972.9 g. The mean number of unique prey taxa was 4.5 (±3.2) with number of prey items per stomach ranging from 1 to 61 (mean 12.1 ± 14.6).

Within the south coast stomach samples, *Trisopterus* spp. (specifically poor cod, *T. minutus*) were the most numerically dominant, and most frequently occurring prey with the highest contributors to the seals diet in terms of biomass. Both whiting (*Merlangius merlangus*) and sandeels (*Ammodytes* spp.) were also key species in the diet of the south coast by-caught seals while cephalopods too, contributed substantially in terms of biomass (Table 5.1).

Regional differences in diet were apparent among the two study areas. Within the west coast samples whiting, as opposed to *Trisopterus* spp., was the most important prey species in terms of percentage number, frequency of occurrence and biomass (Table 5.1). Cephalopods featured strongly among all indices in the diet in this region, while sandeels were the second most numerically dominant species and occurred frequently in the diet along with *Trisopterus* spp., although neither were particularly significant contributors in terms of biomass.

Fishery catch composition and depredation percentage rates from nets containing by-caught seals were calculated for both sites (Table 5.2). The west coast fishery catch comprised mainly of target species, crawfish (19% N) and ray (46% N), with the remaining percentages made up of various other commercial fish species and lobster (*Homarus gammarus*). 33% (n=2) of all cod, 44% (n=8) of all monkfish, and 47% (n=14) of all pollock caught in nets in the west coast fishery were depredated. Within the south coast fishery, spider crab (62% N), ray (18% N), and monkfish (5% N) accounted for the greatest proportion of the catch. Of the catch, 22% (n=4) of all monkfish, 20% (n=1) of all cod, and 25% (n=1) of all ling caught in the south coast fishery displayed seal damage (see Table 5.2).

Table 5.1: Diet composition of by-caught seals from the south & west coasts of Ireland. %F: percentage frequency of occurrence; %N: percentage by number; %B: percentage biomass

Species	South			West		
	%F	%N	%B	%F	%N	%B
CHONDRICHTHYES						
Ray *Raja* spp.	-	-	-	4.8	0.6	-
Dogfish *Scyliorhinus canicula*	-	-	-	9.5	1.1	-
OSTEICHTHYES						
Conger eel *Conger conger*	4.8	0.3	0.4	4.8	0.6	0.2
Herring *Clupea harengus*	-	-	-	9.5	1.1	1.2
Sprat *Sprattus sprattus*	4.8	0.3	-	4.8	0.6	0.3
Cod *Gadus morhua*	19.0	8.2	9.9	9.5	1.1	3.0
Haddock *Melanogrammus aeglefinus*	19.0	1.8	4.8	19.0	2.2	4.6
Pollock/Saithe *Pollachius* spp.	14.3	0.9	9.3	14.3	1.7	6.3
Haddock/Pollock	-	-	-	4.8	1.1	2.1
Whiting *Merlangius merlangus*	33.3	9.7	15.3	52.4	18.5	18.5
Poor cod *Trisopterus minutus*	85.7	31.8	10.3	33.3	6.7	1.2
Poor cod *Trisopterus minutus*	23.8	3.9	7.2	9.5	1.7	3.7
Poor cod/bib	14.3	3.0	1.2	-	-	-
Unidentified *Trisopterus* spp.	14.3	3.6	0.2	9.5	1.1	0.0
Torsk *Brosme brosme*	-	-	-	4.8	0.6	0.3
Greater forkbeard *Phycis blennoides*	9.5	0.6	0.2	-	-	-
5-bearded rockling *Ciliata mustela*	-	-	-	4.8	0.6	-
3-bearded rockling *Gaidropsarus vulgaris*	4.8	0.3	2.6	4.8	0.6	1.9
Ling *Molva molva*	14.3	0.9	7.3	9.5	1.1	3.2
Hake *Merluccius merluccius*	23.8	2.4	7.6	-	-	-
Unidentified Gadidae	4.8	2.1	1.3	4.8	0.6	0.3
Dragonet *Callionymus spp.*	14.3	1.8	0.7	9.5	1.1	0.3
Garfish *Belone belone*	4.8	0.3	-	-	-	-
Grey gurnard *Eutrigla gurnardus*	-	-	-	9.5	1.1	0.1
Cuckoo wrasse *Labrus mixtus*	14.3	0.9	0.7	4.8	0.6	0.4
Ballan wrasse *Labrus bergylta*	-	-	-	9.5	1.1	1.9
Horse mackerel *Trachurus trachurus*	4.8	0.3	0.8	23.8	6.7	6.0
Sandeels *Ammodytes spp.*	28.6	15.5	1.0	42.9	16.9	3.4
Mackerel *Scomber scomber*	-	-		9.5	4.5	9.6
Norwegian Topknot *Phrynorhombus norvegicus*	4.8	0.3	<0.1	4.8	0.6	0.0
Brill *Scophthalmus rhombus*	-	-	-	4.8	0.6	1.7
Megrim *Lepidorhombus* spp.	4.8	0.6	0.9	9.5	1.1	0.7
Unidentified Bothidae	-	-	-	4.8	0.6	1.0
Plaice *Pleuronectes platessa*	9.5	0.6	1.2	9.5	4.5	6.2
Dab *Limanda limanda*	4.8	0.3	0.2	-	-	-
Long rough dab *Hippoglossoides platessoides*	4.8	0.6	0.1	4.8	0.6	0.8
Lemon sole *Microstomus kitt*	19.0	1.2	1.7	4.8	0.6	0.7
Unidentified Pleuronectidae	-	-	-	4.8	0.6	0.6
Solenette *Buglossidium luteum*	-	-	-	4.8	0.6	0.1
Sole *Solea solea*	4.8	0.3	1.3	9.5	1.1	0.9
Unidentified Soleidae	4.8	0.6	2.1	4.8	0.6	0.2
Unidentified flatfish	9.5	0.6	<0.1	4.8	0.6	0.1
Unidentified fish species	14.3	0.9	-	-	-	-
CEPHALOPODA						
Common cuttlefish *Sepia officionalis*	-	-	-	14.3	1.7	3.9
Squid *Loligo* spp	4.8	0.3	0.9	23.8	3.9	5.5
Curled octopus *Eledone* spp.	9.5	1.5	3.0	4.8	0.6	0.3
Octopus spp.	14.3	2.4	5.7	23.8	7.3	8.8
Unidentified Cephalopods	9.5	0.9	2.0	-	-	-
Total *Trisopterus* spp.	90.5	42.4	18.9	42.9	9.5	4.9
Total Gadidae	95.2	69.4	77.3	90.5	37.4	45.1
Total flatfish	23.8	5.2	7.6	28.6	13.4	13.1
Total fish	100.0	94.9	88.4	100.0	86.6	81.5
Total Cephalopoda	23.8	5.2	11.6	42.9	13.4	18.5

Table 5.2: The total percentage catch composition and percentage depredation rate of the total number of each landed species, from the west coast fishery over 27 days between June 2011 – July 2012, and the south coast fishery over 16 days between November 2012 – April 2014.

Species	West		South	
	% Catch composition	% Dep rate	% Catch composition	% Dep rate
Ray *Raja* spp.	45.9	-	17.8	-
Cod *Gadus morhua*	2.4	33.3	1.6	20.0
Haddock *Melanogrammus aeglefinus*	-	-	0.4	-
Pollock/Saithe *Pollachius* spp.	9.4	46.7	-	-
Ling *Molva molva*	2.4	-	1.2	25.0
Monkfish *Lophius* spp.	5.9	44.4	5.4	22.2
Grey gurnard *Eutrigla gurnardus*	-	-	0.4	-
John Dory *Zeus faber*	1.2	-	-	-
Plaice *Pleuronectes platessa*	-	-	0.4	-
Turbot *Scophthalmus maximus*	7.1	-	-	-
Brill *Scophthalmus rhombus*	1.8	-	0.8	-
Megrim *Lepidorhombus* spp.	-	-	0.4	-
Dogfish *Scyliorhinus canicula*	-	-	0.4	-
Lobster *Homarus gammarus*	5.3	-	0.4	-
Crawfish *Palinurus elephas*	18.8	-	2.7	-
Spider crab *Maja squinado*	-	-	62.4	-
Brown crab *Cancer pagurus*	-	-	5.8	-

5.4.2 Net contents versus stomach contents

When all species (commercial and non-commercial in both nets and digestive tracts) were included in the analysis, nMDS plots showed clear distinctions between fish assemblages from fisheries and by-caught seal stomachs (Figure 5.2). Multivariate assemblage structure was similar when including only commercial species in the analysis, suggesting a lack of overlap in fish composition between seal stomachs and fisheries nets. This was tested using PERMANOVA+, which detected significant differences between all stomach and net contents at both sites ($P = 0.001$ in all cases). Of the four sub-adult seals, one stomach from the west coast contained no prey remains and was thus excluded from further analysis. Within the nMDS plots, prey assemblages from sub-adult seals lay within the spread of juvenile seals, suggesting a lack of ontogenetic differences in diet between by-caught juvenile and sub-adult grey seals in this study.

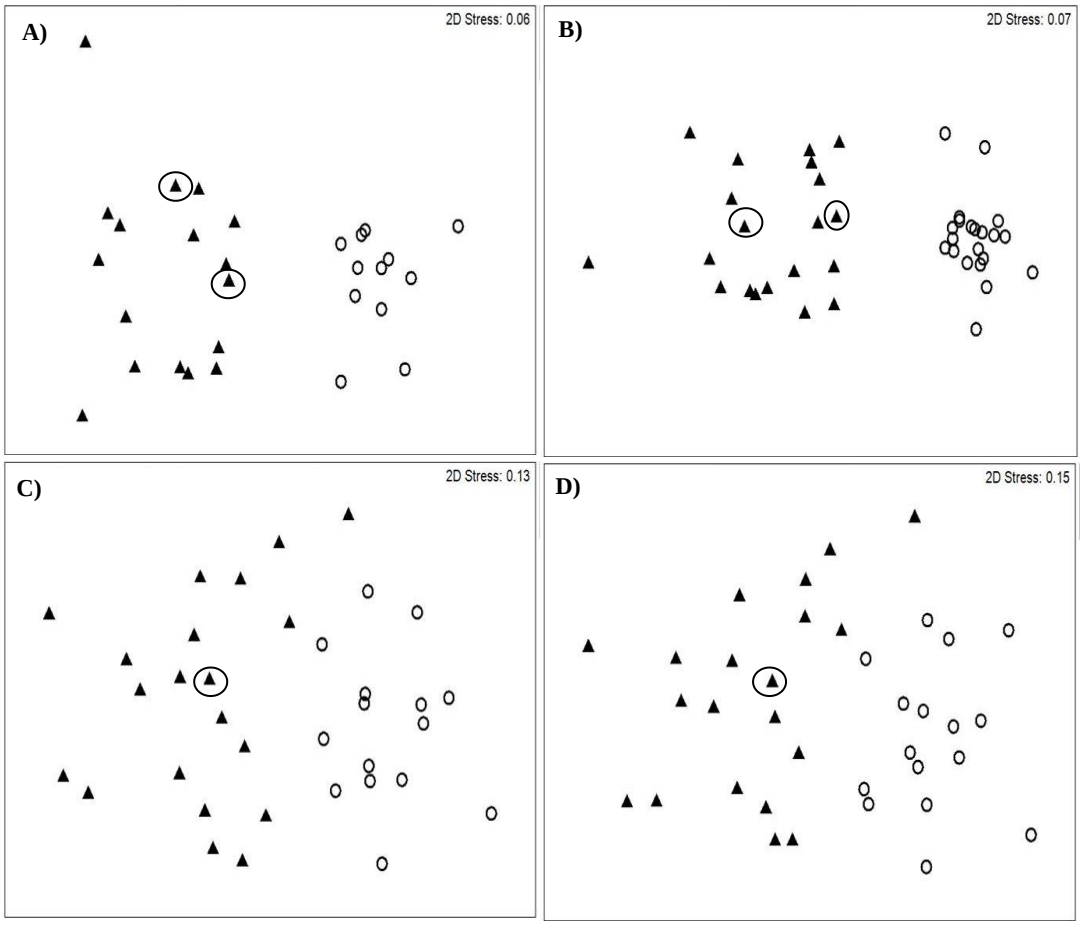


Figure 5.2: nMDS plots showing the multivariate patterns of net versus stomach composition. Closed triangles are from digestive tracts of by-caught seals, open circles are fish assemblages from nets. A,B samples from south coast fishery using a presence/absence and square root transformation respectively, C,D samples from west coast fishery using a presence/absence and square root transformation respectively. Circled points denote sub-adult grey seals stomachs as opposed to juvenile seal stomachs.

The SIMPER routine was run to identify the species responsible for the greatest differences between stomach and net composition. Unsurprisingly, this routinely identified species commonly occurring in nets but rarely occurring in digestive tracts as accounting for the greatest difference. Within both the west and south coast fisheries, depredated species (ling, pollock, monkfish and cod) accounted for large differences between net and digestive tract samples (Table 5.3). On the west coast ling, cod and pollock occurred more frequently in nets than in the diet of seals, while on the south coast, ling, cod and pollock occurred in the diet of by-caught seals, but were rarely recorded in nets. In both sites monkfish was routinely recorded in nets, but was not found in digestive tracts.

Table 5.3: Species accounting for the greatest difference between net and stomach contents along the West and South coast of Ireland. Pres/Abs = Presence/Absence transformation; Square-root = Square-root transformation; Avg. Abund = percentage average abundance of species; %Contrib = percentage contribution to the Bray-Curtis dissimilarity.

West	Pres/Abs: Avg dissimilarity = 93.09			Square-root: Avg dissimilarity = 94.64		
Species	**Stomach Avg. Abund**	**Net Avg. Abund**	**% Contrib**	**Stomach Avg. Abund**	**Net Avg. Abund**	**% Contrib**
Ray *Raja* spp	0.07	0.80	15.32	0.07	1.64	22.36
Cephalopoda	0.64	0.00	13.72	0.96	0.00	14.50
Crawfish *Palinurus elephas*	0.00	0.60	11.10	0.00	0.86	11.70
Pollock/Saithe *Pollachius* spp.	0.21	0.50	9.46	0.21	0.62	8.54
Turbot *Scophthalmus maximus*	0.00	0.40	8.08	0.00	0.47	5.83
Monkfish *Lophius* spp.	0.00	0.45	7.38	0.00	0.47	5.93
Lobster *Homarus gammarus*	0.00	0.35	5.85	0.00	0.39	5.05
Haddock *Melanogrammus aeglefinus*	0.29	0.00	5.28	0.29	0.00	4.22
Cod *Gadus morhua*	0.14	0.20	5.26	0.14	0.20	4.03
Ling *Molva molva*	0.14	0.20	4.79	0.14	0.20	3.80
Brill *Scophthalmus rhombus*	0.07	0.15	3.11	-	-	-
Plaice *Pleuronectes platessa*	-	-	-	0.28	0.00	3.33
Mackerel *Scomber scomber*	0.14	0.00	2.70	0.28	0.00	3.60

South	Pres/Abs: Avg dissimilarity = 97.72			Square-root: Avg dissimilarity = 98.25		
Species	**Stomach Avg. Abund**	**Net Avg. Abund**	**% Contrib**	**Stomach Avg. Abund**	**Net Avg. Abund**	**% Contrib**
Spider crab *Maja squinado*	0.00	0.90	20.17	0.00	2.28	29.25
Ray *Raja* spp	0.00	0.86	18.73	0.00	1.29	17.70
Hake *Merluccius merluccius*	0.33	0.00	7.97	0.40	0.00	5.69
Monkfish *Lophius* spp.	0.00	0.43	7.45	0.00	0.52	6.06
Cod *Gadus morhua*	0.27	0.10	7.27	0.66	0.13	9.55
Brown crab *Cancer pagurus*	0.00	0.43	7.26	0.00	0.53	5.99
Cephalopoda	0.33	0.00	6.66	0.57	0.00	6.89
Ling *Molva molva*	0.20	0.14	5.10	0.20	0.14	3.46
Haddock *Melanogrammus aeglefinus*	0.27	0.05	4.52	0.32	0.05	3.61
Lemon sole *Microstomus kitt*	0.27	0.00	4.36	0.27	0.00	3.01
Pollock/Saithe *Pollachius* spp.	0.20	0.00	2.67	-	-	-

The contribution of depredated species to the overall diet was small when compared with non-commercial small fish species in the diet. Pollock accounted for 14.3 %F in both sites and 0.9 %N, 9.3 %B in the south coast site and 1.7 %N, 6.3 %B in the west coast site. This is not disproportionate when compared to grey seal scat data (n=494) collected over a 5-year period (2009 – 2013) from the southwest coast of Ireland, with pollock accounting for 10.5 %F, 1.0 %N, and 11.1 %B after correcting for partial erosion (see Chapter 3). Cod and ling feature more prominently in the diet of by-caught

seals (Table 5.1) when compared with the larger dataset (1.4 %F, 0.1 %N, 1.6 % corrected biomass; 5.7 %F, 0.4 %N, 2.8 % corrected biomass, respectively) (Chapter 3).

Fish length data were available for the landed catch from the west coast fishery. When possible ($n \geq 4$ individual fish), the length-frequency distributions of all commercial species common to both the fishery nets (with and without by-catch) and seal stomachs from both sites were compared in order to ascertain whether the fishery and by-caught seals were selecting the same fish sizes. Fish lengths from scat data (Chapter 3 & 4) were also included to assess whether by-caught seal prey size range fell within the range for naturally caught prey (assuming that scat contents do not represent systematic contribution from depredated fish) (Figure 5.3). The majority of commercial species recovered from stomachs were smaller than those caught in the nets, and fell within the size range of prey identified from scat analysis. Three pollock (48 cm, 54 cm & 57 cm) and one ling (71 cm) from by-caught seal stomachs did occur within the size range selected by the fishery. However, prey lengths from scat analysis also overlapped to some extent with species sizes caught by the fisheries, particularly in the case of pollock and ling.

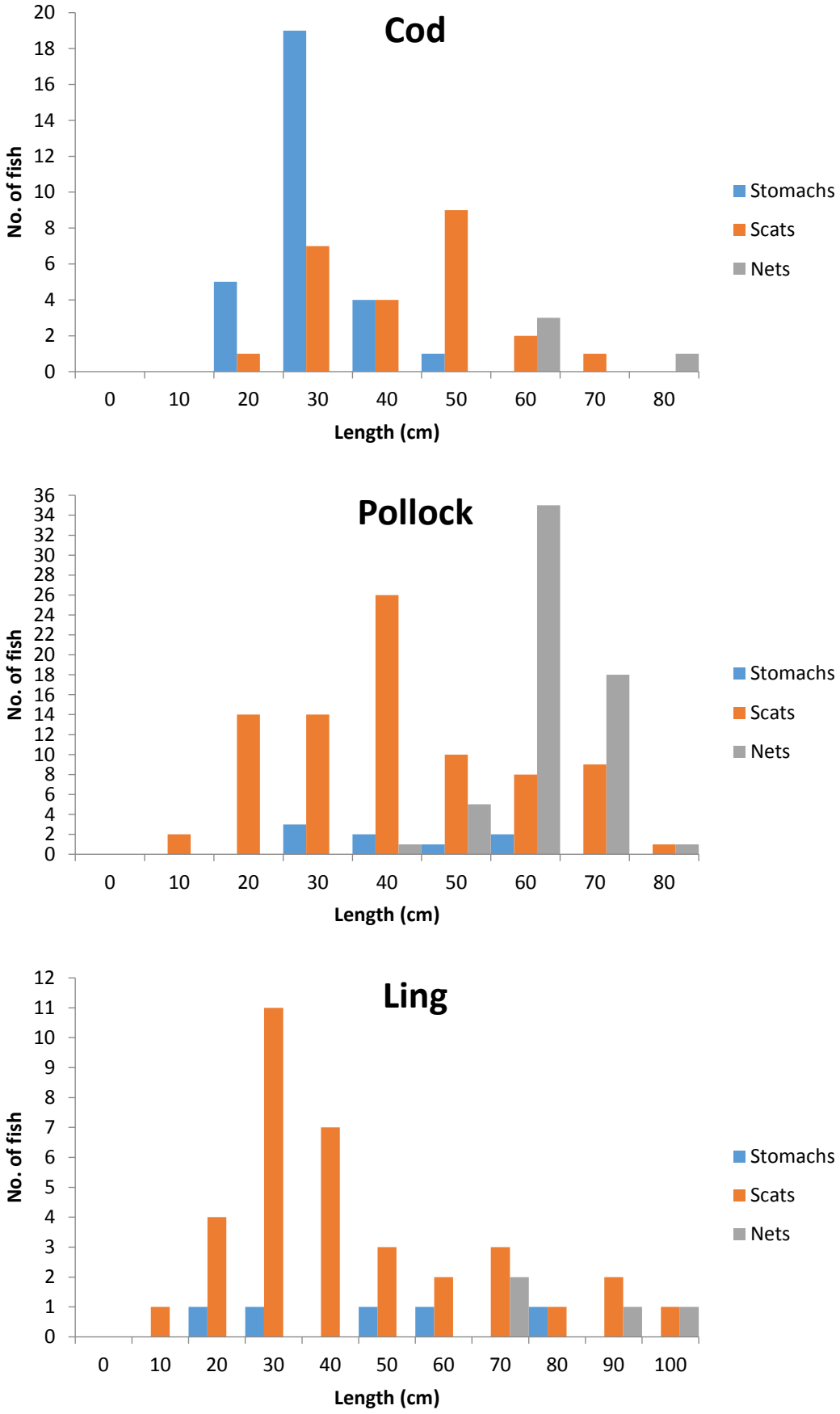


Figure 5.3: Length-frequency distributions of all cod, pollock, and ling recovered from south & west coast seal stomachs, scat analysis (Chapters 3 & 4), and all west coast fishery nets.

5.4. DISCUSSION

While previous studies have demonstrated a low overlap for shared resources between grey seals and specific fisheries in Irish waters (Cronin *et al*., 2012; Houle *et al*., 2015), operational interactions consisting of seal depredation and by-catch are known to be problematic in Irish set-net fisheries (Cosgrove *et al.*, 2013; Cronin *et al.*, 2014; Cosgrove *et al*., 2015; Cosgrove *et al*., 2016). While the latter studies demonstrate high levels of depredation and by-catch in specific fisheries on the west coast of Ireland, it is not evident if these interactions are linked. This study endeavoured to determine whether juvenile and sub-adult by-caught seals were depredating inshore fishing nets in which they were entangled to better understand the nature of these interactions. While similar approaches have been adopted to examine common bottlenose dolphins (*Tursiops truncatus)* fisheries interactions (Scheinn *et al*., 2014), this appears to be the first such study to examine grey seal and static-net fisheries interactions using stomach contents data. Because stomach contents reflect the previous few meals (Pierce & Boyle, 1991), we can test the hypothesis that if depredating nets, by-caught seal stomachs will contain fresh fish remains from species that are also present in the nets.

We found that the by-caught juvenile seals fed on a wide range of prey species, totalling 37 unique taxa, the majority of which were small non-commercial species not caught or landed by fisheries. This wide variety of prey species within the by-caught seal diet reflects the general diet of grey seals observed in studies using prey hard part remains in scat collected at terrestrial sites (Bowen and Harrison, 1994; Hammond *et al*., 1994a; 1994b; Ridoux *et al*., 2007; Gosch *et al*., 2014).

Some commercial species landed by both fisheries were observed in the seals digestive tracts (e.g. cod, pollock, ling). However, many other species not found in the nets occurred in the stomachs of the by-caught seals. Community analysis showed clear distinctions in fish assemblages from seal stomachs compared to fishery nets. This was the case regardless of whether Presence/Absence or Square-Root transformations were applied in the nMDS analysis, or when only commercial species were included in the analysis. Indeed, the SIMPER analysis showed that depredated species such as pollock, ling, cod and monkfish, were consistent contributors to the dissimilarities observed between seal diet and net contents. This suggests that by-caught seals were

not feeding predominantly on net contents, and that natural foraging was also occurring.

Despite overall differences in stomach and net contents suggesting that by-caught seals are not routinely depredating, seals may target particular 'higher value' species in the net. If this is the case then it would be expected that depredated species would be disproportionately represented in the stomachs of by-caught seals, unless by-caught seals are entangled on their first attempt to depredate. Pollock contribution to the diet in by-caught seals was consistent with that of the wider seal population within the same time period, determined through analysis of scats. Cod and ling were over-represented in the stomachs compared to seal scat diet analysis, although it should be noted that the overall contribution of these depredated species to the diet was still small when compared with non-commercial species such as sandeels and *Trisopterus* species. Seal diet is also known to vary both temporally and spatially (Hammond *et al.*, 1994a; 1994b; Brown & Pierce, 1998). The dataset analysed from seal scats was collected off the southwest coast of Ireland, and it is possible that species such as cod and ling are more freely abundant in the areas assessed in this study compared to the southwest coast. However, if these depredated species represent opportunistic encounters with nets, the fish in the stomachs should be the same length as those caught in the nets. To address whether by-caught seals were indeed supplementing their diet with net contents, we looked at the length-frequency distribution of depredated species caught in the nets and compared them to the size of these species found in the stomachs of by-caught seals. All depredated species found within the diet, apart from 3 pollock and 1 ling, were smaller than fish caught in nets, suggesting that the majority of these fish were caught via natural foraging rather than taken from fishing nets. Previous studies have demonstrated that generally grey seals select prey within a narrow size range (Grellier & Hammond 2005; Gosch *et al.*, 2014; Houle *et al.*, 2015; Chapter 3). The three pollock recovered from stomach contents that were consistent with sizes taken by the fishery were also consistent with the size range taken through natural foraging (Chapter 3 & 4). However, it should be noted that of the three pollock recovered from stomachs, one was clearly freshly depredated, while the other two were identified from otoliths in the absence of fresh remains. This suggests that two of the pollock were consumed some time previous to the entanglement. Apart from being consistent with pollock sizes within nets, the head was absent while the

entire body of the fish remained intact, clearly severed below the anterior abdominal vertebrae. This is characteristic of seal damage to farmed salmon (Northridge *et al*., 2013). The soft body of larger fish tend to be targeted by seals with bites either taken out of the belly or the entire soft tail being removed, leaving the heads/hard parts behind in the nets. From the number of depredated fish observed in this study, it is clear that grey seals are depredating large fish from nets, particularly pollock in the west coast fishery (58% of the entire catch) and monkfish in the south coast fishery (67% of the entire catch). The low numbers of depredated species such as pollock, ling and cod identified within the diet of by-caught juvenile seals may be due to the lack of diagnostic structures present in the seals digestive tracts. While juvenile and sub-adult seals may have difficulties swallowing large fish and take bites out of the belly of the fish, the vast majority of pollock depredation occurring in the west coast fishery was characterised by complete removal of the body, leaving the head intact (personal observation). This would have resulted in diagnostic structures being present in the digestive tract if they had been consumed by the by-caught seals. Given that one clearly depredated pollock was detected, we would expect that if by-caught juvenile seals were responsible for the high levels of depredation recorded by the fishery, we would have found more examples of depredation within the digestive tracts than this one example. No evidence of monkfish was detected within the seal stomachs in this study. However, there is a long-standing issue with seal predation on monkfish in the south coast fisheries (Collins *et al*., 1993). It is possible that the by-caught seals in this study did not consume monkfish, or more likely, monkfish was undetected due to a lack of diagnostic structures in the stomachs. The flesh contained within the stomachs of the by-caught juveniles had no diagnostic structures from which to identify the species, an acknowledged limitation to this study. To address this problem, further genetic analysis would be required to determine if the flesh originated from monkfish, either by testing pieces of flesh found within the stomach, or testing the digestive tracts of by-caught seals using species-specific DNA primers (e.g. Méheust *et al*., 2015). However, the time monkfish DNA takes to degrade would need to be taken into consideration and furthermore genetic analyses would not be able to determine if the fish had been depredated or consumed naturally.

While there is currently little evidence to suggest that by-caught juvenile seals in this study were specifically targeting the nets, it is conceivable that juvenile seals can

supplement their diet with the opportunistic removal of fish from nets. Some commercial fish species of sizes similar to those caught by the fisheries and pieces of flesh that may have originated from target species e.g. monkfish, were found within the stomachs of by-caught seals. As 91% of seals in this study were juveniles, lack of built-up fat reserves may lead juvenile seals to apply riskier foraging strategies with the hopes of a larger food reward. One would have expected to have found fresh evidence of depredated fish within the stomachs if the seals had learned how to take fish from nets prior to the by-catch event, particularly if they had previously associated nets with food availability. However, within our sample size of 44 stomachs, only 2 stomachs showed any sign of fresh remains in them, and only one had a clearly depredated fish in a large sample size. This makes it unlikely that over 40 seals all failed to successfully depredate any net contents before becoming entangled if juvenile seals are responsible for the observed depredation levels in the fishery. The fact that these animals are young lends weight to the idea that they are unfamiliar with removing fish without becoming entangled themselves. Those few that do successfully depredate, may go on to become problem seals. Alternatively, juveniles may not have perceived the nets in the water and became entangled while foraging in the same area. There are three major Irish seal breeding colonies located within foraging range of both fisheries used in this study; Inishkea Islands, the Blasket Islands and the Saltee Islands. Both the west and the south coast fisheries operate in shallow to medium depths (<50 m), and telemetry studies conducted on the west coast of Ireland demonstrated that tagged seals primarily undertook dives to the benthos between 40-160 m (Cronin *et al*., 2012; Jessopp *et al*., 2013). This suggests that juvenile seals are likely to be foraging in the part of the water column containing nets, increasing the likelihood of encounters with nets if fishing in the same areas.

We found a definite depredated pollock in the digestive tract of a by-caught juvenile grey seal. While it is therefore conceivable that juvenile seals can supplement their diet with the opportunistic removal of fish from nets, the limited occurrence of definite depredated fish in the digestive tracts, and lack of evidence for indiscriminate, targeted or opportunistic depredation indicates that this cohort are not responsible for the high reported depredation rates. This suggests that other parts of the population such as adult grey seals may be largely responsible for the depredation reported off Ireland's coasts. This may be a learned behaviour and not necessarily true of all adult seals.

Such ‘rogue’ seals are not unusual (Graham *et al*., 2011). The ability to perfect such learned behaviour may have enabled adult grey seals to specialise in the depredation of fishery nets. As adult seals are rarely recovered as by-catch (Cosgrove *et al*., 2013; 2016), it may be their experience around nets has allowed them to remove fish without the risk of becoming entangled.

This study raises important implications for the management of fisheries. Despite the rate of grey seal population increase being less sensitive to changes in juvenile survival (Harwood & Prime, 1978), high juvenile mortality through by-catch (see Cosgrove *et al*., 2016) may still have population level consequences. The implementation of appropriate mitigation measures that reduce both the level of depredation, along with negating the incidence of seal by-catch is necessary. In order to alleviate the seal-fishery conflict, close collaboration is required between researchers, fishers and resource managers. The shift globally towards a multi-species ecosystems approach to fisheries management is encouraging for long-term solutions to the seal-fisheries conflict. In the short-term, modifications to fishing practices and gear offer the best promise of alleviating seal depredation and by-catch. These may include faster hauling speeds or shorter net soak times so as to reduce the amount of time fish are available to passing seals, or gear modifications such as a move away from static nets (Cosgrove *et al*., 2013). While fish traps and fish pots have worked successfully in other areas such as the Baltic (Suuronen *et al*., 2006; Holma *et al*., 2014; Königson *et al*., 2015) they may require seal exclusion devices to reduce by-catch incidents (Königson *et al*., 2015) and thus can be an expensive option, requiring substantial financial investment by fishers with returns not guaranteed over a short time frame (Meek *et al*., 2011). Other options such as the implementation of jigging reels and pollock boards have been suggested, however fishers have reported that these too are subject to depredation. Recent advances in acoustic deterrent technologies, such as target-specific ADDs (which do not seem to affect non-target species such as cetaceans) have proved successful in reducing the numbers of seals around fish farms in Scotland (Götz & Janik, 2014). Food motivation or reinforcement has an accelerating effect on habituation to aversive stimuli (Götz & Janik, 2011), so deterring juveniles before they associate nets with available food may be effective in preventing seals from opportunistic depredation and/or by-catch. Furthermore, robust assessment of by-catch risk, examining the spatial and temporal overlap of seals and specific fisheries,

using telemetry data, seal population data, fishing effort and by-catch data from observer studies would identify key problem areas where future mitigation efforts could be targeted.

CHAPTER 6

General Discussion

6.1 DISCUSSION

Against a backdrop of direct and indirect pressures on marine ecosystems (Lotze *et al*., 2006), effective conservation of species and their habitat requires an understanding of the trophic interactions that drive the functioning of an ecosystem. Information on the diet composition of marine predators can provide an indication of prey species availability in the ecosystem (Meynier *et al*., 2008). These marine predators are susceptible to ecosystem changes and can indicate potential changes occurring in fish stocks (Montevecchi, 1993; Wanless *et al*., 2007), making them useful indicator species of environmental health (Rice, 2003).

Challenges of reconstructing marine mammal diet:

To obtain insights into predator-prey dynamics, diet composition must first be estimated using appropriate methods (Chapter 2). Baseline data on diet composition can be obtained using the standard dietary indices (%N, %F, %B). As has been demonstrated in this study, these indices indicate which prey species are consumed both regularly and infrequently by grey seals in Ireland, which prey species are the largest contributors to the diet, and how prey assemblages differed over time and space (Chapters 3 and 4).

While normally, scat samples are thought to be representative of the animals last few meals, digestion of prey typically occurs 2 – 56 hours after its ingestion, depending on the type of prey and the activity/state of the predator (Tollit *et al*., 2003). However, this may not always be true as smaller prey diagnostic structures may be retained for up to 92 hours within the folds of the digestive tract (Tollit *et al*., 2003). Therefore, one scat sample is not necessarily representative of a distinct meal (Dellinger & Trillmich, 1988; Tollit *et al*., 2003; Casper *et al*., 2006; Lundström *et al*., 2007). Instead, they more likely reflect the diet of the predator over a period of days (Casper *et al*., 2006). While the traditional method of pinniped diet analysis provides quantitative information at a high taxonomic resolution, the approach adopted depends on the questions being asked. Furthermore, the investigator must be aware of several assumptions associated with this methodology, to minimise the biases it produces (da Silva & Nielsen, 1985; Marie & Lavigne, 1986; Pierce & Boyle, 1991; Bowen & Iverson, 2013).

The primary purpose of this study was to provide robust baseline information on the composition of grey seal diet in Ireland. By implementing the "all structures" approach as opposed to the traditional use of otoliths/beaks alone, it is possible to more accurately reconstruct diet. For example, large prey that may have not been consumed entirely can still be quantified if vertebrae are present, and minimum estimates of cartilaginous fish such as rays can be attained. The inclusion of all diagnostic structures clearly increased prey detection (by 31% in fact for all scat samples examined), with a number of fish prey species from each sampling location identified solely through the use of non-otolith structures. Such an increase in prey detection is similar to previous dietary studies incorporating non-otolith structures (Olesiuk *et al*., 1990; Pierce *et al*., 1991a; Cottrell *et al*., 1996; Tollit *et al*., 1997; 2003; Browne *et al*., 2002; Fernandez *et al*., 2009; Hernandez-Milian & Rogan, 2011). Also noteworthy was the increase in cephalopod detection due to the presence of eye lenses, which would support previous findings suggesting large beaks can be regurgitated rather than excreted (Ridoux *et al*., 2007, Lundström *et al*., 2007). If this is the case than there is the possibility that cephalopods are being under-represented within seal diet studies. The presence of these robust structures can facilitate a conservative estimate of cephalopod abundance and frequency within the predators' diet. Inclusion and accurate quantification of prey items in diet composition have important implications for effectively assessing the trophic interactions taking place in Irish waters, particularly if species that would otherwise have gone undetected are of economic value.

As seen in Chapter 2, a limitation to employing the "all structures" method is the lack of published regression equations making prey size reconstruction from non-otolith structures difficult. In the case of Cephalopod beaks, few regression equations are available for the numerous species that exist (e.g. Clarke, 1986, Pierce *et al*., 1993, Santos *et al*., 2007), with weight reconstruction often reliant on generic family level equations. Within this study, family-level regressions and average weights (attained from others of the same species identified within the diet) were used to enable inclusion of prey items with no species-specific regressions for diet estimates. Average sizes were assigned to Cephalopoda prey identified from eye lenses while family regressions were employed for size reconstruction from beaks when no species-specific equations were available. Total Cephalopoda biomass contribution estimates

to grey seal diet in the southwest and southeast coast were 18% and 13%, respectively. Although, Clarke (1985) warns against applying regressions greater than the lowest taxonomic level due to the large degree of variation in body form between cephalopods, the exclusion of many prey items for which size reconstruction is not possible will underestimate this prey group within the diet. Furthermore, given that many large beaks may not be excreted, the use of average sizes and family regressions may negate some of the bias associated with unrecovered beaks in scat samples. Chapter 2 also demonstrated that the use family level regression equations did not significantly alter the biomass contribution of *Trisopterus* and haddock/pollock species to grey seal diet. Furthermore, while average fish sizes attained from Fishbase tended to overestimate prey size, average sizes from calculated from the same species in recovered in the diet increased the biomass contribution of less important prey within the diet.

While these approaches are based on assumptions they endeavour to assign values to all prey items identified within the diet, thus eliminating some of the biases associated with hard part dietary analysis. Given that the alternatives are to either identify all prey to a species level, which is not always possible, or exclude entirely from biomass estimates those prey items for which size cannot be calculated, the application of general equations and average sizes is perhaps better than not using them. It would be extremely difficult to produce regression equations for items such as cephalopod eye lenses and diagnostic structures which are rare in the diet or occur in fragments. However, it would be enormously beneficial for marine mammal diet studies if further work on producing species-specific regression equations for a wider number of Cephalopoda species was conducted, together with creating species-specific regressions for other non-otolith diagnostic structures commonly recovered within scat and stomach samples. As has been demonstrated in this study, published regression equations have the potential to overestimate the size of particular species (e.g. 5-bearded rocklings, *Ciliata mustela*). Furthermore, the lack of available species level regression equations for squid species means that the use of generic and family level equations can underestimate body length when applied to small beaks, and may overestimate weight due to the degree of variation that exists between squid body sizes. Further studies to produce robust species level regression equations for common marine mammal prey species are clearly necessary.

As seen in Chapter 2, application of correction factors is a complex issue and must account for myriad factors such as prey retention times, digestibility of prey species and prey sizes, the amount and type of other species ingested and the size and biological state of the predator (Cottrell *et al*., 1996; Tollit *et al*., 1997; Marcus *et al*., 1998). Applying numerical correction factors to account for complete erosion may however be counterintuitive when using the "all structures" approach to pinniped diet estimation. This is due to the substantial likelihood of increased prey detection even though otoliths may not always be present (e.g. Browne *et al*., 2002; Fernandez *et al*., 2009; Hernandez-Milian & Rogan, 2011; Gosch *et al*., 2014). Applying numerical correction factors to account for digested otoliths may potentially overinflate the biomass of a species if individuals have already been accounted for through the inclusion of other diagnostic structures e.g. sandeels identified from atlas vertebrae or dentaries' etc. (Chapter 2). Furthermore, given that large otoliths are less likely to be completely eroded (Tollit *et al*., 1997), numerical correction factors may potentially overestimate biomass contributions of large prey. Both of the latter issues are of particular concern when estimating biomass contribution of economically valuable fish. In contrast, large otoliths will undergo larger size reductions due to increased exposure to digestive processes (Prime & Hammond, 1990). The application of digestion coefficients to counteract the effects of partial erosion is therefore beneficial when investigating potential overlap in commercial fish sizes selected by seals and fisheries. However, as has been demonstrated in Chapter 2 and other studies (e.g. da Silvia & Neilson, 1985; Browne *et al*., 2002; Laake *et al*., 2002), gadoid biomass contribution increased substantially after digestion coefficient application, while biomass values for most other prey types declined.

Correction factors should theoretically be applied to avoid biases associated with temporal retention and differential erosion (e.g. Bowen, 2000; Grellier & Hammond, 2006; Tollit *et al*., 2007). However, despite the evidence that the "all structures" approach increases prey detection, a comprehensive study on the effects of erosion on non-otolith structures has not been undertaken, but would be useful. Additionally, there remains a large deficit in the availability of correction factors for Octopus species beaks and many correction factors are only available for a limited number of fish species. By only applying correction factors to some prey items identified within the diet and excluding prey for which none are available, this unavoidably introduces

further bias. As demonstrated in Chapter 2, biomass contribution of some species increased/decreased after the application of correction factors, however overall the most important contributors to the diet remained unchanged.

Murie & Lavigne (1986) noted that even within one meal, the degree of structural digestion is random. While the composition of a meal may influence digestion (e.g. mixed/single species, large/small meal), the many variables that affect free-swimming seals such as extended periods of swimming, diving, foraging, fasting, meal size, meal frequency, meal composition, and prey lipid content cannot be comprehensively replicated in captive feeding trials from which correction factors are generated. Due to the many uncertainties surrounding prey digestion, the widespread application of correction factors requires further robust investigations, particularly when analysing the diet of a generalist with a varied diet.

The many limitations associated with the traditional method of dietary analysis, have therefore propelled the advancement of a variety of molecular dietary techniques, each with their own associated advantages and caveats (Tollit *et al*., 2010). Older serological methods, while successful when attempting to detect the presence of certain target species, may not distinguish between several species due to the degradation of proteins during digestion (e.g. Pierce *et al*., 1993). Other techniques such as enzyme-linked immunosorbent assays (ELISA) or those utilising monoclonal antibodies are more accurate and have many advantages. However, drawbacks include the lengthy time delay (up to a year) in order to obtain a suitable clone, in addition to the cost required to produce the antibodies and the difficulties in acquiring specialised tissue culture facilities. Although monoclonal antibodies are rarely used in predation studies due to the aforementioned disadvantages, the potential to screen large numbers of field samples is immense as once created, antibodies can be easily propagated and applied in ELISA (Symondson, 2002).

Based on the identification of DNA fragments from prey species, polymerase chain reaction (PCR) can be used to amplify degraded DNA from homogenised samples and using group-specific primers (Jarman *et al*., 2004; Deagle *et al*., 2005), the DNA is then sequenced and matched with prey DNA contained within a database (Tollit *et al*., 2010). Alternatively, species-specific primers for DNA amplification are relatively inexpensive to design and have also proven successful in dietary studies (Jarman *et*

al., 2002; Casper *et al*., 2007). Many advantages to conventional and real-time PCR techniques exist (e.g. Purcell *et al*., 2004; Parsons *et al*., 2005; Wright *et al*., 2007; Matejusová *et al*., 2008; 2012), however DNA degradation, the lack of quantitative information on prey species contribution to the diet, and the associated expense are still fundamental drawbacks to using DNA based techniques.

Within marine mammal and seabird diet studies in particular, stable isotopes to determine trophic ecology has been used extensively (Abend & Smith, 1997; Burns *et al*., 1998; Kelly, 2000; Kurle & Worthy, 2001; Sunderland *et al*., 2005; Hammill *et al*., 2005; Hückstädt *et al*., 2007; Aubail *et al*., 2011; Stauss *et al*., 2012; Mèndez-Fernandez *et al*., 2012). While this method supplies information on long-term diet enabling the detection of temporal dietary trends (e.g. Hall-Aspland *et al*., 2005), it is often restricted to coarse taxonomic resolution of prey and subject to many variables (Tollit *et al*., 2010; Pompanon *et al*., 2012). Prior knowledge of baseline isotopic values in the study system is required and of most relevance to predator diet studies, and quantitative estimates are typically not achievable unless prey species consist of three or less (Bowen & Iverson, 2013).

Another widely used method of marine mammal diet estimation is fatty acid profiling (Koopman *et al*., 1996; Møller *et al*., 2003; Walton & Pomeroy, 2003; Bradshaw *et al*., 2003; Ridoux *et al*., 2007; Kavanagh *et al*., 2010), with the latest development of quantitative fatty acid signature analysis (QFASA) also enabling count data to be derived (Iverson *et al*., 2004; Beck *et al*., 2007; Nordstrom *et al*., 2008; Bromaghin *et al*., 2016). However, similar to the previous techniques, caveats exist when using QFASA. It requires previous knowledge on the diet of the predator (Bronaghin *et al*., 2016) with sufficient numbers of prey species previously sampled in the same manner as they are consumed (Iverson *et al*., 2004; Budge *et al*., 2006), otherwise multiple species with similar signatures can lead to a degree of confounding among prey results (Bronaghin *et al*., 2016). This is particularly true when investigating the diet of a predator which contains a diverse array of prey species, as there is an increased risk of inconsistent estimates and misclassifications (Tollit *et al*., 2010). However, while the time period of integration for only a few species has been thoroughly investigated, both qualitative and quantitative predator dietary information can be obtained regarding the most recently consumed meals using blood samples (Cooper *et al*.,

2005), or regarding meals consumed over a period of weeks to months from adipose tissue stores (Iverson *et al*., 2007).

General diet of grey seals in Ireland:

Grey seals in Ireland exhibit a varied diet, feeding on a wide range of prey species. This study (Chapters 2, 3, and 4) suggests that grey seals in Irish waters display a generalist feeding strategy, in line with findings from other studies across the species range in the Northeast Atlantic (Benoit & Bowen, 1990; Hammond *et al.*, 1994a; Bowen *et al*., 1993; 2006; Austin *et al*., 2006; Svensson, 2012; Smout *et al*., 2014). From all samples analysed a minimum of 63 prey taxa were identified, although only a few prey species occurred in high abundances and frequencies in the diet. These consisted of sandeels, *Trisopterus* species, and to a lesser extent, dragonets. Other prey groups of considerable importance to the diet in terms of biomass included haddock/pollock species, whiting, flatfish, and Cephalopoda. The general reliance of grey seals on seven particular types of prey is consistent with findings by Matthiopoulos *et al*. (2008) who analysed grey seal diet data from several previous studies (see Hammond & Prime, 1990; Prime & Hammond, 1990; Hammond *et al*., 1994a; 1994b; Hall *et al*., 2000).

Although stomach sample sizes were smaller than scat sample sizes and stomach contents represent a shorter period of prey retention time, within the grey seals diet there were broad similarities in key prey biomass contributions across study sites. Key prey such as haddock/pollock species varied only slightly from 13% biomass within the diet off the west coast of Ireland to 18% biomass within samples collected from the southeast site. *Trisopterus* contribution to biomass within the seals diet was at its lowest within west coast samples (5%) and at its highest in south coast stomach samples (19%), while sandeel biomass contribution ranged from 1% in the south coast diet to 11% biomass in the diet at the southwest site. Cephalopoda biomass contribution to grey seal diet was at its minimal at the southeast site (8%B) and increased steadily reaching its highest value within the west coast diet (18%). Amongst this class, octopus species were the largest biomass contributors (5-9%) in all sites apart from the southwest where squid species were more important to the diet in terms of biomass (6%).

The overall diet composition in this study is broadly similar to many dietary studies conducted on grey seals in the North Atlantic (e.g. Pierce *et al*., 1990; Hammond & Prime, 1990; Hammond *et al*., 1994b; Bowen & Harrison, 1994; Harvey *et al*., 2012), although quantities of particular prey species varied and *Trisopterus*, whiting and haddock/pollock species as opposed to cod were the dominant gadoid species within the Irish diet (e.g. Prime & Hammond, 1990; Hammond *et al*., 1994a).

Temporal and spatial variation in grey seal diet:

Grey seal diet in Ireland displays characteristics typical of the species right across its range, in so far as significant regional, seasonal, and annual variation in diet occurs (Chapters 3 and 4; Hauksson, 1984; Hauksson & Bogason, 1997; Prime & Hammond, 1990; Benoit & Bowen, 1990; Hammond & Prime, 1990; Pierce & Boyle, 1991; Hammond *et al*., 1992; Murie & Lavigne, 1992; Bowen *et al.*, 1993; Hammond *et al*., 1994a; Hall *et al*., 2000; Walton and Pomeroy, 2003; Hammond & Grellier, 2006, Hammill *et al*., 2007). Spatial and temporal variation exhibited in seal diet is presumed to be a result of prey species abundance in areas close to seal haul-out sites (Prime & Hammond, 1990; Hammond *et al*., 1994a; Hall *et al*., 2000; Walton and Pomeroy, 2003). Previous tagging studies in southwest Ireland identified that most grey seal foraging trips were within 50 km of the haul out site (Cronin *et al*., 2013). The high site fidelity demonstrated by grey seals as a consequence of needing to return to haul-out sites to rest, means that access to offshore habitat may be limited (Matthiopoulos *et al*., 2008).

As was demonstrated from scat samples collected in this study, grey seal prey assemblages and their relative contribution to the diet varied significantly between regions (Chapter 4). Diet appears to be associated with habitat and substrate type in the region of the haul-out sites, with differences in prey abundances in the diet presumably related to prey availability in each region. This was demonstrated by the high abundance of pelagic species in the diet of grey seals using the southwest haul-out site, compared to the southeast site. The prevalence of pelagic prey in the diet of seals using waters off southwest Ireland is not surprising given the relative proximity of the haul-out site to the shelf edge and open water. Conversely the sandy and course sediments of the Irish Sea support demersal and benthic prey assemblages, e.g. flatfish

and rays, that were found in higher abundances within the diet of seals utilising the southeast coast haul-out site, than in the diet of seals from the southwest coast

While particular prey such as sandeels and *Trisopterus* species were consistently present in substantial quantities within the diet, grey seal diet varied seasonally and inter-annually. For example, Cephalopoda and dragonets were of greater importance during spring, blue whiting were larger contributors to the diet in the summer, while flatfish formed a major component of grey seal diet in the autumn. Haddock/pollock species appeared to be most important in grey seal diet during winter months, which is consistent with findings from Hammond *et al*. (1994a) and Pierce *et al*. (1990) who also found that the presence of large gadoids in the diet increased towards the end of the year.

Inter-annual differences displayed in the diet were primarily as a result of variations in the relative abundances of sandeels and *Trisopterus* species in the diet between years. When abundances of these species were low in the diet, the contribution of other prey taxa experienced noticeable increases. For example, sandeel abundances were lower in the diet of seals hauling-out on the southwest coast of Ireland in 2010 compared to subsequent years, while *Trisopterus* species quantities was lower than experienced in previous years. Instead blue whiting abundances were at their highest within the entire diet during summer 2010. Sandeel abundances then increased reaching a peak in summer 2012 before reaching pronounced lows in winter 2012 to winter 2013 (with a brief increase only in spring 2013). Winter 2012 instead saw haddock/pollock species reaching their highest abundances in the diet while their prevalence in the diet was at its second highest during winter 2013. Such prey switching in the diet of grey seals has previously been recognised (Hammond *et al*., 1994a; Smout *et al*., 2014).

Subtle shifts in spawning/migration timings and climate induced changes in species distributions may account for some of the seasonal and yearly variations of prey abundances exhibited in the seals diet in Ireland. Variability in blue whiting spawning distribution and migration route in the Northeast Atlantic has been reported and attributed to changes in the circulation strength and extent of the sub-polar gyre (Hátún *et al*., 2007). Both *Trisopterus* species and sandeels were found in the highest abundances in the diet of grey seals in southwest Ireland. An increase in *Trisopterus*

species on Irelands north and west shelf over the last decade has been recorded (Lynam *et al*., 2010). Northward shifts of *T. minutus* and southward shifts of *T. luscus* in the North Sea have been attributed to potential climate change (Dulvy *et al*., 2008) and may similarly be responsible for the observed increases in *Trisopterus* species experienced in Irish waters. Sandeel recruitment has also been linked to the influence of warmer waters on plankton abundance (Frederiksen *et al*., 2004). However, while climate change has been linked to changes in fish abundances in Irish waters (Pinnegar *at al*., 2002), with no reliable baseline data on grey seal diet from this region it is impossible to assess any climate related impact on the diet of this top predator over the longer term.

While this study has attempted to relate prey composition to the habitats surrounding the sampling sites, it is not currently possible to definitively state that higher prey species abundances in diet is a direct result of their availability. Similarly, increased temporal abundances of particular prey in the diet is assumed to be due to an increase in their availability. Findings from a harbour seal study conducted in Skagerrak and Kattegat found that not all abundant species were consumed by seals, either due to avoidance or inability to catch them (Härkönen, 1987). The prevalence of sandeels and *Trisopterus* species over other prey types in the diet be as a result of these species being more locally abundant. Alternatively, the high abundances of these prey species in the diet may also be as a result of seals operating according to optimal foraging theory, however without measuring the swim speed of seals while foraging and those of their prey this is difficult to infer. Studies by Onsrud *et al*. (2005) indicate that *Trisopterus* have slower swimming speeds than fish such as whiting, herring and sprat, while underwater camera observations by Kubilius & Ona (2012) suggest sandeels typically swim at low speeds. Additionally, both taxa are energy rich prey with higher nutritional values (approximately 1100 kcal kg^{-1}) relative to gadoids such as haddock, pollock, and whiting (less than 800 kcal kg^{-1}) (Wilson *et al*., 2002). Grey seals may therefore receive a higher reward while expending less energy if foraging for sandeels and *Trisopterus* species over lower energy and/or faster moving prey species. This may also explain why lower quantities of oily fish such as mackerel and herring (Murray & Burt, 1977) were recovered in the diet of grey seals in this study compared with abundances of sandeels and *Trisopterus*. It would also support the theory suggested by Armstrong (1999) that seals may find it difficult to catch schooling

shoals of fish off the seabed. Further studies in the area of prey availability and predator/prey swimming speeds are clearly necessary to determine the drivers behind grey seal prey selection.

Seal-fishery interactions:

Seal-fishery interactions comprise indirect biological interactions, where both seals and fisheries compete for shared resources away from nets, and direct operational interactions, where seals become entangled, or damage fishing gear and/or catch.

Grey seal abundance has increased in recent decades across their entire range in the North Atlantic (Ridoux *et al*., 2007; Thomas, 2011; Kauhala *et al*., 2012; Ó Cadhla *et al*., 2013; Waring *et al*., 2014). It is conceivable that the increase in grey seal abundance in Ireland may be contributing to the increase in seal-fishery operational interactions reported in Ireland (Cronin *et al*., 2015; Cosgrove *et al*., 2015; 2016). Such a correlation has been demonstrated in other parts of the species range e.g. the Baltic Sea (Oksanen *et al*., 2015). A number of studies have also linked the increase in grey seal population abundance to the failure of cod stock recovery in certain areas across the north Atlantic, with increased natural mortality a direct result of grey seal predation (Cook *et al*., 1997, 2015; Trzcinski *et al*., 2006). Seal-fishery interactions along the Irish coast is of growing concern, in particular direct interactions at the nets where high levels of depredation of valuable commercial species (up to 50% of the catch) have been recorded (Collins *et al*., 1993; Wickens, 1995; Cronin *et al*., 2013; Cosgrove *et al*., 2015). Interestingly modelling studies, using size- and trait-based dynamic marine community models, as well as the data presented in Chapter 3, suggest seals in southwest Ireland are not competing with fishers for commercial fish stocks (Houle *et al*., 2016), unlike other parts of their range in the North Atlantic (Cook *et al*., 1997; Trzcinski *et al*., 2006; Königson *et al*., 2007; Swain & Benoît, 2015).

Telemetry studies have demonstrated relatively low spatial overlap between grey seals and an offshore whitefish trawl fishery off the west coast of Ireland (Cronin *et al*., 2012). However, in the Celtic and Irish Seas, overlap between seals and passive fisheries were significantly higher (Cronin *et al*., 2016) suggesting seals are potentially targeting passive or set-net fisheries (e.g. gill nets, tangle nets, trammel nets), or the areas in which they operate. Oksanen *et al*. (2014) showed how Baltic grey seals and

trap-net fisheries overlapped both spatially and temporally, and suggest that such intensity of overlap may be as a result of high site fidelity demonstrated by grey seals. Previous studies have also demonstrated concentrated movements of grey seals within small areas close to haul-out sites (McConnell *et al*., 1999; Sjöberg & Ball; 2000). However, high levels of depredation have been shown to occur within an offshore gillnet hake fishery off the southwest coast of Ireland (Cosgrove *et al*., 2015) suggesting that grey seals in this region do not necessarily remain close to their haul-out sites.

Within the current study juvenile grey seals in particular experienced high rates of by-catch within inshore fisheries, which is consistent with previous by-catch findings (e.g. BIM, 1997; Cosgrove *et al*., 2016). The study sites were located within foraging range of the three largest grey seal breeding colonies in Ireland. While it is possible that remaining close to their haul-out sites would have brought juvenile seals into contact with the passive set-net fishing gear, telemetry studies have shown that juvenile grey seals often range much further than adults on exploratory trips (McConnell *et al*., 1984; Sjöberg & Ball; 2000). However, high incidents of by-catch are evidence that juvenile grey seals do regularly come into contact with set-net gear. It is conceivable that they may be attracted to the nets as a result of the chemical detection (taste) of the fish caught in the nets. It is also therefore possible that given their inexperience, juveniles may become entangled while trying to opportunistically remove these fish from the nets. However, results from this study indicate that this is not the case. Instead it appears that juveniles either do not perceive nets in the water as they swim past or do not recognise the danger they pose.

Results from the forty-four by-caught grey seal stomach samples examined in Chapter 5 indicate that juvenile seals are not indiscriminately depredating fishing nets, with significant differences between prey assemblages within nets and seal diet apparent. They also did not appear to target specific species in the nets, with commercial fish occurring in relatively low abundances within the seals diets from both sites. Indeed, only one stomach contained clear evidence of a depredated fish whilst just two stomachs contained fresh remains of flesh. Fish sizes reconstructed from hard-parts recovered from the stomachs indicated that by-caught juvenile grey seals were generally selecting prey below the sizes targeted by the fisheries in question, with only four fish of economic value overlapping in size with those selected by the fisheries.

By-caught grey seals in this study fed predominantly on smaller fish species with a large proportion of these being of non-commercial origins, suggesting that this cohort at least may not be contributing to the high levels of depredation reported by the Irish fishing industry (Cronin *et al*., 2014). However, although fish species targeted by the fisheries did not occur in high abundances within the diets of the by-caught seals from both the south and west coast sites, stomach contents identified using hard-part analysis cannot account for prey which may not have been consumed in its entirety. This is quite likely the case with certain species such as monkfish, where seals will seldom eat the head, therefore diagnostic structures such as otoliths will not appear in the stomach and monkfish depredation at the net may go un-recorded or under-estimated. Therefore, to definitively confirm that depredation of target species such as monkfish and pollock had not occurred, further analysis of stomach contents using molecular methods for identifying target prey is required (e.g. Méheust *et al*., 2015). However, flesh removed by the seals would remain undigested within the stomach had the by-caught seals recently depredated the nets, and little flesh was present within the stomachs examined in this study.

It is therefore probable that another cohort of grey seals is responsible for the high levels of depredation reported. Adult seals may have learned to forage successfully with experience enabling them to remove fish from nets without becoming entangled themselves. Within this study, three adult grey seals were by-caught on three separate occasions, however due to their weight, they fell out of the nets as they were being hauled aboard (*pers. obs*.). If adults are indeed targeting larger commercial fish, this would support finding by Lundström *et al*. (2010). The authors demonstrated how Baltic grey seal diet composition varied significantly between juveniles (<2 years) and adults, with juveniles similarly feeding primarily on small non-commercial species, and adult diet characterised by large commercially important fish species. Furthermore, a study by Beck *et al*. (2007) using QFASA, identified juvenile grey seals as being less selective with regards to prey type, with the authors suggesting this cohort may be naïve predators.

While this may also be the case in this study, it is not possible to establish if the observed small fish prey sizes in this study is juvenile specific, as there are insufficient by-caught adult seals for robust comparison. Furthermore, as mentioned, molecular methods to examine by-caught seal stomach contents is still required to conclusively

rule out depredation of monkfish by juvenile seals. However, data from scat analyses (Chapter 3 & 4) suggests grey seals using haul-out sites in southwest and southeast Ireland are generally not selecting fish of commercial size, with the exception of pollock/haddock. Assuming that scat samples represent the diet of a mixed colony (i.e. adults and juveniles), and all types of foraging (i.e. natural and some depredation), the larger fish individuals may be reflective of adult grey seal prey selection. However, even within scat samples, economically valuable fish species occurred in relatively low abundances in the diet (≤ 3%N, each). Therefore, dietary analysis from this study suggests grey seals in Ireland are taking small quantities of economically valuable fish and are selecting sizes smaller than those targeted by the commercial fisheries.

Bowen *et al.* (1993) reported that 80% of certain economically valuable species identified within grey seal diet from the west Atlantic were within commercial sizes, the authors attributed it to variations in the seasonal energy requirements of seals and suggest that most gadoids consumed are typically pre-recruits to fisheries. Therefore, while results from this study suggest that some resource overlap between grey seals and fisheries occurs, given the low quantities consumed by seals, the extent of resource competition should remain minimal provided the status of these fish stocks remain favourable.

Houle *et al.* (2016) suggests that grey seals tend to target lower trophic level species which are both more productive and abundant. This is consistent with the findings of Morissette *et al*. (2012) who demonstrated that the global trophic level of marine mammal prey species is significantly lower than that of trophic levels targeted by fisheries, inferring that they were not significant competitors for shared resources. It has been demonstrated that the wider the range in a predator's diet preference, the more they increase overall biomass within an ecosystem by inducing beneficial predation i.e. by keeping in check potential predators or competitors (Parsons, 1992). Therefore, seals which actively select smaller lower trophic level prey species, may theoretically be of an indirect benefit to fisheries by removing smaller fish species which compete with juveniles of large commercial species (Houle *et al*., 2013).

However, the phenomenon of "fishing down the food web" has seen a shift in global fishery landings from large piscivorous fish toward smaller meso-consumers and invertebrates (Pauly & Palomares, 2005). If such shifts in fishery target species

towards lower trophic level species continue, this may result in an increase in competition between marine mammals and fisheries in the future. Furthermore, according to foraging theory, "depression" of a prey population through exploitation by predators may lead to a reduction of that natural resource within a region (Charnov *et al*., 1976). Pinnegar *et al*. (2002) revealed a decline in mean trophic level of fish communities as a result of intensive fishing and long-term climate variability within the Celtic Sea, including off the southwest coast of Ireland. If both seals and fisheries are targeting similar trophic level species, then a reduction in their availability due to species being "depressed" could also potentially result in a rise in operational interactions between seals and fishers in Ireland.

Robust knowledge on the status of local fish stocks and rigorous management plans for commercially valuable species is imperative when dealing with stocks that are of importance to the wider ecosystem. The status of many fish species that occur regularly in the diet of grey seals are data deficient within Irish waters. Whiting by-catch and discarding within the Irish and Celtic Sea, is a serious issue (Borges *et al*., 2005; Enever *et al*., 2007), although recent reform of the EU Common Fisheries Policy aims to significantly reduce discarding of commercial species. Indications are that in the Irish Sea, the present stock size of whiting is particularly low with noticeable declines in relative spawning stock biomass and landings (Marine Institute, 2015). Whiting was an important contributor to the diet of grey seals that haul-out in southeast Ireland. Thus an ecosystems approach to managing this fishery in the Irish Sea is necessary given its importance as a prey species to higher predators such as seals and cetaceans and its vulnerability as a discard species within the *Nephrops* fishery.

To date, there is no management plan for any of the skate/ray stocks within the Irish Sea, where certain ray species are commercially targeted. Though some survival is known to occur, rays constitute a high proportion of discards in trawl and gill-net fisheries within the Irish Sea and Celtic Sea but very little data are available on the level of discarding. Both *Raja montagui* and *R. brachyura* appear to be overexploited in these regions (Marine Institute, 2014). Over-exploitation has already led to the local demise of one species of ray in the Irish Sea, the common skate (*Dipturus batis*). A study by Dulvy *et al*. (2000) has also demonstrated local disappearances of long-nosed skate (*D. oxyrhinchus*) and white skate (*Rostroraja alba*) within the Irish Sea, Bristol channel and northeast Celtic Sea. Alarmingly, declines in ray species can often go

unnoticed for decades (Brander, 1981; Dulvy *et al*., 2000). Benoît *et al*. (2011) hypothesised that grey seal predation may explain the elevated natural mortality observed among winter skate (*Leucoraja ocellata*) in the southern Gulf of St. Lawrence. Given the presence of relatively high numbers of *Raja* species within scat samples in this study collected from the southeast coast (with abundances conservatively estimated) it is advisable that further diet studies be conducted to facilitate annual seal consumption rates on rays and biomass removal estimates. Rays in general are slow growing, mature at a high age and have low fecundity (Brander, 1981). Overexploitation by fisheries may already have led to recent noticeable declines in other larger ray species in the Irish Sea (Dulvy *et al.*, 2000), and seal predation may potentially be a source of elevated naturally mortality that has not been considered.

Stock assessment of fish species in Irish waters is temporally patchy, inconsistent and lacking in fine geographic scale resolution for certain species. Furthermore, the Irish Groundfish survey which generates the current information used in fish stock assessments, is limited spatially, and occurs only along the northwest to the southwest of Ireland, and is conducted annually during autumn months. The implementation of frequent robust stock assessments in all Irish waters would allow long term monitoring of status trends in fish stocks, and would provide the data necessary to assess competition between seals and valuable commercial fish species. Additionally, long term analysis of seal diet could be compared with stock assessment data to evaluate whether there is a correlation in predator diet and prey availability over time. Indeed, Wilson *et al*. (2002) demonstrated how harbour seal (*Phoca vitulina*) diet in Dundrum Bay, northeast Ireland reflected survey data of commercial species within that area. Given that the ecosystems approach to fisheries management promotes sustainable fishing within a greater ecosystem, seals could be used as sentinels for ecosystem health as has been previously suggested (Aguirre & Tabor, 2004; Moore, 2008). Close monitoring of seal diet could provide indications of instability within the ecosystem. Just like fledgling success of kittiwakes (*Rissa tridactyla*) is used as an indicator of sandeel stock status in parts of the North Sea, an overall reduction of large piscivorous fish (e.g. haddock/pollock) and key prey in grey seal diet (e.g. sandeels and *Trisopterus* spp.) could be reflective of the status of fish stocks off the coast of Ireland.

6.2 CONCLUSIONS AND FUTURE RECOMMENDATIONS

Food consumption estimates of predators are based on several variables (see review in Pierce & Boyle, 1991), and require accurate prey biomass descriptions. Errors in biomass estimations associated with biases pertaining to the traditional method of diet analysis can be misleading if using those data for modelling predator-prey interactions, and have potentially significant consequences in the context of assessing predator-fishery resource competition.

A single faecal sample may contain vast quantities of bones from various species which may also be substantially degraded due to chemical abrasion. Subtle differences in diagnostic features can easily result in the incorrect identification of prey, however if recognised they can help differentiate between species. Therefore, familiarisation with bone fragments, advanced taxonomic training, access to a very good reference collection, reference guides, published regression equations, and considerable expertise are a necessity when reconstructing pinniped diet.

Feeding trials dedicated to specifically cataloguing the effects of erosion on various diagnostic structures would allow regression equations and correction factors for non-otolith structures to be generated, and would help to reduce the bias towards those species for which published regressions and correction factors exist. However, feeding trials should ideally be designed to mimic the activity state of seals in the wild, and to date, no such facility exists.

Within marine mammal diet studies, no one investigatory approach will offer all the information, and each method has its own associated limitations. Newer sophisticated DNA based techniques are being created and refined (e.g. Kaneko & Lawler, 2006; Rothman *et al*., 2009; Deagle *et al*., 2009; Pompanon *et al*., 2012; Méheust *et al*., 2015) and these offer real potential for future predator diet studies. Similarly, QFASA has proven reasonably successful when estimating diverse diets of pinnipeds and seabirds, albeit with corroborated data from other methods of dietary analysis (Iverson *et al*, 2004; 2007; Beck *et al*., 2007; Nordstrom *et al*., 2008). The ability to gather integrative information from stable isotopes over long time frames is also advantageous when used in conjunction with other techniques that provide higher

taxonomic detail regarding recently ingested meals e.g. DNA-based methods, and/or traditional hard part analysis (Tollit *et al*., 2010; Pompanon *et al*., 2012).

Therefore, to accurately investigate marine mammal diet, a suite or combination of methods is ideally required. For example, in depredation studies, genetic based techniques alone could not provide information on the size of fish consumed to determine whether prey is likely to have been actively depredated, or whether it represents smaller fish (below the sizes caught by the fishery) consumed via natural foraging. Thus using genetic techniques alone may produce misleading conclusions given that this study suggests juvenile by-caught seals are selecting pre-recruits to commercial fisheries and scat samples indicate for the most part grey seals target smaller size classes of non-commercial species. To accurately estimate marine mammal diet, molecular tools should therefore be used in tandem with conventional dietary hard part analysis, so as to produce informed high resolution qualitative and quantitative diet descriptions.

The relatively high by-catch mortality of juvenile grey seals in specific fisheries in Ireland, in particular the tangle-net fishery for crawfish off the mid-west coast. (Cosgrove *et al*., 2016) is concerning and may pose a threat to the conservation of this species particularly around major breeding colonies. Additionally, the increasing issue of depredation of catches by grey seals in certain passive fisheries urgently requires mitigation measures to be developed and implemented, which will ideally reduce both by-catch and depredation. If adults grey seals rather than juveniles are responsible for the majority of depredation events, then this has important implications for conservation and mitigation measures. Targeted measures to reduce juvenile by-catch, with additional measures to mitigate against depredation by adult seals would be required. Smaller mesh size, improved net visibility as well as reintroduction of pots have major potential to mitigate seal by-catch in the tangle net fishery, whilst acoustic deterrents have potential to reduce both depredation and bycatch (Cosgrove *et al*., 2015; 2016). Much work has been conducted in the Baltic Sea to combat seal-fishery interactions, with mitigation tools working to varying degrees (Lunneryd *et al*., 2003; Lehtonen & Suuronen, 2004; 2010; Hemmingsson *et al*., 2008). For example, a novel device (seal sock) tested by Oksanen *et al*. (2015) demonstrated a 70% reduction in ringed seal (*Phoca hispida*) bycatch mortality, yet only 11% of grey seals survived when the seal sock was deployed. Graham *et al*. (2011) suggests that selective

removal of problem seals may be a focused method of mitigating seal induced catch damage, particularly if only a low number of individuals specialise in depredating nets and display foraging site fidelity. The refinement of seal exclusion devices that successfully prevent seals entering cod pots while simultaneously generating higher catches have proven successful in the Baltic (Königson *et al*., 2015), however such devices/cod pots are unlikely to be used by the industry in Irish waters, as their efficiency is apparently habitat and species specific (P. Tyndall, BIM *pers. comm*.). The development of species-specific targeted acoustic deterrent devices (e.g. Götz & Janik, 2014) offer high potential in Irish waters for mitigating against seal-fishery interactions at nets, with research currently underway.

By adhering to management plans which safeguard sustainable fishing effort and establishing robust plans for those species for which none exist so far, the real or perceived threat of competition over shared resources between seals and fisheries can be reduced. Furthermore, robust monitoring of seal diet with comprehensive sampling over multiple seasons at multiple sites/colonies will enable the determination of temporal and spatial trends in diet, enhancing our understanding of resource competition and the role this top marine predator plays in the marine ecosystem.

Key findings:

- Grey seals in Ireland exhibited high levels of seasonal, inter-annual and regional variation in diet
- The diet was characterised as containing a wide range of prey species
- Gadoids (particularly *Trisopterus*, haddock/pollock and whiting), flatfish, sandeels and Cephalopoda were the main biomass contributors to the diet
- Most prey consumed by grey seals were of non-commercial origins and occurred in small sizes
- Commercially important fish species were found in low abundances within the diet suggesting low levels of direct competition between seals and fisheries
- Sizes of commercial species in the diet were generally pre-recruits suggesting potential indirect competition between seals and fisheries
- There was little evidence that by-caught juvenile grey seals were depredating nets
- Additional correction factors and regression equations for more species and non-otolith structures are required to minimise biases in diet estimations
- A combination of traditional hard-part and molecular techniques have the greatest potential to account for biases in diet estimation

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Appendix I: Regression equations used to reconstruct prey length and weight from sources (S). FL = total length of fish (mm), FW = total fish weight (g), DML = total dorsal mantle length (mm), BW = total cephalopod body weight (g), OL = otolith length (mm), OW = otolith width (mm), PMXHH = premaxilla head height (mm), PMXHL = premaxilla head length (mm), PMXL = total length of premaxilla, PMXAH = premaxilla articular height, VL = vertebra length (mm), LRL = lower rostral length (mm), LHL = lower hood length (mm). Sources are as follows: Ba = Bayhan *et al*. (2008), Be = Bedford *et al*. (1986), Bo = Bowen & Harrison (1994), Br = Brown & Pierce (1998), Cl = Clarke (1986), Co = Coull *et al*. (1989), Fr = Froese & Pauly (2015), Hä = Härkönen (1986), İl = İlkyaz *et al*. (2010), La = Landa & Piñeiro (2000), Le = Leopold *et al*. (1998), Mo = Moutopoulos & Stergiou (2002), Pe = Pereda & Villamor (1991), Ro = Robson *et al.* (2000), Sa = Santos *et al*. (2007), Sn = Santos *et al*., 2001, Su = O'Sullivan *et al*. (2003), Tu = Tuset *et al.* (2008), Wa = Watt *et al*. (1997).

Fish species	Estimated prey length (mm)	S	Estimated prey weight (g)	S
Rays *Raja* spp.	Estimated from literature		FW = 0.00187 (FL/10) ^ 3.173	Fr
Eels Anguilliformes	FL = (0.1+15.04 (OL/2))*10	Su	FW = 0.0002 (FL/10) ^ 3.509	Sa
Conger eel *Conger conger*	FL = (0.1+15.04 (OL/2))*10	Su	FW = 0.0002 (FL/10) ^ 3.509	Sa
Herring *Clupea harengus*	FL = -87.49 + 184.39 (OW)	Hä	FW = 4.910 (OW) ^ 5.193	Hä
	ln FL = 4.4552 + 1.0204 ln VL	Wa	FW = 0.006030 (FL/10) ^ 3.0904	Br
Sprat *Sprattus sprattus*	FL = -25.28 + 137.24 (OW)	Hä	FW = 9.7343 (OW) ^ 4.695	Hä
	ln FL = 4.2524 + 0.9616 ln VL	Wa	FW = 0.002168 (FL/10) ^ 3.474600	Co
Twait shad *Alosa fallax*	See Note 1		FW = 0.0059 (FL/10) ^ 3.0777	Le
Argentine *Argentina sphyraena*	FL = -35.049 + (OL) * 46.370	Br	FW = 0.082530 (OL) ^ 3.830400	Br
Cod *Gadus morhua*	FL = -202.13+48.37 (OL)	Hä	FW = 0.006855 (OL) ^ 4.435	Hä
	ln FL = 3.9304 + 0.9839 ln PMXHH	Wa	FW = 0.0124 (FL/10) ^ 2.93	Bo
Haddock *Melanogrammus*	FL = 8.785 (OL) ^ 1.38	Hä	FW = 0.002096 (OL) ^ 4.58	Hä
aeglefinus	FL = 45.897*(OW) ^ 1.215	Br	FW = 0.723869 (OW) ^ 3.79377	Br
	ln FL = 3.7898 + 1.0110 ln PMXHH	Wa	FW = 0.0074 (FL/10) ^ 3.06	Fr
	ln FL = 4.3571 + 0.9701 ln VL	Wa		
Pollock/Saithe *Pollachius* spp.	FL = 13.20 (OL) ^ 1.329	Hä	FW = 0.01192 (OL) ^ 4.205	Hä
	FL = 42.391 (OW) ^ 1.525	Br	FW = 0.762794 (OW) ^ 4.513928	Br
	ln FL = 4.6252 + 0.7651 ln PMXHH	Wa	FW = 0.0134 (FL/10) ^ 2.94	Bo
	FL = 173.20 + 11.33 (PMXL)	Wa		
	FL = 65.030 (VL) + 4.0112	Wa		
Haddock/Pollock/Saithe	FL = 16.274 (OL) ^ 1.197	Br	FW = 0.039122 (OL) ^ 3.600289	Br
	FL = 49.497 (OW) ^ 1.269	Br	FW = 1.066829 (OW) ^ 3.844856	Br
Whiting *Merlangius merlangus*	FL = -54.114 + (OW) * 79.671	Br	FW = 0.790806 (OW) ^ 3.705954	Br
	ln FL = 3.8872 + 0.9745 ln PMXHH	Wa	FW = 0.010961 (FL/10) ^ 2.9456	Co
	ln FL = 2.6165 + 0.9954 ln PMXL	Wa		
	FL = 73.108 (VL) + 1.906	Wa		
Blue whiting *Micromesistius*	FL = -40.94 + 25.394 (OL)	Hä	FW = 0.0067267 (OL) ^ 3.892	Hä
poutassou	FL = -17.800 + (OW) * 70.770	Sa	FW = 0.0019350 (FL/10) ^ 3.34372	Sa
	FL = 72.33 + 48.37 PMXHH	Wa	FW = 0.0041 (FL/10) ^ 3.15	Fr
	FL = 61.90 + 57.23 PMXAH	Wa		
	FL = 30.71 + 13.21 PMXL	Wa		
	ln FL = 4.6688 + 0.8300 ln VL	Wa		
Whiting/Blue whiting	FL = -26.438 +22.547 (OL)	Hä*	FW = 0.00970935 (OL) ^ 3.7135	Hä*
Norway pout *Trisopterus esmarkii*	FL = -42.6 + 29.522 (OL)	Hä	FW = 0.0020805 (OL) ^ 4.729	Hä
	FL = -1.640 + (OW) * 55.204	Br	FW = 0.886564 (OW) ^ 3.279030	Br
	ln FL = 3.9133 + 1.1262 ln PMXAH	Wa	FW = 0.0066 (FL/10) ^ 3.000	Fr
	ln FL = 4.0081 + 1.1290 ln PMXHL	Wa		
Poor cod *Trisopterus minutus*	FL = -49.9 + 28.091 (OL)	Hä	FW = 0.00354 (OL) ^ 4.57	Hä
	FL = -34.836 + (OW) * 56.691	Br	FW = 0.218384 (OW) ^ 4.211111	Br
	FL = 41.13 (PMXHH) + 23.49	Wa	FW = 0.0072 (FL/10) ^ 3.13	Fr
	FL = 62.80 (PMXAH) + 0.77	Wa		
	FL = 15.05 PMXL - 10.24	Wa		
	FL = 60.480 (VL) + 13.51	Wa		
Bib *Trisopterus luscus*	FL = -160.42 + 41.95 (OL)	Hä	FW = 0.000291 (OL) ^ 5.878	Hä
	ln FL = 4.3288 + 0.6810 ln PMXHH	Hä	FW = 0.0079 (FL/10) ^ 3.15	Fr
	ln FL = 4.3910 + 0.8672 ln VL	Wa		
Poor cod/Bib	FL = -109.100 + (OL) * 36.13900	Hä*	FW = 0.00079 (OL) ^5.38000	Hä*
	FL = 41.13 (PMXHH) + 23.49	Wa	FW = 0.002796 (FL/10) ^ 3.40400	Hä*

Trisopterus spp.	FL = -5.886 + 23.443 (OL)	Br	FW = 0.033918 (OL) ^ 3.531259	Br
(*T. minutus* used for bone length)	FL = 15.515 + (OW) * 45.404	Br	FW = 0.916531 (OW) ^ 3.157323	Br
	FL = 41.13 (PMXHH) + 23.49	Wa	FW = 0.002796 (FL/10) ^ 3.40400	Hä*
	FL = 60.480 (VL) + 13.51	Wa		
Silvery pout *Gadiculus argenteus*	FL = 19.449 (OL) ^ 1.053	Hä	FW = 0.0021289 (OL) ^ 3.785	Hä
	ln FL = 4.2064 + 1.0392 ln VL	Wa	FW = 0.0058 (FL/10) ^ 3.15	Fr
Tadpole fish *Raniceps raninus*	FL = -20.37 + 22.96 (OL)	Hä	FW = 0.151155 (OL) ^ 2.912	Hä
Greater forkbeard *Phycis blennoides*	FL = (1.555 (OL) ^ 1.28500) *10	Pe	FW = 0.0037 (FL/10) ^ 3.20	Fr
	See Note 1			
3-bearded rockling *Gaidropsarus vulgaris*	FL = -74.6 + 92.29 (OL)	Hä	FW = 0.0044 (FL/10) ^ 3.21	Fr
	ln FL = 4.1697 + 0.9140 ln PMXHH	Wa		
Four-bearded Rocking *Enchelyopus cimbrius*	FL = -28.8 + 70.344 (OL)	Hä	FW = 0.1752 (OL) ^ 3.482	Hä
5-bearded rockling *Ciliata mustela*	FL = -74.6 + 92.29 (OL)	Hä	FW = 1.0736 (OL) ^ 3.444	Hä
	FL = 79.52 (PMXHH) -6.45	Wa	FW = 0.00640 (FL/10) ^ 3.000	Fr
	FL = 78.51 (VL) -55.70	Wa		
Northern Rockling *Ciliata septentrionalis*	FL = -52.7 + 81.317 (OL)	Hä*	FW = 0.6244 (OL) ^ 3.463	Hä*
	See Note 1		FW = 0.0083 (OL) ^ 3.18	Fr
Rockling spp.	FL = -52.7 + 81.317 (OL)	Hä*	FW = 0.6244 (OL) ^ 3.463	Hä*
	G. vulgaris used for premaxilla		FW = 0.0035 (FL/10) ^ 3.106	Fr
Ling *Molva molva*	FL = -128.038 + (OL)* 67.634	Br	FW = 0.198199 (OL) ^ 3.620808	Br
	FL = -130.941 + (OW) * 186.906	Br	FW = 6.559731 (OW) ^ 3.738733	Br
	ln FL = 4.2651 + 1.0308 ln PMXHL	Wa	FW = 0.0040 (FL/10) ^ 3.07	Fr
	ln FL = 4.7590 + 0.8693 ln PMXHH	Wa		
	ln FL = 4.6663 + 0.9385 ln PMXAH	Wa		
	ln FL = 4.3205 + 1.0306 ln VL	Wa		
	ln FL = 4.6687 + 0.8512 ln VH	Wa		
Hake *Merluccius merluccius*	FL = -0.63 + 23.884 (OL)	Hä	FW = 0.02628 (OL) ^ 3.484	Hä
	FL = -68.180 + (OW) * 76.276	Sa	FW = 0.009740 (FL/10) ^ 2.91300	Be
	ln FL = 4.4327 + 0.9916 ln VL	Wa		
Unidentified Gadidae	FL = -61.590 + 33.304 (OL)	Hä	FW = 0.016042 (FL/10) ^ 3.035950	Br
	FL = -54.350 + 76.582 (OW)	Br		
Dragonet *Callionymus spp.*	FL = 44.29 (OL) ^ 1.412	Hä	FW = 0.482 (OL) ^ 4.459	Hä
	FL = -68.660 + (OW) * 167.300	Br	FW = 0.022000 (FL/10) ^ 2.590700	Co
	See Note 1	Wa		
Garfish *Belone belone*	FL = 0.000 + (OL) * 140.000	Br	FW = 0.000200 (FL/10) ^ 3.442000	Co
Grey gurnard *Eutrigla gurnardus*	FL = 16.7 + 71.92 (OL)	Hä	FW = 1.007 (OL) ^ 3.616	Hä
Triglidae spp.	*E. gurnardus* used for otolith		*E. gurnardus* used for otolith	
Shorthorn sculpin *Myoxocephalus scorpius*	FL = -9.95 + 34.84 (OL)	Hä	FW = 0.2261 (OL) ^ 3.496	Hä
Sea scorpion *Taurulus bubalis*	FL = 5.36 + 33.71 (OL)	Hä	FW = 0.6398 (OL) ^ 2.988	Hä
Cottidae (Sculpins)	See Note 1		FW = 0.0141 (FL/10) ^ 3.05	Fr
Hooknose *Agonus cataphractus*	See Note 1		See Note 2	
Perch *Perca fluviatilis*	FL = -36.97 + 33.90 (OL)	Hä	FW = 0.0545 (OL) ^ 3.797	Hä
Sea Breams Unidentified Sparidae	See Note 3		FW = 0.01772 (FL/10) ^ 2.951	Mo
Horse mackerel *Trachurus trachurus*	FL = -27.020 + 34.939 (OL)	Br	FW = 0.003400 (FL/10) ^ 3.294300	Co
	FL = -26.110 + (OW) * 79.010	Br		
	See Note 1			
Cuckoo wrasse *Labrus mixtus*	FL = -4.76 + 52.12 (OL)	Hä	FW = 0.688 (OL) ^ 3.51	Hä
	See Note 1		FW = 0.0049 (FL/10) ^ 3.28	Fr
Ballan wrasse *Labrus bergylta*	FL = -31.24 + 67.97 (OL)	Hä	FW = 0.695 (OL) ^ 4.205	Hä
Labridae spp.	FL = 3.320 + 53.440 (OL)	Hä*	FW = 2.330310 (OL) ^ 2.934000	Hä*
	See Note 1		FW = 0.0049 (FL/10) ^ 3.28	Fr
Eelpout *Zoarces viviparus*	FL = -23.65 + 179.96 (OW)	Hä	FW = 12.58 (OW) ^ 4.4321	Hä
Butterfish *Pholis gunnellus*	FL = 1.23 + 173.96 (OW)	Hä	FW = 0.0011 (FL/10) ^ 3.4752	Le
	See Note 1			
Greater Weever *Trachinus draco*	See Note 2		FW = 0.0059 (FL/10) ^ 3.08	Fr
Greater sandeel *Hyperoplus lanceolatus*	FL = -4.024 + 56.84 (OL)	Hä	FW = 1.083343 (OL) ^ 2.446703	Br
	See Note 1		FW = 0.00340 (FL/10) ^ 2.928	Fr
Sandeels *Ammodytes spp.*	FL = 18.376 + 51.441 (OL)	Br	FW = 1.083343 (OL) ^ 2.446703	Br
	FL = 10.589 + 110.199 (OW)	Br	FW = 5.731932 (OW) ^ 2.679693	Br
	ln FL = 5.0687 +1.0489 ln PMXAH	Wa	FW = 0.1248 (FL/10) ^ 1.75	Bo
	ln FL = 4.4758 + 1.0426 ln VL	Wa		
	ln FL = 4.7444 + 0.9370 ln VW	Wa		
Gobiidae spp.	FL = -6.460 + (OW) * 41.770	Sa	FW = 0.232809 (OW) ^ 4.17000	Sa
	See Note 1		FW = 0.0113 (FL) ^ 2.8799	Le

Mackerel *Scomber scomber*	FL = -33.539 + (OW) * 255.071	Br	FW = 78.642882 (OW) ^ 4.046557	Br
	See Note 1		FW = 0.002709 (FL/10) ^ 3.29000	Co
Megrim *Lepidorhombus* spp.	FL = 66.745 (OL/2) ^ 1.1755	La*	FW = 0.0062 (FL/10)^3.367	Ro
(Left)	ln FL = 3.6719 + 1.0078 ln PMXHH	Wa	FW = 0.0046 (FL/10) ^ 3.13	Fr
	FL = 67.97 - 4.28 PMXHL	Wa		
	FL = 14.83 + 30.45 PMXL	Wa		
	ln FL = 4.2805 + 0.9400 ln VL	Wa		
Scaldfish *Arnoglossus* spp.	See Note 3		FW = 0.0073 (FL/10) ^ 3.011	Ba
	See Note 1			
Bothidae spp.	FL = -11.420 + (OL) * 54.770	Hä	FW = 0.024920 (FL/10) ^ 2.857000	Be
	Lepidorhombus spp. used for bones		*Lepidorhombus* spp. used for bones	
Plaice *Pleuronectes platessa*	FL = -3.81 + 47.63 (OL)	Hä	FW = 0.498 (OL) ^ 3.408	Hä
(Right)	ln FL = 3.4364 + 1.0013 ln (PMXL)	Wa	FW = 0.0099 (FL/10) ^ 3.0209	Le
	ln FL = 4.4671 + 0.9520 ln VL	Wa		
Dab *Limanda limanda*	FL = -50.96 + 58.47 (OL)	Hä	FW = 0.170 (OL) ^ 4.117	Hä
(Right)	FL = 42.44 (PMXHH) - 6.87	Wa	FW = 0.007400 (FL/10) ^ 3.112800	Co
(Left)	FL = 66.36 (PMXAH) - 9.51	Wa		
(Right)	FL = 35.48 (PMXL) - 25.94	Wa		
(Left)	FL = 24.31 (PMXL) + 14.70	Wa		
	ln FL = 4.2920 + 0.9802 ln VL	Wa		
Flounder *Platichthys flesus*	FL = -51.06 + 59.10 (OL)	Hä	FW = 1.578 (OL) ^ 2.899	Hä
(Right)	ln FL = 3.1277 + 1.2552 ln PMXHH	Wa	FW = 0.0103 (FL/10) ^ 2.9976	Le
(Right)	ln FL = 3.6493 + 1.2931 ln PMXAH	Wa		
(Right)	FL = 34.53 (PMXL) - 37.49	Wa		
	ln FL = 4.3757 + 0.8605 ln VL	Wa		
Plaice/Flounder	FL = -27.435 + 53.365 (OL)	Hä*	FW = 1.038 (OL) ^ 3.1535	Hä*
Dab/Flounder (Right)	FL = 42.44 (PMXHH) - 6.87	Wa	FW = 0.007400 (FL/10) ^ 3.112800	Co
(Right)	FL = 112.29 (PMXHL) - 42.14	Wa		
Lemon sole *Microstomus kitt*	FL = 10.93 + 88.46 (OL)	Hä	FW = 4.89 (OL) ^ 3.45	Hä
	FL = -71.440 + (OW) * 176.450	Br	FW = 0.026520 (FL/10) ^ 2.764300	Co
(Right)	ln FL = 3.8654 + 0.8913 ln PMXHH	Wa		
(Left)	ln FL = 3.7714 + 0.9246 ln PMXHH	Wa		
(Right)	ln FL = 4.2277 + 0.8353 ln PMXL	Wa		
	ln FL = 4.4164 + 0.9124 ln VL	Wa		
Long rough dab *Hippoglossoides platessoides*	FL = -24.52 + 48.35 (OL)	Hä	FW = 0.166 (OL) ^ 3.788	Hä
	ln FL = 4.4390 + 0.8832 ln VL	Wa	FW = 0.00400 (FL/10) ^ 3.203900	Co
Witch *Glyptocephalus cynoglossus*	FL = - 100.65 + (OL) * 78.29	Hä	FW = 0.0770 (OL) ^ 4.633	Hä
	ln FL = 3.7231 + 1.0495 ln PMXHH	Wa	FW = 0.001700 (FL/10) ^ 3.389800	Hä
Pleuronectidae spp.	FL = -90.57 + 69.44 (OL)	Hä**	FW = 1.0568 (OL) ^ 3.907	Hä**
	L. limanda used for bones		*L. limanda* used for bones	
Solonette *Buglossidium luteum*	See Note 2		FW = 0.0101 (FL/10)^3.008	İl
(Left)	FL = 22.23 (PMXHH) + 20.45	Wa		İl
	ln FL = 4.2338 + 0.9427 ln VL	Wa		İl
Sole *Solea solea*	FL = -12.622 + 80.901 (OL)	Hä	FW = 2.535 (OL) ^ 3.444	Hä
	See Note 1	Wa	FW = 0.0072 (FL/10) ^ 3.0646	Le
Solidae spp.	*S. solea* used for otoliths		*S. solea* used for otoliths	
	B. luteum used for bones		*B. luteum* used for bones	
Unidentified Flatfish	FL = -25.950 + (OL) * 53.274	Hä	FW = 0.009923 (FL/10) ^ 3.03595	Be/Co
	FL = -38.100 + (OW) * 76.600	Hä		Be/Co
Cephalopoda	**Estimated prey length (mm)**	**S**	**Estimated prey weight (g)**	**S**
Flying squid *Todaropsis eblanae*	DML = -10.320 + LRL * 35.040	Cl	BW = 1.803990 LRL ^ 3.17000	Cl
Squid *Loligo* spp.	DML= -42.220 + LRL * 84.274	Cl*	BW = 6.195360 (LRL) ^ 3.24200	Sn*
Unid Ommastrephidae	*Loligo* spp. used for beaks		BW = 2.337310 (LRL) ^ 2.82000	Br*
Octopus *Eledone cirrhosa*	DML = 3.380 + (LHL) * 26.570	Cl	BW = 5.365600 (LHL) ^ 2.85000	Cl
Unid. *Octopus* spp.	*E. cirrhosa* used for beaks		*E. cirrhosa* used for beaks	

Notes: 1) No bone regression was available so length was estimated based on a proportion from Watt *et al*. (1997). 2) No otolith regression was available length &/or weight was estimated based on a proportion from Härkönen. 3) No otolith regression was available so length was estimated based on a proportion from Tuset *et al*. (2008). 4) Asterisk (*) indicates data were combined from more than one species. 5) Two Asterisk (**) indicates combined data excluding Greenland halibut (*Reinhardtius hippoglossoides)*

Appendix II: Digestion Coefficients (DC) and Numerical Correction Factors (NCF) applied to fish otoliths, bones and squid beaks to account for partial and complete erosion. OL = otolith length, OW = otolith width, LRL = lower rostral length

Species	DC	NCF	Source
Anguilliformes	OL=1.25/OW=1.24	–	Tollit et al. (1997)
Conger conger	OL=1.25/OW=1.24	–	Tollit et al. (1997)
Clupea harengus	OL=1.18/OW=1.40	2.867	Grellier & Hammond (2006)
M. aeglefinus/Pollachius spp.	OL=1.40/OW=1.40	1.113	Grellier & Hammond (2006)
Merlangius merlangus	OL=1.49/OW=1.24	1.027	Grellier & Hammond (2006)
Micromesistius poutassou	OL=1.49/OW=1.24	1.027	Grellier & Hammond (2006)
Trisopterus spp.	OL=1.21/OW=1.18	1.087	Grellier & Hammond (2006)
T. esmarkii	OL=1.25/OW=1.22	1.157	Grellier & Hammond (2006)
T. minutus	OL=1.17/OW=1.14	1.025	Grellier & Hammond (2006)
Rocklings	OL=1.54/OW=1.52	1.069	Grellier & Hammond (2006)
Molva molva	OL=1.54/OW=1.52	1.069	Grellier & Hammond (2006)
Unidentified Gadidae spp.	OL=1.54/OW=1.52	1.069	Grellier & Hammond (2006)
Merluccius merluccius	OL=1.68/OW=1.63	1.081	Grellier & Hammond (2006)
Perca fluviatilis	OL=1.25/OW=1.24	–	Tollit et al. (1997)
Trachurus trachurus	OL=1.25/OW=1.24	–	Tollit et al. (1997)
Labridae spp.	OL=1.25/OW=1.24	–	Tollit et al. (1997)
Ammodytes spp.	OL=1.56/OW=1.65	2.861	Grellier & Hammond (2006)
Callionymus spp.	OL=1.59/OW=1.47	3.273	Grellier & Hammond (2006)
Gobiidae spp.	OL=1.25/OW=1.24	–	Tollit et al. (1997)
Scomber scomberus	OW=1.19	1.391	Grellier & Hammond (2006)
Hippoglossoides platessoides	OL=1.34/OW=1.36	1.163	Grellier & Hammond (2006)
Microstomus kitt	OL=1.25/OW=1.27	1.539	Grellier & Hammond (2006)
Glyptocephalus cynoglossus	OL=1.16	1.037	Grellier & Hammond (2006)
Solea solea	OL=1.25/OW=1.31	1.241	Grellier & Hammond (2006)
Buglossidium luteum	OL=1.25/OW=1.31	1.241	Grellier & Hammond 2006
Unidentified flatfish	OL=1.25/OW=1.31	1.241	Grellier & Hammond 2006
Loligo spp.	LRL=1.02	1.062	Grellier & Hammond (2006)

Appendix III: Grey seal diet composition during February & April 2009 - 2010. %F= Percentage frequency of occurrence, %N= Percentage by number, %B= Uncorrected percentage biomass, %DC B= Percentage biomass corrected for partial erosion when possible, NCF %B= Percentage biomass corrected for complete erosion when possible.

Species	%F	%N	%B	DC %B	NCF %B
AGNATHANS					
Lamprey *Petromyzon marinus*	2.3	0.3	4.63	2.28	3.97
CHONDRICHTHYES					
Ray *Raja* spp.	1.5	0.2	-	-	-
OSTEOCHTHYES					
Eels Anguilliformes	0.8	0.1	<0.01	<0.00	<0.01
Conger eel *Conger conger*	0.8	0.1	0.03	0.04	0.02
Herring *Clupea harengus*	1.5	0.2	0.18	0.50	0.43
Haddock *Melanogrammus aeglefinus*	1.5	0.2	0.32	0.34	0.29
Pollock/Saithe *Pollachius* spp.	10.6	2.2	6.21	10.06	5.83
Whiting *Merlangius merlangus*	15.9	3.1	2.47	2.72	2.16
Blue whiting *Micromesistius poutassou*	14.4	3.2	1.27	0.65	1.11
Norway pout *Trisopterus esmarkii*	2.3	0.3	0.06	0.05	0.05
Poor cod *Trisopterus minutus*	19.7	3.8	2.34	2.02	2.04
Bib *Trisopterus luscus*	14.4	2.9	2.85	4.16	2.64
Poor cod/Bib	16.7	6.6	3.46	4.71	3.22
Unidentified *Trisopterus* spp.	32.6	8.4	2.01	1.30	1.79
3-bearded rockling *Gaidropsarus vulgaris*	2.3	0.3	3.85	14.82	3.91
5-bearded rockling *Ciliata mustela*	0.8	0.1	0.33	0.71	0.30
Ling *Molva molva*	0.8	0.1	0.68	2.88	0.62
Hake *Merluccius merluccius*	3.8	0.6	0.81	2.18	0.78
Unidentified Gadidae	33.3	7.1	5.7	6.46	4.98
Dragonet *Callionymus spp.*	31.8	6.8	2.47	4.42	4.05
Triglidae spp.	1.5	0.2	1.21	0.60	1.04
Perch *Perca fluviatilis*	0.8	0.2	1.21	0.03	0.02
Cuckoo wrasse *Labrus mixtus*	1.5	0.2	0.41	0.20	0.35
Ballan wrasse *Labrus bergylta*	0.8	0.1	0.31	0.10	0.17
Unidentified Labridae	6.1	1.8	1.78	1.81	1.63
Eelpout *Zoarces viviparus*	3.0	1.1	3.15	1.55	2.70
Horse mackerel *Trachurus trachurus*	2.3	0.3	0.60	0.42	0.52
Sandeels *Ammodytes spp.*	37.9	32.7	5.39	7.31	12.20
Scaleless worm goby *Caragobius urolepis*	2.3	0.3	0.03	0.19	0.03
Mackerel *Scomber scomber*	0.2	0.1	2.36	2.31	2.81
Scaldfish *Arnoglossus* spp.	0.8	0.1	0.15	0.07	0.13
Plaice *Pleuronectes platessa*	2.3	0.4	1.46	0.72	1.25
Dab *Limanda limanda*	1.5	0.2	1.24	0.61	1.06
Flounder *Platichthys flesus*	0.8	0.1	2.34	1.15	2.01
Lemon sole *Microstomus kitt*	6.1	1.0	2.41	1.50	1.69
Long rough dab *Hippoglossoides platessoides*	1.5	0.2	0.24	0.36	0.24
Witch *Glyptocephalus cynoglossus*	1.5	0.2	0.04	0.03	0.03
Solenette *Buglossidium luteum*	2.3	0.3	0.19	0.13	0.18
Sole *Solea solea*	2.3	0.4	2.28	2.42	2.42
Unidentified flatfish	9.8	1.6	3.97	2.08	3.45
Unidentified fish	42.4	10.1	-	-	-
CEPHALOPODA					
Squid *Loligo* spp.	3.8	0.7	28.97	15.21	26.35
Curled octopus *Eledone* spp.	3.8	0.6	1.80	0.88	1.54
Total Haddock/*Pollachius* spp.	11.4	2.5	6.52	10.40	6.12
Total *Trisopterus* spp.	51.5	22.1	10.71	12.24	9.75
Total rocklings	2.3	0.4	4.18	15.53	4.21
Total Gadidae	79.5	39.1	32.34	53.06	29.73
Total Labridae	7.6	2.1	2.50	2.11	2.15
Total flatfish	25.0	4.7	14.32	9.07	12.45
Total fish	99.2	98.8	69.24	83.90	72.11
Total Cephalopoda	7.6	1.2	30.76	16.10	27.89

Appendix IV: Protocol and result of attempted feeding trial for the purpose of creating a reference collection, regression equations and correction factors for salmonid bones.

Feeding trials using captive grey seals housed in a local seal sanctuary were conducted to investigate levels of erosion and passage rates that salmonid bones and otoliths undergo during the digestive process. This would enable grade-specific correction factors for otoliths and suitable regression equations and correction factors for salmonid bones to be derived. A total of 34 adult salmon were obtained from Ballycotton Sea Food Ltd and 20 sea trout smolts were provided by Inland Fisheries Ireland. All fish were assigned a unique code, with their length and weight recorded and otoliths removed and labelled according to the fish code. The fish were then boiled for 2 minutes to soften the flesh, which facilitated the removal of head bones and vertebrae. All bones were then labelled with the unique fish code, sterilised in 70% ethanol and dried. 4,668 length, width and thickness measurements were taken from 881 diagnostic structures consisting of paired otoliths, primary premaxillae, secondary premaxillae, maxillae, dentaries, articulars, retroaritculars, quadrates, post-temporals, cleithrums, upper and lower palatal teeth plates, and unpaired uroyhal head bones along with anterior abdominal vertebrae.

Given that seals in the sanctuary were comprised of juveniles (<2 years) and were therefore unable to consume large fish in their entirety, bones were inserted into the belly of small herring (*Clupea harengus*) and the unique fish code for each bone was recorded. An inert coloured polystyrene bead was also placed into the body cavity and its colour and size recorded alongside the unique fish code. The beads were used to mark specific salmon/trout positive scats, and to provide a structure for passage rate analysis.

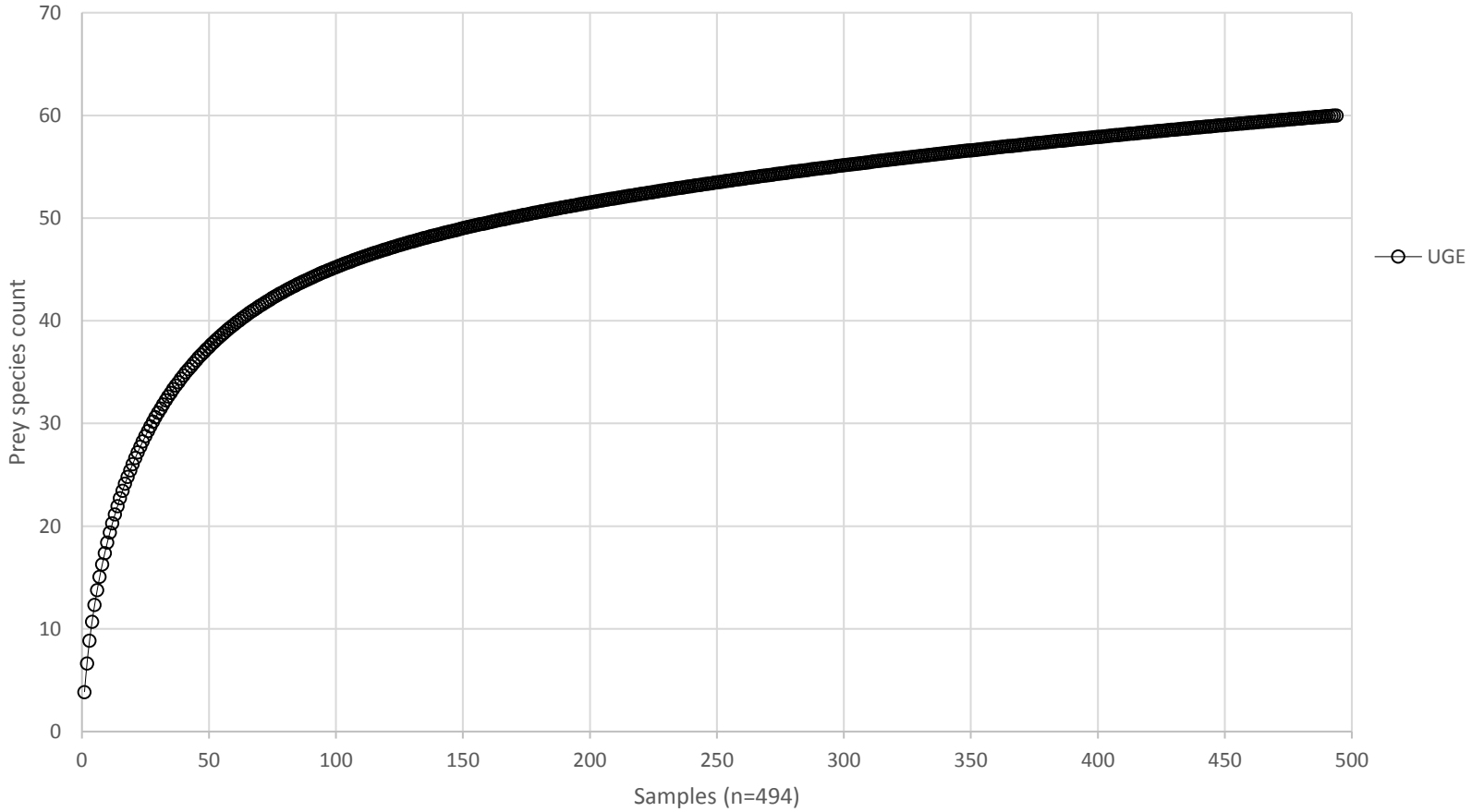
Seals were fed three times a day and ideally kept in a dry-run. When this was not possible a nylon mesh was placed over the hole which drained the pool so as to capture salmonid bones after defecation. The name of the seal to which each fish was fed was recorded, together with the time of feeding, time of scat collection, and condition of the scat sample (i.e. whole/collected in water/out of water). A note was also taken as to whether each herring was consumed whole or if the seal merely scratched at the fish without eating it entirely. Scat samples were then collected from the enclosures up to

7 days after the herring had been consumed. This was done to ensure that any bones which may have been retained in the digestive gut of the seal had successfully passed through. All samples were labelled in a polythene bag and returned to the laboratory to be washed through the nest of sieves. Any salmonid remains recovered were matched to the original unique code when the polystyrene bead was also present, and re-measured.

While several attempts were made to feed salmonid bones to captive juvenile grey seals, and subsequently record the passage rate and extent of erosion the structures had undergone, the experiment proved unsuccessful. Seals housed in the sanctuary are typically very young and often sick, with only two seals capable of consuming whole fish. The seals did not show much interest in consuming the fish, even when feeding was reduced to once a day, and often just played with or ignored them. This resulted in bones being broken or discarded along with the herring.

In total 10 scat samples were collected from one seal over the course of a week, however defecation occurred within the water on 8 occasions and the nylon mesh was insufficiently able to capture bones and beads. Only one cleithrum was recovered from the remaining 2 scats, however no bead was present so the bone could not be allocated to its unique fish code. Trials were then discontinued because the facility proved inadequate for conducting feeding trials for a number of reasons; the sanctuary would not allow non-staff/volunteer members to remain on-site for the course of the week to feed the seals and recover scat samples; seal were not kept in dry runs and the nylon mesh was incapable of stopping bones and beads from escaping along with the water; this consequently resulted in the drainage system being effected.

Appendix V: Species accumulation curve plotting all prey species identified within the total number of scat samples collected from the Great Blasket Island, Kerry. UGE = Rarefaction curve repeatedly re-sampling subsets of the total sample.



Appendix VI: Reconstructed grey seal prey length and weights from southwest Ireland, 2009-2013 (n=8559).

Species	N	Prey Length (g)		Prey Weight (g)	
		Range	Mean ± SD	Range	Mean ± SD
OSTEICHTHYES					
Eels	2	160.5 – 171.2	165.9 ± 7.5	3.4 – 4.3	3.8 ± 0.6
Conger eel	36	257.2 - 745.5	514.6 ± 122.9	17.8 - 743.7	265.7 ± 190.0
Herring	47	55.9 - 315.2	197.4 ± 63.6	1.3 - 283.7	79.1 ± 68.2
Sprat	32	45.9 - 106.6	73.0 ± 14.1	0.4 - 8.1	2.5 ± 1.7
Twait shad	1	238.6	-	102.6	-
Unid. Clupeidae	5	66.1 - 206.9	141.1 ± 72.8	1.2 - 87.9	47.5 ± 43.7
Argentine	1	194.5	-	37.8	-
Cod	8	211.4 - 478.0	310.5 ± 87.9	93.2 - 845.9	294.4 ± 247.6
Haddock	65	109.8 - 538.8	265.0 ± 89.2	9.2 - 1470.2	237.7 ± 264.6
Pollachius spp.	84	44.8 - 574.9	282.6 ± 114.1	0.6 - 1828.5	319.8 ± 378.8
Haddock/*Pollachius* spp.	60	158.2 - 512.9	299.7 ± 72.4	36.6 - 1272.8	295.3 ± 218.6
Whiting	194	27.8 - 641.1	194 ± 88.0	0.9 - 2303.0	106.6 ± 229.6
Blue whiting	280	30.9 - 576.9	168.8 ± 72.1	0.4 - 1497.0	54.6 ± 134.6
Whiting/Blue whiting	91	88.6 - 264.6	150.4 ± 36.2	4.1 - 129.6	25.2 ± 20.7
Norway pout	22	39.0 - 173.3	96.5 ± 38.0	0.3 - 34.2	7.8 ± 8.4
Bib	118	12.2 - 333.1	178.7 ± 52.9	1.2 - 571.1	87.2 ± 86.0
Poor cod	797	2.5 - 277.6	108.6 ± 52.9	0.1 - 265.3	20.2 ± 25.3
Bib/Poor cod	231	7.6 - 281.2	136.2 ± 50.3	0.4 - 286.7	35.3 ± 37.0
Unid. *Trisopterus* spp.	381	27.3 - 280.9	95.5 ± 39.9	0.1 - 238.4	12.6 ± 22.7
Silvery pout	8	43.7 - 114.5	73.7 ± 24.6	0.1 - 12.5	3.7 ± 4.5
Tadpole fish	1	172.0	-	73.7	-
Greater forkbeard	3	131.6 - 323.3	217.0 ± 97.5	14.1 - 250.6	105.1 ± 127.3
3-bearded rockling	7	156.9 - 904.3	479.1 ± 272.4	30.3 - 8380.4	2245.9 ± 3022.4
5-bearded rockling	19	90.7 - 940.6	453.9 ± 283.8	4.8 - 4143.8	978.5 ± 1250.5
Unid. rocklings	4	81.4 - 423.7	278.0 ± 173.3	3.7 - 1154.4	598.0 ± 643.1
Ling	34	86.3 - 777.5	328.5 ± 143.6	3.0 - 2549.7	306.8 ± 467.2
Hake	17	163.7 - 310.3	240.6 ± 44.4	21.8 - 215.9	100.7 ± 63.8
Unid. Gadidae	180	18.1 - 265.7	142.3 ± 48.1	0.1 - 338.4	77.0 ± 61.8
Dragonet	189	58.4 - 311.7	158.7 ± 39.9	1.5 - 163.0	36.2 ± 24.6
Garfish	22	585.2 - 673.9	629.5 ± 13.7	242.2 - 393.5	317.8 ± 23.4
Grey gurnard	18	210.8 - 340.3	244.8 ± 25.0	43.2 - 231.8	70.6 ± 41.1
Unid.Triglidae	2	210.8	210.8 ± 0.0	39.4	39.4 ± 0.0
Shorthorn sculpin	1	149.1	-	45.7	-
Unid. sculpins	1	113.4	-	23.2	-
Unid. Cottidae	2	177.7 - 238.2	208.0 ± 42.8	91.4 - 223.4	157.4 ± 93.3
Perch	1	130.7	-	23.6	-
Sea Breams	1	110.4	-	21.2	-
Cuckoo wrasse	12	56.3 - 288.4	200.4 ± 75.7	1.4 - 295.5	124.5 ± 95.0
Ballan wrasse	6	209.1 - 300.8	240.8 ± 32.8	140.8 - 548.2	258.2 ± 149.2
Unid. Labridae	27	118.3 - 287.4	207.5 ± 36.7	18.7 - 313.5	136.3 ± 66.0
Horse mackerel	67	83.3 - 397.6	230.0 ± 65.3	3.7 - 631.8	151.7 ± 126.8
Greater sandeel	231	101.9 - 383.5	237.5 ± 60.2	3.6 - 147.4	42.1 ± 23.0
Sandeels	4715	12.8 - 313.5	130.0 ± 28.9	0.2 - 77.8	8.4 ± 6.5
Scaleless worm goby	3	68.7 - 103.5	90.4 ± 18.9	2.7 - 13.2	9.0 ± 5.5
Unid. Gobiidae	2	89.3 - 128.6	108.9 ± 27.8	6.2 - 17.7	11.9 ± 8.1
Mackerel	19	104.5 - 391.5	229.1 ± 85.2	6.1 - 620.8	141.8 ± 161.9
Megrim	112	61.9 - 432.0	201.7 ± 65.2	1.4 - 605.1	123.7 ± 101.7
Scaldfish	15	32.3 - 186.2	128.3 ± 46.9	0.2 - 48.7	21.6 ± 15.6
Unid. Bothidae	1	192.1	-	47.9	-
Plaice	25	103.4 - 323.8	223.2 ± 57.2	7.9 - 356.0	131.9 ± 88.3
Dab	14	74.1 - 376.3	198.6 ± 85.2	3.9 - 593.6	130.8 ± 167.9
Flounder	11	78.1 - 333.1	165.6 ± 84.4	5.1 - 358.7	90.2 ± 106.0
Lemon sole	47	113.5 - 336.8	221.3 ± 53.4	21.9 - 439.7	148.6 ± 91.8
Long rough dab	11	138.7 - 426.5	219.1 ± 77.8	16.6 - 666.8	117.1 ± 185.9
Witch	3	143.2 - 325.1	206.4 ± 102.9	14.1 - 196.8	76.0 ± 104.6
Unid. Pleuronectidae	12	96.1 - 387.1	195.9 ± 87.1	23.5 - 1977.4	423.3 ± 593.3
Solenette	10	71.4 - 229.9	136.6 ± 45.1	3.7 - 125.8	38.0 ± 34.7
Sole	12	100.0 - 481.5	283.6 ± 99.8	8.4 - 1289.4	319.6 ± 353.0
Unid. Soleidae	36	91.9 - 398.2	254.2 ± 66.0	8.0 - 683.2	242.4 ± 153.0

Unid. flatfish	40	94.6 - 237.6	154.7 ± 28.4	9.1 - 149.2	51.0 ± 27.0
CEPHALOPODA					
Flying squid	1	29.6	-	2.7	-
Squid	22	<0.1 - 800.5	146.0 ± 247.8	0.7 - 10816.0	1073.9 ± 2668.5
Unid. Squid	13	0.1 - 587.6	76.9 ± 156.5	0.3 - 679.2	64.3 ± 186.5
Curled octopus	20	14.6 - 157.1	82.5 ± 36.5	0.5 - 789.6	186.1 ± 219.8
Unid. octopus	25	17.8 - 159.9	88.6 ± 33.2	0.9 - 840.3	206.1 ± 205.7
Unid. Cephalopoda	82	48.9 - 519.8	132.2 ± 101.6	42.2 - 5327.5	559.0 ± 1118.8
Total Clupeidae	85	45.9 - 315.2	147.8 ± 78.4	0.4 - 283.7	48.7 ± 63.3
Total Haddock/*Pollachius* spp.	209	44.8 - 574.9	282.0 ± 96.5	0.6 - 1828.5	287.2 ± 305.9
Total *Trisopterus* spp.	1549	2.5 - 333.1	114.7 ± 54.2	0.1 - 571.1	25.5 ± 39.8
Total rocklings	30	81.4 - 940.6	436.3 ± 269.4	3.7 - 8380.4	1223.5 ± 1802.4
Total Gadidae	2604	2.5 - 940.6	151.0 ± 93.7	0.1 - 8380.4	78.1 ± 274.0
Total Triglidae	20	210.8 - 340.3	241.4 ± 25.8	39.4 - 231.8	67.4 ± 40.1
Total Cottoidae	4	113.4 - 238.2	169.6 ± 52.7	23.2 - 223.4	95.9 ± 89.6
Total Labridae	45	56.3 - 300.8	210.0 ± 50.1	1.4 - 548.2	149.4 ± 96.2
Total Ammodytidae	4946	12.8 - 383.5	135.0 ± 38.5	0.2 - 147.4	10.0 ± 10.7
Total Gobiidae	5	68.7 - 128.6	97.8 ± 21.8	2.7 - 17.7	10.2 ± 5.9
Total Bothidae	128	32.3 - 432.0	193.0 ± 67.3	0.2 - 605.1	111.1 ± 100.9
Total Pleuronectidae	123	74.1 - 426.5	211.1 ± 68.8	3.9 - 1977.4	160.2 ± 226.5
Total Soleidae	58	71.4 - 481.5	240.0 ± 85.5	3.7 - 1289.4	223.1 ± 216.4
Total flatfish	349	32.3 - 481.5	202.8 ± 71.8	0.2 - 1977.4	140.1 ± 178.8
Total Cephalopoda	163	<0.01 - 800.5	116.3 ± 126.3	0.7 - 10816.0	485.7 ± 1285.3

Appendix VI: PEMANOVA+ results highlighting the effects of combined seasons within combined years, using square-root transformed abundance data.

Groups	**n**	***t* statistic**	**P**
Spring, Summer	288	3.7225	0.001
Spring, Autumn	318	3.5991	0.001
Spring, Winter	270	2.4057	0.001
Summer, Autumn	224	2.6842	0.001
Summer, Winter	176	2.7407	0.001
Autumn, Winter	206	2.3546	0.001

Appendix VIII: PERMANOVA+ results highlighting the effects of seasons between each sampling year, using square-root transformed abundance data.

	t-statistic	P
Spring		
2009, 2010	2.3933	0.001
2009, 2011	2.8027	0.001
2009, 2012	3.5390	0.001
2009, 2013	2.4912	0.001
2010, 2011	1.4253	0.059
2010, 2012	2.3644	0.001
2010, 2013	1.8994	0.004
2011, 2012	1.4602	0.049
2011, 2013	1.4673	0.064
2012, 2013	1.6928	0.024
Summer		
2009, 2010	1.4988	0.031
2009, 2011	1.6021	0.011
2009, 2012	2.2414	0.001
2009, 2013	1.8583	0.002
2010, 2011	1.4946	0.034
2010, 2012	1.9710	0.002
2010, 2013	1.2557	0.142
2011, 2012	1.3036	0.125
2011, 2013	1.7703	0.004
2012, 2013	2.4020	0.001
Autumn		
2009, 2011	1.7199	0.004
2009,2012	1.7205	0.005
2009,2013	1.6843	0.007
2011,2012	0.9382	0.526
2011,2013	1.1379	0.271
2012, 2013	1.2363	0.174
Winter		
2009, 2011	1.4170	0.046
2009, 2012	1.7906	0.001
2009, 2013	1.6259	0.004
2011, 2012	1.7603	0.003
2011, 2013	1.4201	0.060
2012, 2013	1.7097	0.004

Appendix IX: Commercial species (species landed by fisheries) used in the community analysis model.

Commercial Species
Ray *Raja* spp.
Cod *Gadus morhua*
Haddock *Melanogrammus aeglefinus*
Pollock/Saithe *Pollachius* spp.
Ling *Molva molva*
Monkfish *Lophius* spp.
Grey gurnard *Eutrigla gurnardus*
Hake *Merluccius merluccius*
Mackerel *Scomber scomber*
Turbot *Scophthalmus maximus*
Brill *Scophthalmus rhombus*
Plaice *Pleuronectes platessa*
Lemon sole *Microstomus kitt*
Sole *Solea solea*
Cephalopoda
Lobster *Homarus gammarus*
Crawfish *Palinurus elephas*
Spider crab *Maja squinado*
Brown crab *Cancer pagurus*