Defining Sources of Variation in Diets of Northern Phocids using Stable Isotopes and
Quantitative Fatty Acid Signature Analysis

by

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ABSTRACT

What animals consume is perhaps one of the most fundamental questions in ecology. Diet has important consequences with respect to energy intake, overall foraging costs and influences the degree of competitive interactions amongst organisms. Recent collapse of fisheries in the northwest Atlantic has renewed concerns over the role of seal predation in marine food webs. Harp (*Phoca groenlandica*), hooded (*Cystophora cristata*) and grey (*Halichoerus grypus*) seals share considerable overlap in foraging range. However they also exhibit distinct differences in body size, degree of sexual size dimorphism, diving patterns and foraging behaviour. Very little is actually known about what these seals consume across their foraging ranges, especially given that previous diet estimates are biased by nearshore sampling and unavoidable biases associated with stomach content analysis. The development of alternative biochemical methods to estimate diet has overcome some of these problems. The two main approaches are fatty acid (FA) signature and stable isotope analysis. Both of these tracer approaches can provide inferences about or quantitative estimates of diet that are time-integrated. Estimates are made at the level of the individual thereby increasing our ability to understand and detect differences among demographic groups.

The main goal of my research was to examine the diet of seals at varying spatial and temporal scales, and by doing so, increase our understanding of factors influencing the dietary niche breath of large marine predators displaying different foraging tactics. Given broad evidence for their importance in other taxa, I sought to evaluate age, size and sex related effects on diet selection for grey, harp and hooded seals. Second, I evaluated large-scale temporal and geographic variation in seal diets over a decade that saw large changes in prey distribution and abundance. Overall I noted broad inter-and intra-specific variation in diets, diet quality and diet breadth. Key findings demonstrate that seals show marked demographic and individual variation in feeding, thus individuals are achieving similar endpoints by exploiting different energy sources. These results lend further support for the idea of multiple foraging strategies with convergent success and underscore the need to account for such variability in developing predation models.

LIST OF ABBREVIATIONS USED

AIC:	Akaike's Information Criterion
ANOVA:	Analysis of Variance
CC:	Calibration Coefficient
DFA:	Discriminant Function Analysis
FA:	Fatty Acid
FAS:	Fatty Acid Signature
GLM:	Generalized Linear Model
MANOVA:	Multivariate Analysis of Variance
OFT:	Optimal Foraging Theory
PCA:	Principal Component Analysis
QFASA:	Quantitative Fatty Acid Signature Analysis
RM GLM:	Repeated-Measures General Linear Model
SI:	Stable Isotope

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"You are what you eat" - grandma

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CHAPTER I: INTRODUCTION

What animals consume is perhaps one of the most fundamental questions in ecology. Diet has important consequences with respect to energy intake, overall foraging costs and influences the degree of competitive interactions amongst organisms. Discerning the degree of dietary specialization or niche breadth is important for studies of resource use and understanding general evolutionary processes, including physiological, morphological, behavioural and social adaptations (Bolnick *et al.* 2003). Dietary niche breadth is a metric for measuring the degree of specialization (Krebs 1999). However, it is more than a mere metric, as the concept of niche has pervaded much of ecological theory and directed subsequent empirical work. Here I use a restricted definition as simply the breadth or range of the food resources used by a species or individual.

However, there are more pragmatic, management oriented issues when taking into account the potential impact of predation or grazing on biological resources considered important to human society. The recent collapse of groundfish stocks in the northwest Atlantic has renewed concerns over the role of seal predation in marine food webs (Sinclair and Murawski 1997; Hammill and Stenson 2000; Trzcinski *et al.* 2006). Harp (*Phoca groenlandica*), hooded (*Cystophora cristata*) and grey seals (*Halichoerus grypus*) are abundant pinnipeds in the North Atlantic (Bowen *et al.* 2003; Stenson *et al.* 1997, 2002, 2003). These three species share considerable overlap in foraging range, whelping patches and potentially diet. However they also exhibit distinct differences in body size, diving patterns, as well as time and energy invested in reproduction (Lydersen and Kovacs 1999). In fact, however, relatively little is known about the sources of inter-and

intra-specific variation in diets as well as broad spatial and temporal effects on diet selection. This is both a sampling and an analytical problem.

Relatively few studies have documented diets for harp, hooded and grey seals across their entire range given that these animals are far-ranging and large portions of the population are essentially inaccessible to researchers for most of the year. Thus diet estimates are often biased by near shore sampling during particular times of the year. Information to date is based mostly on conventional stomach content analysis with samples collected in different locations, seasons, and years and has often suffered from small sample sizes across age classes. Moreover, there are certain analytical limitations associated with stomach content analysis (Jobling and Breiby 1986; Jobling 1987; Carss and Parkinson 1996) further biasing our estimation of what these seals consume. These include differential rates of digestion, the lack of diagnostic hard parts of some soft bodied prey and the fact that these assessments provide only a snapshot of the most recent meal and may not be representative of the longer term diet. Despite the paucity of data and potential biases associated with this analysis, diet data to date suggest intriguing inter- and intra-specific variation in diets for these seals with additional geographical, annual and seasonal effects (e.g. Bowen *et al.* 1993; Bowen and Harrison 1994; Lawson *et al.* 1995; Lawson and Stenson 1995; Lawson and Stenson 1997; Lawson *et al.* 1998) warranting further exploration given the perceived importance of these predators in the North Atlantic ecosystem.

Limitations of stomach analysis have led to the development of alternative biochemical methods. The two main approaches are fatty acid signature (e.g. Iverson *et al.* 2004) and stable isotope analysis (e.g. Post 2002). Both of these chemical tracer approaches can provide inferences about or quantitative estimates of diet that are time-integrated and readily applied to most taxa of interest thereby alleviating problems associated with conventional analysis. Moreover, analysis is done at the level of individual predators thereby increasing our ability to detect differences amongst various demographic groups. For example, through the application of these biochemical tracers, there is emerging evidence for large intra-specific variation in diet amongst species of marine mammals related to ontogeny, sex, and body size (e.g. Lesage *et al.* 2001; Iverson *et al.* 1997, 2006; Thiemann *et al.* 2006; Beck *et al.* 2005, 2007). Therefore, through the application of both fatty acid and stable isotope analysis, the main goal of my research has been to examine the diets of seals at varying spatial and temporal scales, and by doing so, increase our understanding of factors influencing the dietary niche breath of large marine predators.

It has often assumed that classes of marine mammals differ in their degree of dietary specialization based on the observed diversity of morphological, physiological and behavioural adaptations (reviewed in Bowen *et al.* 2002). In Chapter Two, I evaluate the degree of dietary specialization amongst species of marine mammals in a comparative manner with terrestrial carnivores in order to define potential factors influencing diet and overall niche breadth of these top predators. I also introduce the novel methods to investigate and estimate diet and emerging concepts of niche breadth related to individual specialization.

In Chapter Three, I apply stable isotope analysis to evaluate diet variation in grey seals. Stable isotopes in marine systems are well differentiated between pelagic and benthic invertebrate and fish due to various physical and biological processes at the base of the food chain (i.e. Davenport and Bax 2002; Sherwood and Rose 2005). My objectives were to test for benthic-pelagic segregation in diets among adults as indicated by sex-differences in diving behaviour (Beck *et al.* 2003), to determine whether sex differences in diet are evident in juveniles, which are considered relatively naïve and physiologically less competent foragers, to investigate within sex effects of body size on isotope signatures and to compare population and individual variability in dietary niche breadth over time through serial sampling of individuals. I also sought to determine the relationship between stable-isotope inferred diet and the rate of energy storage in grey seals.

Subsequently in Chapter Four, stable isotopes were compared with prior fatty acid (FA) estimates for the same individual grey seals (Beck *et al.* 2005, 2007) to evaluate whether or not these independent measures of diet corroborate with each other. This Chapter provides a link between the two methodologies applied in the thesis. Of course, it is difficult to validate diet estimates from either of these methods in the field, particularly for wide-ranging aquatic predators such as a seal or seabird consuming complex diets. However, if these two independent methods provide similar views of the diet then we would have greater confidence in the validity of those estimates. These two approaches represent the assimilated signature from multiple dietary sources. The two methods are independent; one examines the fatty acid composition of lipid stores, the other examines

the isotope ratios of carbon and nitrogen in various tissues or whole body of a consumer and due to a number of factors, potentially offer different insights into the diet of a consumer. In this Chapter, I demonstrate two lines of evidence for the convergence of stable isotope and fatty acid estimates of diet and discuss sources of variation between the two methods and implications for interpretation of diet estimates.

In Chapter Five, I used fatty acid signature analysis to examine the sources of variation in the diets of two sympatric phocid seal species that seem to partition space by both ranging and organizing foraging behaviour in different ways. One species, the harp seal, mainly inhabits the continental shelf (Stenson and Sjare 1997; Folkow *et al*. 2004), while hooded seals are more associated with the continental shelf edge and deep ocean (Folkow and Blix 1999). These species also differ in their diving behaviour with hooded seals diving deeper and longer than harp seals on average (Stenson and Sjare 1997; Folkow and Blix 1999; Folkow *et al*. 2004). Hooded seals also exhibit a far greater degree of sexual-size dimorphism than harp seals, that in other species (i.e., grey seal – Beck *et al*. 2005) has lead to sex-specific difference in diet. Thus I had two main objectives for this Chapter. Given broad evidence for their importance in other taxa, first I sought to evaluate age, size and sex related effects on diet selection for harp and hooded seals. Secondly, to evaluate large-scale temporal and geographic variation seal diets during a decade of expanding population size and large changes in prey distribution and abundance.

In the final Chapter, I defined specific sources of variation in diets of harp and hooded

seals by estimating diets of individuals using quantitative fatty acid signature analysis

(QFASA). Proportional estimates of diet composition can be made at the level of the

individual by statistically matching a consumer's FA signature to an inclusive prey

database, after accounting for predator metabolism effects in a mixing model (Iverson *et*

al. 2004). Subsequently, I evaluated the quality of diets with respect to overall energy

density and niche breadth.

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CHAPTER II: FROM SPECIES TO INDIVIDUALS - FACTORS INFLUENCING DIETARY NICHE BREADTH IN MARINE AND TERRESTRIAL MAMMALIAN CARNIVORES

INTRODUCTION

Quantifying diet has long been considered one of the first steps in understanding the basic ecology of a species. Diet has important consequences with respect to gross energy intake, overall foraging costs, as well as exposure to diet specific risk factors such as predation and parasites (Bolnick *et al.* 2003). Diet can influence the degree of competitive interactions and potential social interactions for individuals sharing similar resources, thereby further affecting fitness and survival. Understanding the degree of dietary specialization is important for studies of resource use and general evolutionary processes, including physiological, morphological, behavioural and social adaptations. All of these components of an animal's ecology converge to facilitate acquisition of basic nutrients. Dietary niche breadth is a metric for measuring the degree of specialization (Krebs 1999). However, it is more than a mere metric, as the concept of niche has pervaded much of ecological theory and directed subsequent empirical work (Chase and Leibold 2003).

The niche concept remains one of the most confusing, variously defined and controversial topics in ecology (as summarized in Chase and Leibold 2003). Perhaps this is due to its dual nature: it is simultaneously used to describe the requirements of an organism from its environment as well as the way in which that organism shapes its environment. In this synthesis, I evaluate the degree of dietary specialization amongst species of marine mammals, in part using what we know about terrestrial carnivores as a

benchmark for comparison. Like their terrestrial counterparts, marine consumers display

a wide array of foraging modes and tactics (Bowen *et al.* 2002). I first review concepts

of ecological niche and the more common indices of niche breadth. I then evaluate

potential factors that may influence the dietary niche breadth of consumers. Finally I

consider the means of evaluating niche breadth and highlight the emerging appreciation

in ecology of the incidence and importance of intra-specific variation in diet selection

through the application of powerful new empirical tools, which are refocusing studies

within the framework of a revised niche concept.

BRIEF OVERVIEW OF THE CONCEPT OF ECOLOGICAL NICHE

It is generally accepted that the founder of the niche concept was Grinnell, who, in a

series of papers (1914, 1917, 1924 as cited in Chase and Leibold 2003) described the

habitat, food and predator-prey relationships of a variety of species. Grinnell simply

outlined the niche as a place in the environment occupied by a species. He used the

concept to qualitatively map all conditions supporting the existence of a species,

including its physiological and morphological tolerances and limitations, as well as

feeding habits and inter- and intra-specific interactions. Conversely, Elton (1927 as cited

in Chase and Leibold 2003) defined the niche of a species as its functional role within the

food web and considered its subsequent impact on the environment instead of Grinnell's

focus on the effects of the environment on the species.

Hutchinson (1957) clarified both the definition and quantification of the niche concept.

He defined niche as the sum of all environmental factors acting on an organism, thus the

"n-dimensional hypervolume" (or space) where n was any number of limiting factors for

a given species. The space occupied by the hypervolume would thus be the space where an organism could exist. Hutchinson (1957) went on to differentiate the realized niche of a species as the component of its fundamental niche to which the species was restricted due to inter-specific competition. This became the crucial framework for quantifying community structure and its development.

Expanding on Hutchinson's approach, MacArthur developed a body of work known as niche theory. This consisted of a group of theoretical models aimed at understanding how many similar species could co-exist within a particular community (McArthur and Levins 1967, MacArthur 1972, Vandermeer 1972). At their foundation were the Lotka-Volterra equations and the view that competition was central to structuring communities. Ecologists went on to measure species niche breadth as well as niche overlap and inter-specific niche partitioning. Perhaps as a result, the term niche became closely associated with the concept of inter-specific competition. In the late 1970's, niche theory fell out of favour, and many ecologists criticized studies of competition and niche theory for lacking appropriate null hypotheses and experimentation (e.g. Simberloff 1978, Strong *et al.* 1979, Simberloff and Boecklen 1981). The role of competition was downplayed for more comprehensive perspectives that included predation and environmental factors. The need to meet the emerging emphasis on experimental and statistical rigour necessitated studies of a smaller, more localized scale (Chase and Leibold 2003).

More recently, Hubbell (2001) suggested that the paradigm of niche perspective should give way to an alternative view in which fundamental patterns in ecology can be

explained by neutral theories and models. Hubbell (2001) proposed that random

fluctuations in birth rates, death rates, immigration and dispersal can reproduce observed

patterns of biodiversity and species composition or relative species abundances.

However, the robustness of the approach is broadly criticized, based on the fact that

models are dependent on unrealistic parameters that cannot be estimated from

observational data (summarized in McGill 2003; Alder 2004). Chase and Leibold (2003)

argue against neutral models suggesting that species do in fact differ in their traits and

often demonstrate tradeoffs that allow them to coexist for long periods of time and

disturbed systems often come back to their original state. They attempt to redefine the

niche concept within a framework that incorporates processes other than simple resource

competition and which reflect both the requirements of a species and the effects of a

species on its environment. These include, for example, growth rates, consumption rates

and death rates. Most importantly, implicit in their proposal is the question of whether or

not ecologists have been defining the appropriate niche parameters.

Recently, and independent of Chase and Leibold (2003), Williams and Martinez (2000)

developed a simple model of trophic niche space. This model predicts important

structural properties of documented complex and comprehensive food webs, including

the fraction of species at the top, intermediate and bottom trophic positions, food-chain

length, and degrees of cannibalism and omnivory. However, interestingly, their model

lacks repulsion of overlapping niches owing to inter-specific competition. Instead, size-

related constraints on feeding are implicated as the potential basis for the model as this

can influence resource partitioning and trophic status within food webs (Williams and Martinez 2000; Woodward and Hildrew 2002).

Occupied niche space implies explicit resource use. Trophic niche breadth is the most studied component of niche space using conventional dietary analyses, namely stomach and fecal content analyses. However, there are practical problems associated with these conventional dietary analyses making it difficult to obtain accurate estimates (as reviewed in Bowen and Siniff 1999). Furthermore, such methods often simply provide a snapshot of most recent diet at the time of sampling. At its simplest, dietary niche breadth is a measure of the degree of dietary specialization of a species or individual. Various indices have been used to characterize the diet (Krebs 1999). Levin's index (B) is perhaps the most commonly used. B estimates niche breadth by quantifying the uniformity of distribution of items in the diet and is the reciprocal of Simpson's index of diversity. As defined, B is maximum when there is an equal proportion of each prey type in the diet, suggesting the species does not discriminate and has the broadest possible niche. B is often standardized for comparing across species by correcting for a finite number of resources. A clear problem with this method is that the index does not allow for the possibility that resources vary in abundance over time and space. Another index is the Shannon-Wiener Index (H), which borrows from information theory. While B tends to weight the abundant prey eaten more heavily, H gives more weight to more rare prey. Thus, the two indices provide a more detailed description of overall dietary niche breadth when combined.

POTENTIAL FACTORS INFLUENCING DIETARY NICHE BREADTH

While many studies have documented the degree of dietary specialization in terrestrial mammals, much less is known about prey selection in marine mammals. It is often assumed that classes of marine mammals differ in their degree of dietary specialization based on the observed diversity of morphological, physiological and behavioural adaptations (Bowen *et al.* 2002). For example, many species of cetaceans display very specialized adaptations of the feeding apparatus. Alternatively, pinnipeds are assumed to be generalist predators given their wide-ranging foraging behaviour and the number of different prey species identified from stomachs. There are of course exceptions within pinnipeds, and it is often found that relatively few prey species account for the majority of ingested energy (e.g. Bowen and Harrison 1994). However, these potential overall differences and the factors influencing dietary specialization have not been fully evaluated given the difficulty of studying marine mammals at sea (Bowen *et al.* 2002). I suggest that a logical starting point to assess niche breadth variation in these marine carnivores is an examination of factors influencing their diets in comparison to those of their terrestrial counterparts in the Order Carnivora. Carnivores living in aquatic environments have many adaptations to an aquatic lifestyle. Studies of adaptations have focused on morphological differences, but it is unclear whether these adaptations extend to other functional traits. Examining 20 morphological, life-history, physiological and ecological traits, Bininda-Emonds *et al.* (2001) found that the adaptive differences between marine and terrestrial mammals are limited and apparently no more numerous than those that occur within each group.

Body size influences the amount of energy an animal requires. Standard metabolic rate generally scales to body mass with an exponent of $M^{0.75}$ (Kleiber 1975; Darveau *et al.* 2002; Weibel 2002). Although the specific exponent is still a matter of contention for marine mammals (as summarized in Boyd 2002), it is thought that they generally conform to the Kleiber relationship. Variation in body size of sympatric terrestrial carnivores with similar morphology and foraging strategies is correlated with mass of their prey (e.g. Woodward and Hildrew 2002), as larger predators often consume larger prey items in order to satisfy larger absolute energy requirements. Thus, variation in predator body mass is thought to have evolved to reduce competition (Rosenzweig 1966, 1968). However, it is commonly found that predator size determines dietary overlap, as emphasized by the observation that ontogenetic shifts in diet, which are of course related to changes in body size, often outweigh overall species differences (Woodward and Hildrew 2002).

For terrestrial vertebrate predators, there is a striking transition in prey selection occurring at a predator mass of approximately 21.5 kg, with those species weighing less than this taking prey on average <45% predator mass and those above taking prey of >45% predator mass (Carbone *et al.* 1999). Additionally, all canid and felid species above the mass threshold feed purely on vertebrates, while those below the threshold may feed omnivorously or include invertebrates in their diet. Animals near the threshold (e.g., badgers, skunks) feed on invertebrate prey or plant matter if it is a superabundant resource. However it appears that omnivory is unsustainable for larger predators who have larger absolute energy requirements. Thus predator body size appears to determine

both the prey size and the type of prey that can be consumed in order to efficiently satisfy energy requirements. As a result, it is likely that there is an interaction between body size and both energy requirements, and prey availability, as well as the overall efficiency with which prey can be consumed and digested, which drives consistent patterns in resource use and diet in terrestrial animals (Carbone *et al.* 1999). The pattern of predator-prey size structuring is not apparent in marine mammals, as most species consume prey that is smaller than themselves, often by many orders of magnitude. However in size-dimorphic marine mammals, the larger sex often consumes larger prey items, or alternatively, the sexes have different diets altogether (reviewed in Bowen *et al.* 2002). This is thought primarily to be an effect of increasing dive and swimming capacity in larger animals, or of differences in reproductive expenses and consequences between sexes.

Space use in animals is associated with body size (in Jetz *et al.* 2004) leading to the inference that spatial use reflects energetic needs. This has led to general scaling rules between body size and area use with respect to overall population density and home range size. Compiling an extensive dataset, Kelt and Van Vuren (2001) demonstrated that home range size is positively related to body mass for all trophic groups (carnivores, omnivores and herbivores). Carnivores have larger home ranges than omnivores of the same mass, which in turn have larger home ranges than herbivores. However they found no differences in slopes among trophic groups, yet home range size scaled to body size with an exponent greater than the 0.75 exponent predicted by energetic needs alone. Thus, Kelt and Van Vuren (2001) suggest that for an animal of a given size, home range area is constrained both by the need to obtain resources sufficient for survival and by

decreasing gains relative to costs associated with larger home ranges. Building on the

same dataset, Jetz *et al.* (2004) demonstrate that factors such as interactions between

individuals and loss of resources to neighbours likely influence the steep rate at which

home range area increases. A common rule for scaling of terrestrial carnivore density has

been found (Carbone and Gittleman 2002) in which there is an inverse relationship

between population density and body size of predators. The suggestion is that resource

requirements and prey availability appear to be driving consistent patterns in consumer

abundance, with the underlying mechanism related to the energy requirements of the

consumer. It is postulated then that home range size should influence dietary niche

breadth. Indeed a positive correlation between range size and dietary niche breadth has

been found for some mammalian species, such as in communities of primates (e.g. Eeley

and Foley 1999; Jones 1997) with an exponent of approximately $M^{0.25}$. Interestingly, a

broad variety of temporal measures including muscle contraction time, cardiac cycle

time, gestation time, time to maturity and life span, generally scale around $M^{0.25}$ as

opposed to the energetic scaling of $M^{0.75}$ (Kelt and Van Vuren 2001). It has also been

found empirically that the day range of terrestrial mammals, or the average distance

traveled in one-day scales as $M^{0.25}$ (Garland 1983, Swihart *et al.* 1988, Carbone *et al.*

2005). It is thought that day range represents a short-term measure of space requirements

that at least in part reflects food resource needs (Garland 1983) as well as the distribution

of food resources and foraging strategy in consumers, as morphology, and modes of

foraging are more consistent within taxonomic groups than within dietary groups

(Carbone *et al.* 2005).

It has been suggested that landscape perception by mammals is dependent on body size, with small-bodied mammals perceiving landscapes as less homogenous than larger mammals (Lidicker and Koenig 1996). As well, more vagile species likely perceive landscape variability on a different scale then more sedentary species (Kolasa and Rollo 1991). Relative to larger, more vagile animals, small mammals may view heterogeneity as a barrier to movement and perceive patches within landscapes as isolated (Gehring and Swihart 2003). In a study of habitat fragmentation in an agricultural landscape, Gehring and Swihart (2003) demonstrated that small species had smaller habitat niches and were more constrained spatially in their resource selection. They observed strong inter-specific differences in species responses to spatial elements as, for example, coyotes and foxes were capable of moving freely among all elements, while weasels were confined to linear elements and forest patches. Therefore, it appears that a species' perception of landscape and behaviour are important in defining habitat use and subsequent resource use and that a range of spatial scales should be considered. Information on spatial scaling patterns is not as well understood in marine predators as there are very few studies in the literature that have explicitly documented home range size for marine mammals.

There are of course other factors beyond energetic considerations which are thought to influence an animal's use of space, such as behaviour and perception of habitat (Gehring and Swihart 2003). Irrespective of body size, predators vary in their hunting or foraging behaviour, with these differences often more pronounced along Family lines (Carbone *et al*. 2005). It is likely that these behavioural differences operate to further influence diet selection. Take for example, a study of sympatric cougar and wolf predation, in which

wolf kills occurred in habitat more reflective of the entire study area than did cougar kills (Husseman *et al.* 2003). This suggests that the hunting behaviour of wolves, which is characterized by a chasing mode of capture, likely operates on a larger spatial scale than the ambush hunting tactic of cougars (Husseman *et al.* 2003). The authors noted that the difference in prey selection was a function of hunting behaviour and capture success. Cougars function as solitary hunters and prey capture is limited by their own size. In contrast, for some predator species, group hunting can serve to reduce morphological disadvantages such that larger prey can be killed. Thus, the success rate of hunting may determine prey selection patterns when prey species are difficult to capture. Canids usually chase swift prey. To counter a potentially low capture success, disadvantaged prey should be favoured. Felids generally stalk prey and rely on concealment and therefore should favour a random choice of individuals. Thus in terrestrial systems, body size and behavioural flexibility should influence niche breadth since more highly mobile species should be able to use more diverse habitats and food items. In marine mammals as a whole, there is a wide diversity of hunting strategies observed, including both group and solo hunting strategies (reviewed in Bowen *et al.* 2002).

It follows that dietary niche breadth is not only influenced by factors intrinsic to consumers, but by broad scale patterns of resource availability and community structure. For example, ecologists have predicted that niche breadth should decrease with decreasing latitude (the latitude-niche breadth hypothesis (MacArthur 1972)). This stems from the observation of a gradient of increasing species richness with decreasing latitude for many taxa, however this does not appear to be a universal phenomenon (reviewed in

Vàzquez and Stevens 2004). MacArthur (1972) assumed that because of greater environmental stability and lower seasonality in the tropics, populations at low latitudes should be more stable than populations at higher latitudes and, in turn, greater population stability should promote narrower niches. An implicit assumption is that there is a trade-off between wider resource use and foraging efficiency, such that specialists use their narrower range of resources more efficiently than generalists. In a recent synthesis of niche breadth parameters (ranging from habitat use to prey number) for different orders of terrestrial organisms, Vàzquez and Stevens (2004) concluded that evidence generally does not support the prediction of the hypothesis. Furthermore, they found that the key assumption of a gradient in environmental and population stability with latitude, on which the hypothesis was founded, is supported only equivocally. They suggested that latitude could affect niche breadth only indirectly through species richness. It is commonly assumed that marine tropical systems tend to have greater species richness and are more stable than marine polar regions which tend to be viewed as less diverse yet highly productive (though blooms in production are temporally constrained) (Vàzquez and Stevens 2004). No study has evaluated the generality of the pattern in marine systems, although Rohde (1992) has raised concerns about the assumed environmental stability of tropical marine systems, a cornerstone assumption of the latitudinal niche hypothesis. Finally, although there are large differences in structure, productivity and biomass between terrestrial and marine systems (Cohen 1994), there is debate as to whether or not the mechanisms operating to control overall food web structure are in fact the same (see Cohen 1994; Chase 2000; Link 2002). Terrestrial systems are thought to be more species rich, yet food webs in marine systems are considered to be more highly

connected than terrestrial food webs (Cohen 1994). Connectence is the total number of observed trophic links divided by the total possible number of trophic links. Thus marine systems overall are thought to be dominated by generalists.

Conclusions drawn about niche breadth are dependent on the calculations of standard indices, which in turn are ultimately dependent on the quality of diet data reported in individual studies. The degree of taxonomic description of prey is highly variable among studies. Many studies report some items only to the genus level and very few report the range in prey size for a given species. Studies also vary in their temporal and spatial scales, and very few attempt to make any kind of distinction amongst sex, age or size classes of predators themselves. How discrete prey identification for different classes of predator species influences our understanding of niche breadth is best exemplified in the following two studies.

In a unique study, Radloff and du Toit (2004) documented > 4000 kills of sympatric lions, cheetah, leopards and wild dogs over a continuous 13-year period in South Africa. For each kill not only the species of prey was recorded, but the respective sex and age class as well. They found that prey profiles of most predators were skewed towards a high representation of prey that were smaller than the predator. However, the maximum prey size increased with predator size, thereby increasing the variation in prey sizes taken. Whether considering prey species or prey types, they found no relationship between predator body size and prey diversity. They did find large dietary overlap among predators. These results were consistent across size dimorphic sexes. Their results

suggest that large predators do not specialize on large prey but exploit a wider range of prey sizes by opportunistic behaviour. However, when calculating niche breadth with very discrete taxonomic data categorizing not only species but also size classes of species, there is a relationship of increasing niche breadth with body size. In an independent study of predator guilds, Sinclair *et al.* (2003) found as well that overall the diet niche of smaller carnivores was nested within that of larger carnivores. So in these cases there is a relationship between predator size and niche breadth. However it is not a function of increasing number of prey species but rather an increasing range of prey sizes for a given set of prey species.

The above studies point to the utility of examining sympatric predators in the same way, in the same area, over a long period of time, and perhaps most importantly, compiling complete prey profiles with greater discretion, though predators were still lumped into broad categories of sex and species. Of course the concept and indices of dietary niche breadth are dependent on the degree and quality of information. What are the implications for our understanding of a species' niche breadth if we were as equally discrete about describing individual predator prey selection instead of simply considering a species' average diet? Naturally, it is not always possible to do so, either because of limitations of standard techniques and their applicability to a predator of interest, or of course, limited resources available to the researcher. The question then, is whether or not it might matter.

INDIVIDUAL VARIATION IN DIET SPECIALIZATION

Niche theory has long treated conspecifics as equivalents in for example, models of competition, predation and food web structure and, the current analysis. However, Bolnick *et al.* (2003) suggest that individual variation has been ignored, as many ecologists believe specialization is rare and weak, or may have trivial impacts on ecological processes such that population averages are sufficient. However, there is considerable evidence of individuals using different resources. On the basis of observations of mainland and island bird populations, Van Valen (1965) suggested that population niche expansion in the absence of inter-specific competition was achieved through increased between-individual niche variation in resource use. Roughgarden (1972, 1974) supported the niche variation hypothesis in subsequent theoretical work where he provided a quantitative framework for considering inter-population niche variation. Roughgarden suggested that the total niche width (TNW) of the population can be portioned into two components. The between-individual component (BIC) is the variation among individuals, while the within-individual component (WIC) is the average variance of items within individuals' diets. Individual variation is large when BIC is a large proportion of TNW. Subsequent empirical data varied from supportive, inconclusive to negative (summarized in Bolnick *et al.* 2003). In recent years there has been renewed interest in the discussion of individual variation and the niche variation hypothesis within the context of adaptive radiation and speciation (e.g. Schluter 2000). Individuals of different age, sex and morphologies are expected to exhibit differences in niches. These are encapsulated in the concepts of ecological sex dimorphism, ontogenetic niche shift, and resource polymorphism. Bolnick *et al.* (2003) assert than there can be

important niche variation beyond those concepts and define an individual specialist as an individual whose niche is narrower than its population's niche for reasons that cannot be attributed to its sex, age, or discrete morphology. Here, individual variation and polymorphism are viewed as ends of a continuum of increasingly discrete variation where individual specialists cannot clearly be assigned to distinct morphotypes (at least not yet). Following this definition of specialization, Bolnick *et al.* (2003) documented 93 cases from the literature of inter-individual variation occurring even within sex, age and morphological groups of various species. Bolnick *et al.* (2003) did not address the frequency or degree of individual specialization amongst animal populations since there is a bias towards only reporting positive results of significant diet variation. However, it does strongly demonstrate that individual specialization does indeed exist.

In the case of marine mammals, Estes *et al.* (2003) found that sea otters selected a large range of prey in any location. Diet diversity was highest where populations were at high levels and food resources were limiting. They noted a total of 32 prey types, but individuals specialized on only 1-4 items, some of them exclusively. There was some overlap, but individuals generally differed on the second and third most abundant prey species in the diet. Diets of most individuals remained unchanged throughout the 7-year study. Pups had a high degree of similarity to mothers as well as weaned offspring. The results suggest that prey selection in otters follows maternal lines and is based on learning, despite overlap in foraging ranges. Studies estimating diets for individuals of other species of marine mammals also demonstrate a high degree of variation, although temporal consistency within individuals has not yet been analyzed (reviewed in Bowen *et*

al. 2002). In addition, foraging behaviour (diving, movement) is highly variable amongst individuals, although a direct link with diet has not been made at this point (e.g. Austin *et al.* 2004). These observations suggest that further examples of individual dietary specialization in other species of marine mammals should be expected.

Why would individuals, each acting strategically to choose resources in a common environment, arrive at different outcomes? Estes *et al.* (2003) argued that there is no generally recognized theoretical framework for understanding the mechanisms by which alternative diet specializations arise or what the implications are for population and community level processes. Optimal diet theory provides a paradigm for explaining and predicting predator diet selection. Basically, predators should prefer prey, which yield more energy per unit handling time and as the abundance of high value prey increases, the proportion of lower value prey in diet should decrease. However, many of the above examples cannot be explained by optimal diet theory and the convergence on an optimal diet, even by models that also include risk-sensitive foraging behaviour and context-dependent optimal strategies (Sih and Christensen 2001; Estes *et al.* 2003; Bolnick *et al.* 2003).

Both Estes *et al.* (2003) and Bolnick *et al.* (2003) make conjectures on the potential mechanisms that produce individual specialization and what these may mean for broader issues of community stability and evolution. It is postulated that individuals will use different resources if they have different resource-use efficiencies or preferences based on variable morphological, behavioural, cognitive or physiological capacities. Tradeoffs

are thought to be one of the most plausible mechanisms for limiting an individual's niche breadth in that there is a potential constraint on generalism (i.e. adopting one strategy to specialize on a prey may limit the ability to efficiently exploit another prey). Tradeoffs have been demonstrated in factors such as prey recognition, capture and digestion (e.g. Werner et al. 1981, Afik and Karasov 1995). Other mechanisms such as territoriality in patchy environments can cause individual specialization. Diversification of specialist types may be favoured when the benefit an individual gains from consuming particular prey depends on what other individuals are doing, thus both frequency- and density-dependent effects. In theory, an equilibrium frequency of different foraging types could be reached where all prey items yield an equal benefit (because most valuable prey would be depleted). Thus specialization could act to limit or reduce intra-specific competition and could likely be important to components of population and community ecology. Even if the incidence of individual specialization proves to be widespread, is it relevant and necessary to incorporate individual level data into ecological models? Variation in niche breadth could facilitate potential frequency-dependent interactions affecting population stability, competition, fitness, response to environmental change and ultimately diversification and speciation (Bolnick *et al.* 2003). Traditional models of evolution emphasize optimization and convergence on a single optimum. However Estes *et al.* (2003) contend it is likely that much variation persists due to complex frequency–dependent interactions where variation is a both a product of and target for selection.

NOVEL APPROACHES: NEW TOOLS FOR ESTIMATING CARNIVORE DIETS

Following from the previous discussion on individual variation, an important question is whether a population that appears to show a large dietary niche breadth is composed of generalist individuals, each taking a wide range of prey, or of individuals all specializing on a different but narrow range of prey. Distinguishing between the two types of population generalization is difficult to achieve through conventional diet analysis. However, there are emerging techniques to estimate diet and niche width that allow for direct, standardized comparison amongst individuals, populations and species and allow for the temporal integration of diet over different timescales. These are stable isotope analysis and quantitative fatty acid signature analysis. Both of these biochemical tracer approaches can provide inferences about or quantitative estimates of diet that are time-integrated and alleviate biases associated with more traditional approaches of fecal and stomach content analysis (Iverson *et al.* 2004). In addition, sampling can be done non-lethally allowing for longitudinal study of individuals over time. Stable isotopes allow for direct comparison among individuals and provide temporal integration of diets over different timescales owing to the analysis of different tissues with different turnover times (Bearhop *et al.* 2004). The concurrent analysis of stable carbon and nitrogen isotopes provides a two-dimensional picture of the dietary space occupied by a consumer, but does not permit the individual prey species to be identified. By contrast, fatty acid signature analysis can provide quantitative estimates of diet (Iverson *et al.* 2004). Estimates of diet can be made at the level of the individual by comparing a consumer's signature to an inclusive prey database. Subsequently, individual diet estimates can be directly linked to foraging variables and other phenotypic traits.

A NEW (OLD) SYNTHESIS

Although the concepts of niche breadth and dietary niche have been with us for the last 80 years, only recently with the application of novel techniques are we on the verge of broadly documenting the degree of specialization in and amongst animal populations in a systematic and efficient manner. This may lead to an understanding of factors influencing dietary selection in predators across many scales.

At is simplest, niche describes differences between individuals or species. Overall, though niche breadth is highly variable it appears to be dependent on different factors such as body size, spatial use and hunting strategies. One might speculate that in turn such factors may be related to physiology, behaviour, population structure, species interactions and differing environments; factors, which require further study. However, if ontogenetic diet shifts (typically related to changes in body size) within species are greater than between species differences in diets, as Woodward and Hildrew (2002) contend, then our understanding is limited in its scope, since the best available data merely describe a species' average diet. That being said, I think it is fair to ask whether we are in fact measuring the most relevant niche parameters at the appropriate taxonomic level. Simply itemizing diets and enumerating diet breadth is limiting and unsatisfying. The rather vague concepts of niche breadth and niche overlap should be brought into context through a more mechanistic synthesis; the most rewarding would be that of a currency-based framework of energy flux, where diet is a component of energy budgets. I agree with Chase and Leibold (2003) who reframe the niche concept in terms of measurable, mechanistic and process-orientated aspects of an organism's biology such as

growth rates, consumption rates, as well as foraging costs and foraging efficiency relative to growth. Such a process-orientated approach allows for an evaluation of both an organism's response to the environment and its impact on the environment. Of course, this approach is as much a proposition as a challenge to ecologists, as we have not yet found efficient means of measuring these parameters in most organisms.

Estes *et al.* (2003) contend that there is no current theory to understand individual variation in foraging behaviour or strategies. However, the invocation of tradeoffs and observation of different strategies is reminiscent of classical bioenergetic theory espoused by Lindeman (1949), Odum and Pinkerton (1955) and Odum (1969). Energy is viewed as the fundamental currency of ecosystem processes and the efficiency of trophic transfer determines growth rates of individuals and the overall production of the system. Therefore, actually quantifying energy flow through individuals and populations leads to a dynamic, mechanistic understanding of community structure. In this context, species or individuals are viewed within a spectrum of energy strategies, with the number of energy 'niches' constrained by the rate of supply of limiting raw materials. Based on the laws of thermodynamics, species (or individuals) are postulated to display maximum efficiency of energy use with inputs and outputs minimized, or alternatively, display maximum output in the form of growth or reproduction with higher throughputs of energy. In the latter strategy there is a sacrifice to efficiency as there is greater energy dissipated through maintenance and activity. This bioenergetic perspective is not equivalent to optimal foraging or optimal diet theories, which assert convergence on some preconceived theoretical optimum, notion of competitive superiority or optimal diet.

Dietary specialization or generalization can be viewed as ends of a continuum of energetic strategies, each with particular tradeoffs.

Ecology seems to be progressing along what appears to be two divergent routes. On the one hand are the large-scale meta-analyses, which have given rise to concepts such as Neutrality. On the other are the development of powerful and specialized empirical tools that allow for greater resolution and increased documentation of variation in nature. Neutral theory postulates that the variation is not really important, while traditional niche concepts are more centered on defining absolute differences, basically focusing on mean values. As Judson (1994) alleges, ecologists have in fact obscured interesting patterns in pursuit of both simplification and generality. It is more likely that there is a middle ground somewhere between neutral based concepts of sameness, accompanied by random processes, and the traditional niche based concept of discrete differences acting to structure biological systems. Emerging concepts of the niche attempt to evaluate the mechanisms, which create, maintain and propagate variation.

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CHAPTER III: DIMENSIONS OF DIET SEGREGATION IN GREY SEALS REVEALED THROUGH STABLE ISOTOPES OF CARBON (δ^{13}C) AND NITROGEN (δ^{15}N)

INTRODUCTION

Vertebrate diets are influenced by factors intrinsic to the organism and by extrinsic or ecological factors. Body size is thought to be a crucial determinant of food web patterns and processes (Chase 1999; Williams and Martinez 2000; Memmott et al. 2000). An increase in predator size is associated with an increase in both mean prey size (Carbone et al. 1999, Radloff and du Toit 2004) and prey diversity (Gittleman 1985; Cohen et al. 1993). It is hypothesized that larger predators consume larger prey items to satisfy greater absolute energy requirements. Moreover, predator size generally determines inter-specific dietary overlap (Sinclair et al. 2003), as ontogenetic shifts in diet often outweigh the variation in diets across similarly sized species (Woodward and Hildrew 2002). Among terrestrial vertebrate carnivores (with body sizes spanning more than three orders of magnitude), body size influences not only relative prey size but also the type of prey eaten. For example, small terrestrial carnivores consume an omnivorous diet (plant, invertebrate and vertebrate), whereas large predators consume a diet comprised primarily of vertebrate prey (Carbone et al. 1999). This switch in diet is concurrent with a change in mean prey size that exceeds predator mass. The transition to an exclusive carnivorous diet with increasing body size is thought to reflect a simple energetic constraint: the inability to sustain body size based on relatively smaller and lower quality prey. Thus for terrestrial carnivores, body size appears to influence both the prey size and the type of prey that can be consumed in order to satisfy energy requirements.

In contrast, a correlation between predator body size and prey size is not as apparent among upper-trophic level marine carnivores, as most species consume prey smaller than themselves, often by several orders of magnitude. However, within size-dimorphic predators, the larger sex often consumes larger prey items, or alternatively, the sexes have different diets altogether (reviewed in Bowen *et al.* 2002a). There is mounting evidence for sex differences in the foraging behaviour of size-dimorphic marine mammals, where males are significantly larger than females (Le Boeuf *et al.* 1993, 2000; Beck *et al.* 2003a, b; Field *et al.* 2005; Breed *et al.* 2006). Differential resource use by the sexes, observed in both size dimorphic (e.g. Clarke *et al* 1998) and monomorphic (e.g. Lewis *et al.* 2002) species, may also be due to variation in the sex-specific costs of reproduction (Ginnett and Demment 1997). Ontogenetic diet shifts are thought to result from either differing energetic costs associated with body size or learning (Estes *et al.* 2003).

There is an also increasing recognition of the relatively high degree of individual variation in foraging behaviour and diet among marine carnivores (e.g., Estes *et al* 2003, Bolnick *et al.* 2003, Austin *et al.* 2004, 2006a). This is in contrast to the idea of a population level optimal diet (Sih and Christensen 2001). Intra-specific variation in diet that cannot be explained by intrinsic factors has been documented in insects, fishes, reptiles, birds, ungulates and mammals (reviewed in Bolnick *et al.* 2003 and Estes *et al.* 2003).

Despite the importance of understanding predator diets, the methods used to estimate diet are often subject to considerable bias (Bowen and Siniff 1999). However, stable isotopes

of nitrogen ($^{15}N/^{14}N$; $\delta^{15}N$) and carbon ($^{13}C/^{12}C$; $\delta^{13}C$) have proven to be useful tools for

estimating trophic positions of, and carbon flow to, consumers in food webs (Post 2002).

Isotopes of nitrogen are enriched in consumers relative to diet by an average of 3-5 ‰

(Hobson and Welch 1992; Hobson et al.1994) thereby providing a measure of trophic

position. Carbon isotopes are enriched by <1 ‰, and are more indicative of carbon source

or habitat. In marine systems, a benthic-pelagic continuum has been identified with $\delta^{13}C$

increasing from negative (depleted) values for pelagic species to more positive (enriched)

values for benthic species, and $\delta^{15}N$ increases with trophic level within each system

respectively (Davenport and Bax 2002; Sherwood and Rose 2005). Isotope signatures of

consumers represent the assimilated portion of diet integrated over periods of weeks to

months (Hobson et al 1996; Kurle and Worthy 2001; Lesage et al. 2001). Taken together,

$\delta^{15}N$ and $\delta^{13}C$ provide a two-dimensional, standardized estimate of the dietary space

occupied by a predator relative to other consumers and prey in an ecosystem. Thus, stable

isotopes indicate trophic relationships related to functional patterns of feeding rather than

taxonomic relationships (Davenport and Bax 2002). Recently, Bearhop et al. (2004)

suggested using stable isotope ratios to estimate dietary niche breadth by examining the

variance within and between populations of consumers. This approach provides a

practical measure of trophic niche breadth since it is relatively simple to obtain and stable

isotopes integrate diet, both prey diversity and evenness, over an ecologically meaningful

time-scale.

Grey seals, *Halichoerus grypus,* are a size-dimorphic phocid species, with males 1.5

times heavier than females. Recent studies have indicated sex-differences in adult

foraging behaviour at the level of individual dives and seasonal habitat use (Beck *et al.* 2003b; Austin *et al.* 2006b; Breed *et al.* 2006). Males dive deeper with more flat bottom shaped dives potentially indicative of benthic foraging, whereas females dive longer, and tend to display strong diurnal patterns in depth of diving suggestive of pelagic foraging. Adult males and females also differ in their seasonal patterns of energy storage and expenditure (Beck *et al.* 2003a). As in other phocid seals, dive capacity of grey seals in their first year of life is constrained by their physiology (Noren *et al.* 2005). Thus, relative to adults, juveniles presumably have poorer foraging ability and may have access to fewer or different types of prey than adults. (e.g. Baker and Donohue 2000; Noren *et al.* 2005). These differences in foraging suggest that diets may vary between the sexes and that this variation may have an ontogenetic component.

My objectives were to test for benthic-pelagic segregation in diets among adults as indicated by sex-differences in diving behaviour, to determine whether sex differences in diet are evident among relatively naïve and physiologically less competent foragers, to investigate within sex effects of body size on isotope signatures and to compare population and individual variability in dietary niche breadth over time. I also sought to determine the relationship between stable-isotope inferred diet and the rate of energy storage in grey seals.

METHODS

Grey seal sampling

The study was conducted on Sable Island (43°55′N, 60°00′W), a vegetated sandbar

approximately 45 km long, about 300 km SE of mainland Nova Scotia, Canada, from

1996-2001. Seals breed on the island in January, return to moult in spring, and haul out

on the Island periodically at other times of the year (Beck *et al*. 2003a). Individuals were

captured onshore using hand-held nets (see Bowen *et al*. 1992) and most animals were

weighed to the nearest 0.5 kg. Skin samples (approximately 0.05-0.1g) were taken from

the rear flipper of known-aged adult male (n=36) and female (n=36) grey seals in May-

June (spring) or September-October (fall) and the same animals were re-sampled in

January (winter) at the start of the breeding season. Twenty-nine juveniles (mostly

yearlings; n=14 male, n= 15 female) were sampled in January 2004. Skin samples were

lipid extracted using a modified Folch method (Iverson *et al*. 2001) and analyzed for

stable isotopes of carbon and nitrogen. Total body fat content was determined in a sub-

sample of these adults using hydrogen isotope dilution (Beck *et al*. 2003a and Austin

unpublished). Mass gains (kg·d^{-1}) were calculated as the change in total mass (kg)

between sampling times (initial capture date in spring or fall and recapture date in

winter), divided by the sampling interval (d). Similarly, fat accumulation rates (kg$_{fat}$·d^{-1})

were calculated as the change in fat content (kg$_{fat}$) between sampling times divided by the

sampling interval.

Fish and invertebrate prey sampling

Fishes and invertebrates were collected and frozen during stratified, random, bottom-trawl surveys conducted in the summer on the Scotian Shelf (Northwest Atlantic Fisheries Organization sub areas 4V, 4W, and 4X) in 2000 and 2001 (see Budge *et al.* 2001). Three individuals each of 12 fish and 3 invertebrate species were thawed and fork length or carapace width was measured to the nearest 0.1 cm and body mass to the nearest 0.1 g. Each individual was then homogenized. Lipids were quantitatively recovered in duplicate from sub-samples (approximately 1.5 g) of the homogenized tissue using the modified Folch method as above (data contained in Budge *et al.* 2002). An additional sub-sample (approximately 1.5 g) was subsequently analyzed for stable isotopes of carbon and nitrogen. Fishes and invertebrates were classified as pelagic or benthic based on previous knowledge of feeding habits (Scott and Scott 1988, Sherwood and Rose 2005). Because my sample of prey and invertebrates represent only a sub-sample of potential prey on the Scotian Shelf, for some analyses, I expanded my dataset by using stable isotope values from the Gulf of St Laurence (Lesage *et al.* 2001) and the southern Grand Banks (Sherwood and Rose 2005). Both areas are part of the foraging range of NW Atlantic grey seals (Bowen *et al.* 2006). Since the samples of Lesage *et al.* (2001) were lipid extracted prior to stable isotope analysis, I standardized my data and the data from Sherwood and Rose (2005) so that all data was directly comparable. Lipid-normalized values of $\delta^{13}C$ were calculated from reported C:N ratios using the equations in McConnaughey & McRoy (1979).

Stable isotope analysis

Seal, fish and invertebrate samples were dried to constant weight (for 48 h at 80 °C in a drying oven) and crushed to a fine powder using a mortar and pestle. Stable carbon and nitrogen isotope ratios of these samples were determined by the analysis of CO_2 and N_2 produced by combustion in a CE Elemental Analyzer followed by gas chromatograph separation and analysis with a Delta plus isotope ratio mass spectrometer (G.G. Hatch Isotope Laboratories, University of Ottawa, Ottawa, Ontario, Canada). Stable carbon and nitrogen ratios were expressed in delta (δ) notation, defined as the parts per thousand (‰) deviation from a standard material: $\delta^{13}C$ or $\delta^{15}N = ([R_{sample}/R_{standard}] - 1)$ X 1000; R = $^{13}C/^{12}C$ or $^{15}N/^{14}N$). Standards used were PDB limestone for $\delta^{13}C$ and N_2 in air for $\delta^{15}N$. A sub-sample (8%) was analyzed in duplicate; the average standard error of the mean for replicates was 0.15 ‰ for $\delta^{13}C$ and 0.18 ‰ for $\delta^{15}N$. Total carbon and nitrogen of samples were measured simultaneously during stable isotope analysis (G.G. Hatch Isotope Laboratories, University of Ottawa, Canada). C:N ratio is considered a relatively good surrogate for tissue lipid content (i.e. higher lipid samples have higher C:N ratios; Tieszen et al. 1983). $\delta^{13}C$ values of skin in pinnipeds is known to fractionate by 2.8‰ over prey (Hobson et al. 1996; Kurle and Worthy 2001). Therefore, when comparing seal to potential prey, $\delta^{13}C$ values for seal skin were corrected for the known fractionation of the tissue.

Statistical analysis

I used General Linear Models (GLMs) with Gaussian error distributions to test the following hypotheses: do stable isotope signatures vary between trophic guilds (pelagic

or benthic) of fishes and invertebrates, is the C:N ratio was a suitable proxy for prey lipid

content, does lipid content (C:N ratio) vary among trophic groups of fish and

invertebrates using my data and the expanded dataset of Lesage *et al.* (2001) and

Sherwood and Rose (2005).

Grey seals are wide-ranging predators, but there is some evidence that those sampled in

the fall may use somewhat different areas than those sampled in the spring (Austin *et al.*

2004; Breed *et al.* 2006). Furthermore, some prey species eaten by grey seals also exhibit

seasonal variation in distribution and abundance (Bowen *et al.* 2006). I ran a GLM on

cross-sectional data to jointly test for the effects of initial sampling period (spring vs. fall)

and sex on the stable isotope values at recapture (January). First, I tested for an effect of

sex on stable isotope values at recapture within each sampling period and secondly, I

compared males and females, respectively, between the two sampling periods.

I used my longitudinal data on each adult to test for the effects of sex, body size, and

season on stable isotope values, using Repeated-Measures General Linear Models (RM

GLM). As prey differ in energy content, using GLM I tested whether isotope values (my

proxy for diet) had an effect on the rate of energy accumulation ($kg_{fat} \cdot d^{-1}$) and overall

energy content (% fat) of seals. Since the highest rate of fat accumulation for both sexes

occurs in the fall (Beck *et al.* 2003a), I used the fall sampled animals to test this

hypothesis. I also ran a GLM to test for differences in diet with age, by comparing winter

stable isotope values of adults and juveniles. To examine temporal changes in diet and

the effects of sex, sampling season and mass gain on the change in isotope signatures, I

ran a GLM on the difference between the final and initial $\delta^{13}C$ and $\delta^{15}N$ values for each adult. I had insufficient samples to examine interannual effects.

I examined the relative dietary niche breadth of grey seals by estimating the relative range of prey species consumed by juveniles and adults, where a wider niche breadth should be reflected in a larger variance of isotope signatures (Bearhop *et al.* 2004). I also examined the degree of dietary specialization among individuals using a repeated-measures GLM by comparing the mean variance within and between individuals (Bearhop *et al.* 2004). Bearhop *et al.* (2004) postulate two types of generalist populations: first, where all individuals are generalists in their diets, and second, where all individuals are specialists on different prey items, but taken as a whole the population can be described as generalist. One would expect the variation measured sequentially within individuals from the former population of generalists to be approximately equal to the variation found in a sample representative of the whole population, while for the later generalist population, one would expect the variance from sequentially measured individuals to be low compared with the variance derived from a single sample of the population at any one time.

All possible models with two-way interactions were examined and residuals were examined for lack of fit. Models having the lowest small sample Akaike's Information Criterion (AIC) were selected. GLM models were fitted in S Plus version 6.2 (©1988, 2003 Insightful Corp.) Other basic statistical analyses were conducted using SPSS

version 11.5 (© 2002 SPSS Inc.). Means and variances are reported throughout with standard error (SE).

RESULTS

Fish and invertebrate stable isotope values

Pelagic species (e.g., capelin, herring, sand lance, redfish) shared similar isotope values that differed significantly from all benthic species (e.g., flounder, plaice, skate), which in turn shared similar $\delta^{13}C$ ($F_{14,45}$= 17.98; $p < 0.001$) and $\delta^{15}N$ values ($F_{14,45}$ = 20.86; $p <$ 0.001). Pelagic species were more depleted in both carbon and nitrogen relative to benthic species (Figure 3.1). The X-axis in Figure 3.1 represents a continuum of feeding types ranging from highly pelagic (depleted in $\delta^{13}C$) to highly benthic (enriched in $\delta^{13}C$) while the Y-axis reflects a continuum of trophic levels.

Pelagic and benthic fish also differed significantly in their lipid concentration ($F_{11,35}$ = 22.55; $p < 0.001$), hence overall energy content also differed (Figure 3.2). As predicted I found a positive relationship between lipid concentration and the C:N ratio in the Scotian Shelf prey ($F_{1,44}$= 45.94; $p < 0.001$). For the expanded dataset of fish and invertebrates in the NW Atlantic, which represents more trophic groups (Figure 3.3), there was a significant effect of both $\delta^{15}N$ and $\delta^{13}C$ on C:N ratio (Table 3.1). Thus, there was a gradient of fat content from low to high with increasing trophic levels as indicated by $\delta^{15}N$, and along the benthic-pelagic continuum, as indicated by $\delta^{13}C$ (e.g. Figure 3.2).

Grey seals

Adult stable isotope values

Overall, the isotope signatures of seals were within the range of the prey carbon values

(Figure 3.3) and were enriched in $\delta^{15}N$ by a factor of 2-3‰ over potential prey, reflecting

higher trophic positions.

Cross-sectional analysis:

In spring and fall cross-sectional samples, neither $\delta^{13}C$ ($F_{1,35}$ = 0.53; p = 0.47) nor $\delta^{15}N$

($F_{1,35}$ = 1.88; p = 0.18) isotope ratios differed significantly among adult males between

seasons (Table 3.2; Figure 3.4). Similarly for females, spring and fall samples did not

differ in $\delta^{13}C$ ($F_{1,35}$ = 2.42; p = 0.13) or $\delta^{15}N$ ($F_{1,35}$ = 0.17; p = 0.68). In the spring, males

were significantly more enriched in $\delta^{13}C$ ($F_{1,39}$ = 9.70; p = 0.003) than females, however

$\delta^{15}N$ values ($F_{1,31}$ = 0.123; p = 0.73) were similar. Similarly in the fall, males were

significantly more enriched in $\delta^{13}C$ ($F_{1,31}$ = 15.10; p = 0.001) than females, however $\delta^{15}N$

values ($F_{1,31}$ = 2.66; p = 0.11) were similar.

On arrival at the breeding colony in January, spring-sampled males had significantly

lower $\delta^{15}N$ values ($F_{1,35}$ = 7.15; p = 0.011) than fall-sampled males, while $\delta^{13}C$ values

($F_{1,35}$ = 0.03; p = 0.865) were similar (Figure 3.4). By contrast, spring-sampled females

had significantly lower $\delta^{13}C$ values ($F_{1,35}$ = 7.04; p = 0.012) than fall-sampled-females,

but their $\delta^{15}N$ values ($F_{1,35}$ = 3.34; p = 0.076) were similar. Fall-sampled males were

significantly more enriched in $\delta^{13}C$ ($F_{1,31}$ = 17.59; p <0.0001) and $\delta^{15}N$ ($F_{1,31}$ = 14.68; p

=0.001) than fall-sampled females (Table 3.3). Spring-sampled males also were more

enriched in $\delta^{15}N$ ($F_{1,39}$ = 5.12; p =0.029) at January recapture than females, however $\delta^{13}C$ values ($F_{1,39}$ = 3.65; p =0.064) were similar.

Longitudinal analysis:

I used longitudinal samples to evaluate differences between spring-winter and fall-winter, respectively, both within and between sexes. Spring and winter samples did not differ significantly within males or within females in either $\delta^{13}C$ (males: $F_{1,18}$ = 0.018; p = 0.90, females: $F_{1,20}$ = 1.56; p = 0.23) or $\delta^{15}N$ (males: $F_{1,18}$ = 0.39; p = 0.54, females: $F_{1,20}$ = 4.22; p = 0.053). Similarly, fall and winter samples did not differ significantly within males or within females in either δ^{13} (males: $F_{1,16}$ = 1.50; p = 0.24, females: $F_{1,14}$ = 0.49; p = 0.49) or $\delta^{15}N$ (males: $F_{1,16}$ = 4.46; p = 0.052, females: $F_{1,14}$ = 0.001; p = 0.97). Males differed significantly from females in $\delta^{13}C$ ($F_{1,38}$ = 8.85; p = 0.005), but had similar $\delta^{15}N$ values in spring and winter ($F_{1,38}$ = 2.25; p = 0.14). By contrast, in fall and winter, males differed significantly from females in both $\delta^{13}C$ ($F_{1,30}$ = 21.31; p < 0.001) and $\delta^{15}N$ ($F_{1,30}$ = 9.32; p = 0.005).

Juvenile stable isotope values

Juvenile males and females sampled in January did not differ in either $\delta^{13}C$ ($F_{1,28}$ = 0.721; p = 0.403) or $\delta^{15}N$ values ($F_{1,28}$ = 0.359; p = 0.554) (Table 3.2). However, $\delta^{13}C$ signatures of juveniles differed significantly from both adult male ($F_{1,64}$ = 59.963; p < 0.001) and adult females ($F_{1,64}$ = 12.34; p = 0.001) (Figures 3.3 & 3.5) whereas $\delta^{15}N$ values of juveniles differed significantly from adult females ($F_{1,64}$ = 7.11; p = 0.010) but not from adult males ($F_{1,64}$ = 3.21; p = 0.078).

Body size, rate of energy accumulation and individual variation

Adult males were approximately 1.5 times heavier than females in each season (Table 3.4). Within individuals, there was a significant positive relationship between $\delta^{13}C$ and body mass (t = 2.54, p = 0.014) and a significant sex effect (t= 2.30, p = 0.024), but no significant interaction between sex and body mass (t =-0.32, p = 0.75) and no effect of season (t=-1.52, p=0.13). There was also a significant positive effect of mass on $\delta^{15}N$ (t = 2.48, p = 0.016), but no effect of sex (t=1.64, p=0.11) or season (t = 0.86, p = 0.40). However, there was a significant interaction between sex and mass (t = -2.377, p = 0.021) indicating that the relationship with mass differed between males and females. This is likely due to the fact that males and females had similar $\delta^{15}N$ in both the spring and fall but differed in winter. Further, as the rate of change in mass differed between males and females in both spring ($F_{1,27} = 4.66$; p = 0.04) and fall ($F_{1,25} = 15.31$; p = 0.001), an effect of sex on the relationship between body size and stable isotopes is not unexpected.

I also examined the effect of body mass on stable isotope signatures using cross-sectional data from winter values only so that juvenile data could also be included in the analysis. There was a significant positive correlation (Figure 3.6) between body mass and $\delta^{13}C$ ($F_{1,73} = 11.26$; p = 0.001), with no effect of age class ($F_{1,73} = 1.12$; p = 0.29) or sex ($F_{1,73} = 0.049$; p = 0.83). Body size in juveniles ranged from 37.5 to 71.0 kg. However, in contrast to adults, I found a significant negative relationship between juvenile body mass and $\delta^{15}N$ ($F_{1,15} = 6.77$; p = 0.02).

There was no relationship between the carbon signature and either the rate of energy accumulation ($F_{1,24}$ = 1.32; p = 0.26) or fat content ($F_{1,24}$ = 0.40; p = 0.53) of seals. However, there was a positive effect of δ^{15}N ($F_{1,24}$ = 5.69; p = 0.02) on the rate of fat gain, but no sex effect ($F_{1,24}$ = 0.27; p =0.61) (Figure 3.6). There was also a positive relationship between δ^{15}N and the winter percent body fat content in males ($F_{1,13}$ = 7.46; p = 0.02), although, this was not the case for females ($F_{1,10}$ = 1.25; p = 0.29).

Individuals differed by an average of 0.49 (abs ‰) in δ^{13}C (range:-1.07 to + 2.13‰) and by 0.99 (abs ‰) in δ^{15}N (range:-3.63 to +2.37) between initial and final capture. Initial and final values of carbon (Pearson's = 0.59, p < 0.001, n = 72) and nitrogen (Pearson's = 0.50, p < 0.001, n=72) were positively correlated. Given that the sampling interval exceeded the isotope turnover time, initial values should not have influenced final values (Lesage *et al.* 2001; Kurle and Worthy 2001). Therefore, on average, changes in isotope values within individuals were relatively small. There was a positive correlation between the change in δ^{13}C and the change in δ^{15}N ($F_{1,53}$ = 18.44; p < 0.001; Figure 3.6). There was no effect of sex (δ^{13}C: $F_{1,53}$ = 0.31; p = 0.58; δ^{15}N: $F_{1,53}$ = 2.57, p = 0.11) or sampling season (δ^{13}C: $F_{1,53}$ = 0.52; p = 0.48; for δ^{15}N: $F_{1,53}$ = 1.25; p = 0.27) on this relationship. Conversely, the temporal change in isotope values within individuals had no significant effect on growth rate, whether calculated as a change in overall mass (for δ^{13}C: $F_{1,53}$ = 0.58; p = 0.45; for δ^{15}N: $F_{1,53}$ = 0.41; p = 0.53) or a change in the amount of fat (for δ^{13}C: $F_{1,53}$ = 2.13; p = 0.15; for δ^{15}N: $F_{1,53}$ = 0.23; p = 0.64).

Niche Breadth

Males (δ^{13}C: $\sigma^2 = 0.43$ ‰; δ^{15}N: $\sigma^2 = 1.98$ ‰) had about a 1.5 fold greater niche breadth than females (δ^{13}C: $\sigma^2 = 0.32$‰; δ^{15}N: $\sigma^2 = 1.11$ ‰), whether considering δ^{13}C ($F_{1,142} = 38.02$; $p < 0.001$) or δ^{15}N ($F_{1,142} = 13.69$; $p < 0.001$; Table 3.5). This difference was observed in both spring and fall samples. Relative to adults (see winter values Table 3.2), niche breadth for juvenile seals (δ^{13}C: $\sigma^2 = 0.25$ ‰; δ^{15}N: $\sigma^2 = 0.52$ ‰) was roughly half for both δ^{13}C ($F_{2,101} = 28.05$; $p < 0.001$) and δ^{15}N ($F_{2,101} = 9.69$; $p < 0.001$).

Within population variance of δ^{13}C (males: $F_{1,18} = 0.018$; $p = 0.90$, females: $F_{1,20} = 1.56$; $p = 0.23$) and δ^{15}N (males: $F_{1,18} = 0.39$; $p = 0.54$, females: $F_{1,20} = 4.22$; $p = 0.053$) was less than the between population variance (i.e., no significant within-subject effects; Table 3.5) for spring and winter sampled animals. Similar results were found in seals samples in fall and winter for δ^{13}C (males: $F_{1,16} = 1.50$; $p = 0.24$, females: $F_{1,14} = 0.49$; $p = 0.49$) and δ^{15}N (males: $F_{1,16} = 4.46$; $p = 0.052$, females: $F_{1,14} = 0.001$; $p = 0.97$). Thus, diets of individual seals changed less over time relative to the total observed dietary space of grey seals.

DISCUSSION

Stable isotope values of fishes and invertebrates from the Scotian Shelf suggest that taxa are organized along a clearly defined axis where pelagic organisms are more depleted in both δ^{13}C and δ^{15}N and benthic organisms are more enriched in δ^{13}C and δ^{15}N. On average, invertebrates were 3‰ lower than fish in δ^{15}N in each trophic guild, thereby reflecting trophic positions of consumers. Sherwood and Rose (2005) and Davenport and

Bax (2002) also found that the baseline of $\delta^{15}N$ is more elevated for benthic systems, resulting in higher overall $\delta^{15}N$ values for equivalent trophic positions of pelagic or benthic piscivores. Consequently, a $\delta^{15}N$ signature must always be interpreted in the context of a corresponding $\delta^{13}C$ signature. Using the ratio of C:N as a proxy for lipid concentration, I found that, on average, pelagic fish at the highest trophic levels have high concentrations of lipid while benthic fish at the lowest trophic level have low concentrations of lipid.

Overall, the carbon isotope signatures of seals were contained within the range of the prey carbon axis (Figure 3.3) and were enriched in $\delta^{15}N$ by 2-3‰, over potential prey, reflecting their higher trophic level. The mean differences in $\delta^{13}C$ and $\delta^{15}N$ values suggests that adult females fed on a greater proportion of pelagic prey whereas adult males consumed a higher proportion of benthic species. Juveniles had a carbon signature even more deplete than adult female seals, suggesting that their carbon was derived primarily from pelagic sources. Thus inferences about diets of adult males and females are consistent with sex-specific seasonal differences in diving behaviour (Beck *et al.* 2003b). Indeed, the sex differences indicated by stable isotopes are similar both in a qualitative (Beck *et al.* 2005) and quantitative (Bowen *et al.* 2006) manner with the results of fatty acid analyses. Males and females had similar $\delta^{15}N$ in the spring and fall but differed in winter samples. As the baseline nitrogen signature of prey changes relative to the position on the carbon axis (Figure 3.1 & 3.3; Davenport and Bax 2002; Sherwood and Rose 2005), overlap in $\delta^{15}N$ signatures of seals with different $\delta^{13}C$ signatures does not necessarily imply convergent diets. The results here suggest that overall, adult males

and females were segregated with respect to diet, as were juveniles, whether it is from consuming different prey items or different proportions of the same prey items. This segregation would operate along two lines, namely the main carbon pool (pelagic/benthic systems) from which energy is derived, and the trophic position within that system. Thus it is likely this segregation in diet is a manifestation of spatial segregation within the water column or geographic segregation (Breed et al. 2006) and may act to reduce intra-specific competition. Similar results in spatial segregation and inferred dietary segregation have been found for other pinnipeds (Field *et al.* 2005; Le Boeuf *et al.* 1993, 2000), and seabirds (González-Solis *et al.* 2000; Weimerskirch *et al.* 1997).

Sex differences remained significant across seasons. Overall, males were more enriched in $\delta^{13}C$ than females in all seasons (Figure 3.4). For $\delta^{15}N$, values were similar in the spring and fall, but were more enriched by winter in males. Within each sex, there were no significant differences in isotope values between spring and fall. However in the winter, there were significant differences related to when animals were initially sampled. Using satellite telemetry, Austin *et al.* (2004) found that those animals captured on Sable during the spring moult were more likely to be long-ranging directed travelers subsequently fanning out across the Scotian Shelf and the Gulf of St Lawrence. In contrast, the majority of animals captured and instrumented in the fall tended to be residents, primarily foraging near Sable Island. Sable Island Bank is a relatively shallow (50-100 m), sandy region, which is habitat for species such as sand lance and capelin (Zwanenburg *et al.* 2002). The remainder of the Shelf and Shelf edges have greater habitat complexity, and greater depth ranges than the shallow banks. Consequently a

different array of fish species are found there (Zwanenburg *et al.* 2002). Furthermore, some prey species eaten by grey seals also exhibit seasonal variation in distribution and abundance (Bowen *et al.* 2006). These seasonal changes in distribution but also seasonal changes in prey presumably both contribute to differences in the final winter stable isotope values for the spring and fall sampled animals

Dietary niche breadth is a metric for measuring the degree of specialization. Based on the variance in stable isotope values dietary niche breadth was approximately 1.5-fold greater in males than in females. On average, adult grey seals had a 2-fold higher niche breadth than juveniles. It is often assumed that juveniles are limited in their foraging ability relative to adults due to lack of experience and cognitive ability and presumably have access to fewer or different types of prey (e.g. Baker and Donohue 2000; Noren *et al.* 2005). In terrestrial systems of sympatric predators, there is a positive relationship between increasing body size and niche breadth (Radloff and du Toit 2004) and the dietary niche of smaller carnivores is nested within that of larger carnivores (Sinclair *et al.* 2003).

There were no significant changes in niche breadth among adults between seasons, although sample sizes were relatively small and more data is needed to confirm this conclusion. However, my results indicated that individual grey seals are relative specialists as diets change less for individuals over time relative to the total observed dietary space of the population. On average, between initial capture in the spring or fall, and recapture in the winter, individual's varied by less than 0.5 ‰ in $\delta^{13}C$ and less than

1‰ in δ^{15}N signatures. There was no difference between sexes in the degree of change, nor was there a consistent pattern in the direction of change among individuals. However, there was a high degree of individual variation in signatures (Figure 3.5). This is not entirely unexpected as foraging behaviour, in particular, as well as movement and feeding frequency have been found to be highly variable among individual grey seals, although a direct link with diet has not yet been made (Beck *et al* 2003b; Austin *et al.* 2004). Studies estimating diets for individuals of other species of marine mammals also demonstrate a high degree of variation (reviewed in Bowen *et al.* 2002a), although with the exception of sea otters (Estes *et al.* 2003), temporal consistency within individuals has not yet been studied.

Sex differences in foraging behaviour of pinnipeds are assumed to reflect differences in sex- specific costs of reproduction, body size or competitive abilities. To that effect, two interesting results emerge from the stable isotope data. The first is that there is a high degree of overlap in diets across sex and age-class and a correlation with both δ^{13}C and δ^{15}N signatures and body size across all age classes; that is, diet changes with body mass. My data suggest a shift from more pelagic to more benthic diets as body size increases. It is probable that δ^{15}N of seals is shifting due to a change in the main δ^{13}C source of the diet, paralleling trends of the prey axis. Indeed, within individuals there is a positive correlation between δ^{13}C and δ^{15}N. The second result is that seals are achieving higher rates of fat gain on diets which are at a higher trophic level. An examination of potential prey data suggest that this is possibly a higher quality diet i.e. more energy rich. The correlation of stable isotope values, or diet, with body size and rate of energy gain

suggests that energetics are a parsimonious, underlying mechanism in diet selection and ontogenetic diet changes in grey seals.

In adults, both sexes increase their rate of energy storage during the 3 months prior to reproduction, and it has been assumed that they may forage more selectively on a few high-quality prey species during the fall/early winter period (Beck *et al.* 2005). Results of the stable isotope analysis suggest that indeed higher rates of energy gain are obtained through different diets. However, based on the variance ratio test of stable isotope values between spring, fall and winter, diets appear to be just as relatively diverse in all those seasons. I found however a positive relationship between the rate of fat accumulation $(kg \cdot d^{-1})$ over the fall period and $\delta^{15}N$ such that seals with the highest rates of fat gain had higher $\delta^{15}N$ values. There was also a positive relationship between the total amount of fat (kg) or the percent body fat (%), and diet only in males. Based on the stable isotope values and prey quality, this suggests that seals are likely consuming prey of higher energy density since both benthic and pelagic fish at higher trophic positions have higher fat concentration of prey. There was no correlation between energy gain and the $\delta^{13}C$ signature, suggesting that benthic-pelagic segregation is not important but relative trophic position is. Thus prey selection appears to affect the efficiency with which energy is gained in both males and females.

Lipid or energy concentration is simply one consideration in diet selection and overall energy gain of a predator. Other considerations include availability of prey and the subsequent costs associated with pursuit, capture, handling and digestion. In fish, diet

shifts with increasing body size are thought to reflect the limiting factor of gap size and the increasing foraging cost of consuming increasingly relatively smaller prey (Sherwood *et al.* 2002). That is, a shift in diet is made when the costs outweigh the benefits of feeding on a particular prey or prey-size class (e.g. Jones *et al.* 1994; Sherwood *et al.* 2002). This, in turn, leads to lower energetic demands, with respect to minimizing time and activity costs spent in burst swimming and pursuit of prey (Sherwood *et al.* 2002). Typically this diet switch is made in the direction of larger prey, but the underlying operative is decreased foraging costs. Therefore, with respect to ontogeny and body size differences in diets for grey seals, one hypothesis is that diet shifts towards a larger fraction of benthic prey are made to reduce foraging costs thereby maximizing gains, since these are such a large fraction of the energy budget. Foraging costs are likely reduced on more sedentary, benthic prey despite their lower quality. The caveat here is that the capacity to digest this prey comes with larger body size (Ginnett and Demment 1997).

Stable isotopes indicate representative trophic relationships related to functional patterns of feeding (i.e. benthic-pelagic, higher-lower trophic level) rather than an explicit taxonomic description of diet. In certain cases, functional feeding patterns provide more meaningful insight into overall food web properties and dynamics (e.g. Williams and Martinez 2000). Through stable isotope analysis I found mean differences in diets between adults and juveniles and between adult males and females. The divergence among these groups lends support to the idea of dietary segregation in grey seals. The lack of sex differences in the diets of juveniles is probably indicative of the lack of

dimorphism at that stage. Therefore, it is unlikely that sex dimorphism is an important factor until male and female body sizes diverge dramatically. However, the data were characterized by a high degree of variation and in fact grey seals were found to be relative specialists in their diets. Although we can make general inferences based on age-class or sex, we essentially see a continuum of diets (along the prey axis) across individuals, where overlap between age-class and sex groups is correlated with body size. The relative trophic position of the diet was seen to affect the rate or efficiency with which energy was stored in both adult males and females, and in the case of males, diet had an influence on total fat content. However, position along the $\delta^{13}C$ axis, or degree of benthic feeding had no effect on energy storage. Thus individuals are achieving similar endpoints by exploiting different energy sources. It has previously been found as well, that mean differences between sexes in foraging behaviour of grey seals are marked by a high degree of individual variability. These two results lend further support for the idea of multiple foraging strategies with convergent success (Estes *et al.* 2003; Bolnick *et al.* 2003).

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TABLES

Table 3.1: Results from GLM with stable isotopes and trophic guild predictive of the fat content in fish (n = 40). Akaike's Information Criteria (AIC), the delta AIC (Δ_i) and the Akaike weights (w_i). Best fitting models are given in bold print.

ID	Model	df	AIC	Δ_i	w_i
1	**$\delta^{13}C$**	**40**	**4.68**	**0.00**	**0.341**
2	**$\delta^{15}N$**	**40**	**4.88**	**0.20**	**0.308**
3	trophic guild	39	6.90	2.22	0.112
4	$\delta^{13}C + \delta^{15}N$	39	6.62	1.94	0.129
5	$\delta^{13}C$ + trophic guild	38	8.64	3.96	0.047
6	$\delta^{15}N$ + trophic guild	38	8.74	4.06	0.045
7	$\delta^{13}C + \delta^{15}N$ + trophic guild	37	10.61	5.93	0.018

Table 3.2: Mean (σ^2) $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰) for adult male and female and juvenile grey seals sampled in spring, fall and winter (mean values from Table 3.3 are presented for adults).

Sample	Spring		Fall		Winter	
	$\delta^{13}C$ (‰) mean (σ^2)	$\delta^{15}N$ (‰) mean (σ^2)	$\delta^{13}C$ (‰) mean (σ^2)	$\delta^{15}N$ (‰) mean (σ^2)	$\delta^{13}C$ (‰) mean (σ^2)	$\delta^{15}N$ (‰) mean (σ^2)
adult males (spring n=17 fall n=19)	-15.73 (0.54)	17.09 (2.66)	-15.89 (0.36)	17.79 (1.78)	-15.73 (0.43)	17.81 (1.64)
adult females (spring n=21 fall n=15)	-16.34 (0.25)	16.95 (0.93)	-16.58 (0.12)	17.08 (1.08)	-16.34 (0.43)	16.69 (1.23)
juvenile males (n=15)	-	-	-	-	-16.79 (0.21)	17.25 (0.39)
juvenile females (n=14)	-	-	-	-	-16.95 (0.31)	17.42 (0.73)

Table 3.3: Mean and σ^2 of $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰) in January for spring- and fall-sampled adult male and female grey seals.

Sex	Season	Winter	
		$\delta^{13}C$ mean (σ^2)	$\delta^{15}N$ mean (σ^2)
males	spring (n=19)	-15.74 (0.36)	17.31 (1.75)
	fall (n=17)	-15.71 (0.53)	18.37 (0.99)
females	spring (n=21)	-16.12 (0.42)	16.41 (1.41)
	fall (n=15)	-16.66 (0.29)	17.08 (0.80)

Table 3.4: Mean± SE mass (kg), fat content (%), growth rate ($kg \cdot d^{-1}$) and fat accumulation rate ($kg_{fat} \cdot d^{-1}$) for adult males and females in spring, fall and winter sampling periods.

Sample	Season	n	Mass (kg)	Fat (%)	Mass gain ($kg \cdot d^{-1}$)	Fat accumulation ($kg_{fat} \cdot d^{-1}$)
adult male	spring	13	209.7 ± 11.4	13.1 ± 1.6	-	-
	fall	14	238.0 ± 8.1	22.4 ± 1.6	0.549 ± 0.067	0.320 ± 0.046
	winter	25	296.0 ± 7.9	28.7 ± 1.2		
adult female	spring	15	135.0 ± 6.2	14.6 ± 1.4	-	-
	fall	11	165.9 ± 6.6	26.0 ± 2.3	0.240 ± 0.050	0.191 ± 0.064
	winter	23	196.8 ± 5.5	34.6 ± 1.8		
juveniles	winter	16	47.7 ± 2.1	-	-	-

Table 3.5: Between population level (population) and within population level (within) variance (σ^2) for $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰) of adult male and female seals in spring, fall and winter sampling periods. Winter values, as well as the within population variance from repeated measures analysis for spring-sampled (s-s) and fall-sampled (f-s) animals are shown separately.

Sex		Spring σ^2 (‰)		Fall σ^2 (‰)		Winter (s-s) σ^2 (‰)		Winter (f-s) σ^2 (‰)	
		$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
male	*Population*	*0.53*	*2.66*	*0.35*	*1.78*	*0.36*	*1.75*	*0.53*	*0.99*
	Within s-s	0.35	1.14	-	-	0.35	1.14	-	-
	Within f-s	-	-	0.24	0.68	-	-	0.24	0.68
female	*Population*	*0.25*	*0.93*	*0.12*	*1.08*	*0.42*	*1.41*	*0.29*	*0.80*
	Within s-s	0.001	0.39	-	-	0.001	0.39	-	-
	Within f-s	-	-	0.09	0.26	-	-	0.09	0.26

FIGURES
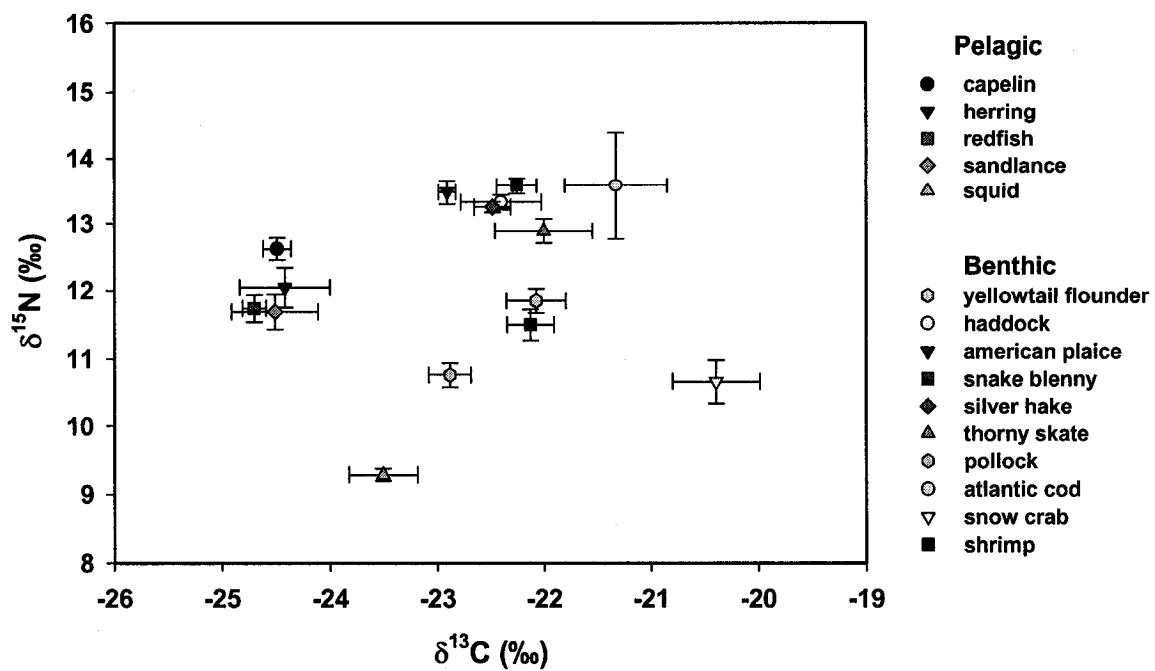
Figure 3.1: Mean (n=3) δ^{13}C and δ^{15}N values for fish and invertebrate species from the Scotian Shelf. Error bars represent ±1 SE.
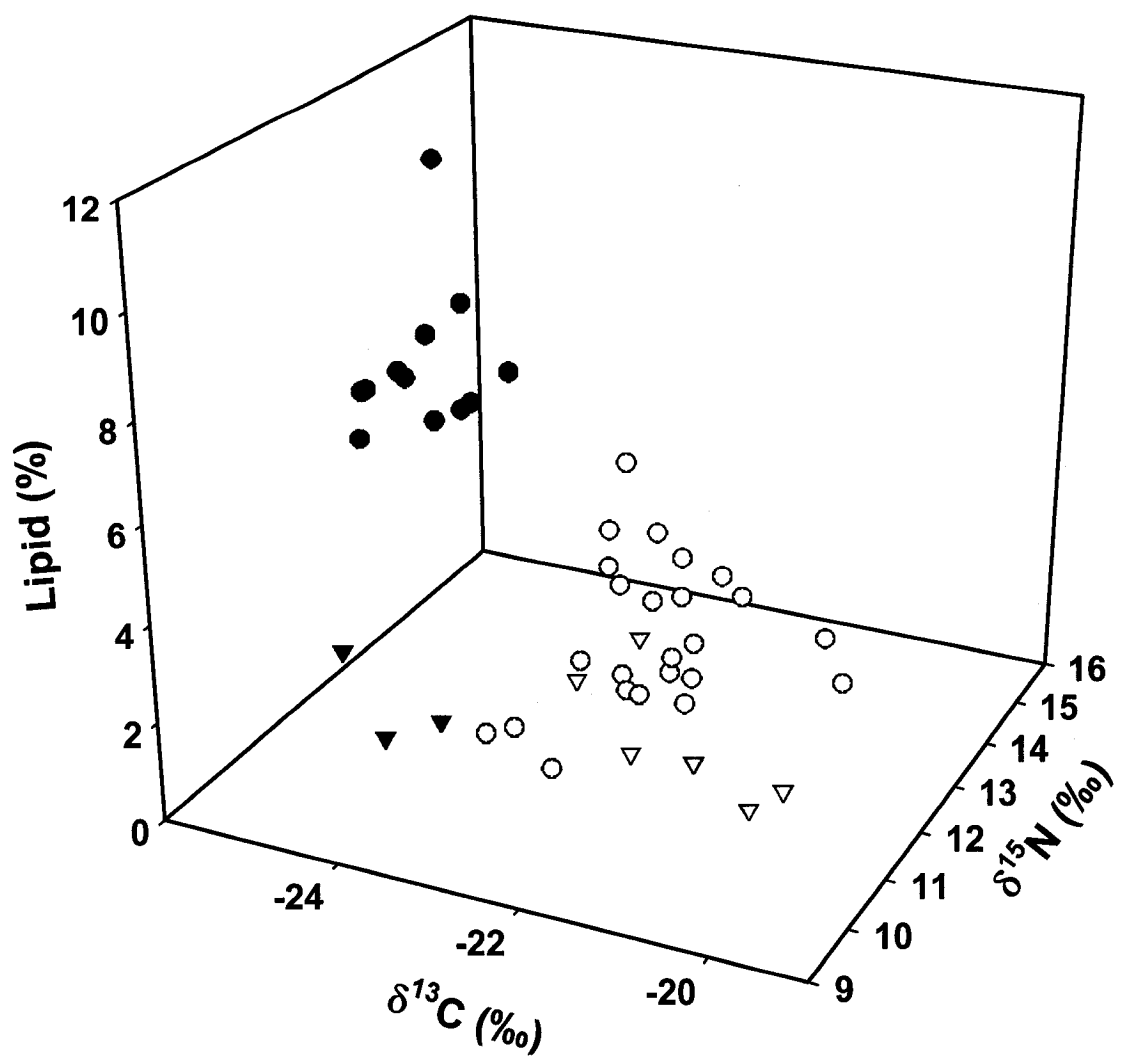
Figure 3.2: $\delta^{13}C$ and $\delta^{15}N$ and lipid concentration (%) in fish (circles; pelagic:closed, benthic:open) and invertebrates (triangles; pelagic:closed, benthic:open) from the Scotian Shelf.
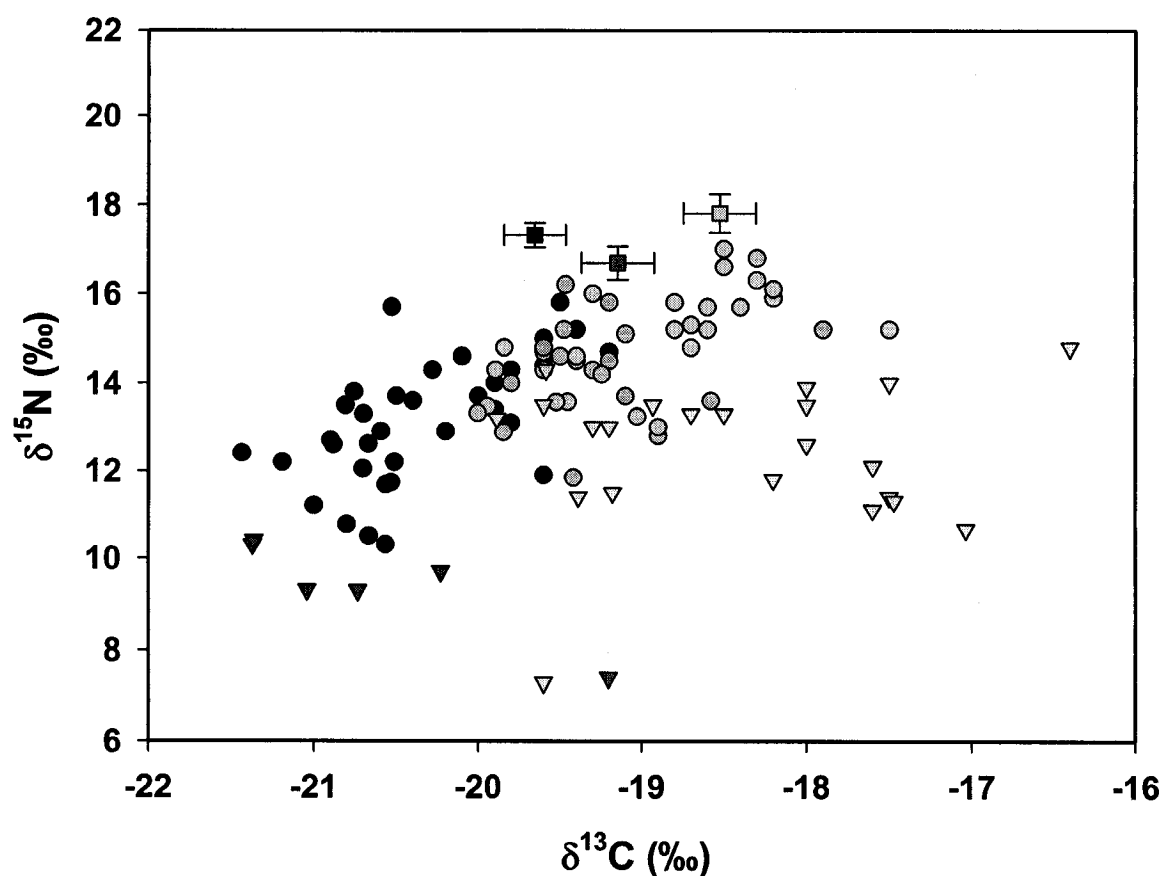
Figure 3.3: Mean $\delta^{13}C$ and $\delta^{15}N$ for fish species (circles: pelagic black; benthic light grey) invertebrates (inverted triangles: pelagic dark grey; benthic light grey) and seals (squares: juveniles black; adult females dark grey; adult males light grey) from the NW Atlantic and Gulf of St Lawrence. Error bars are ± 1SE. Values for fish and invertebrates are from Scotian Shelf (this study), the Grand Banks (Sherwood and Rose 2005) and the Gulf of St Lawrence (Lesage *et al.* 2001).
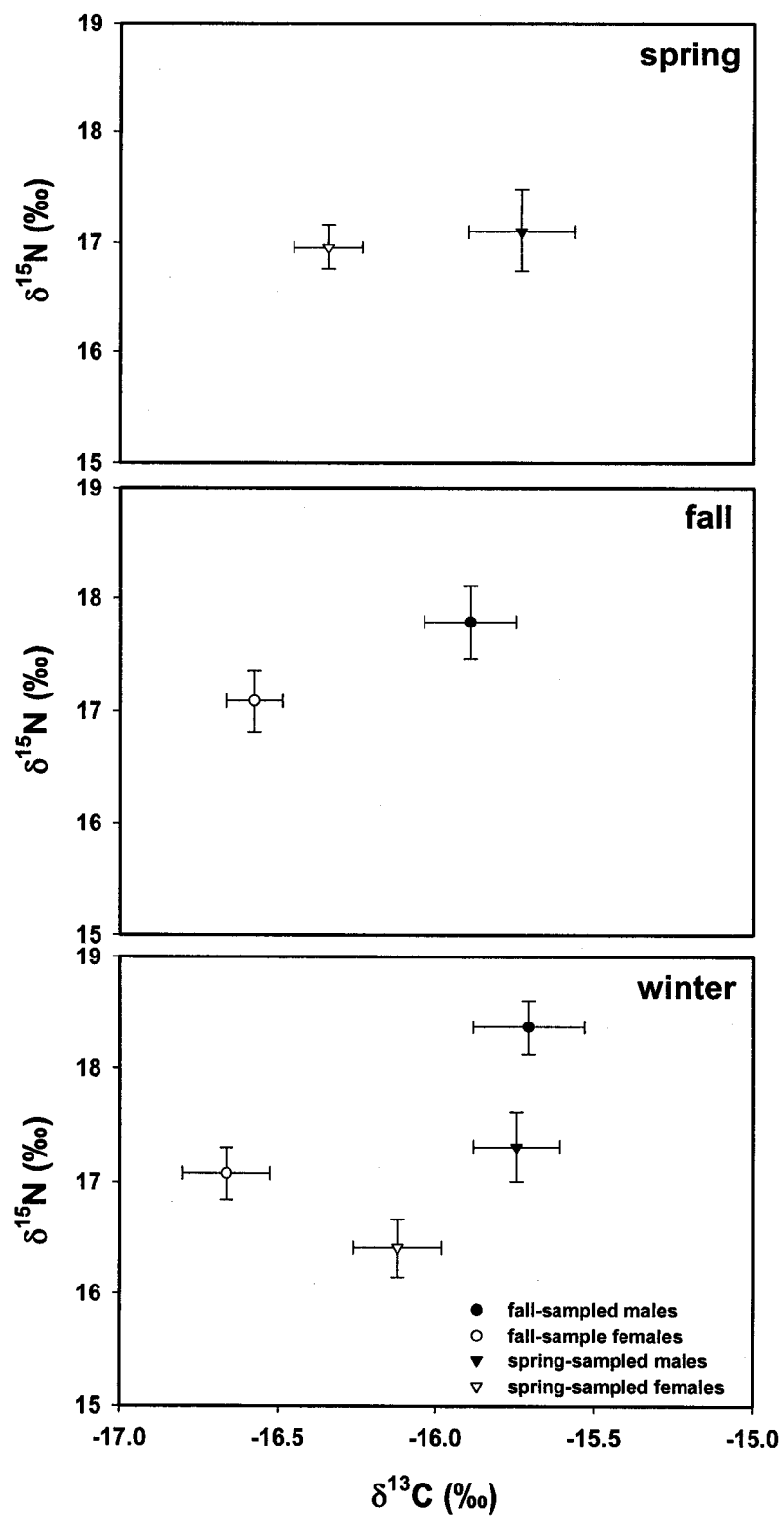
Figure 3.4: Mean $\delta^{13}C$ and $\delta^{15}N$ by season for adult male and female grey seals. Error bars represent 1SE.
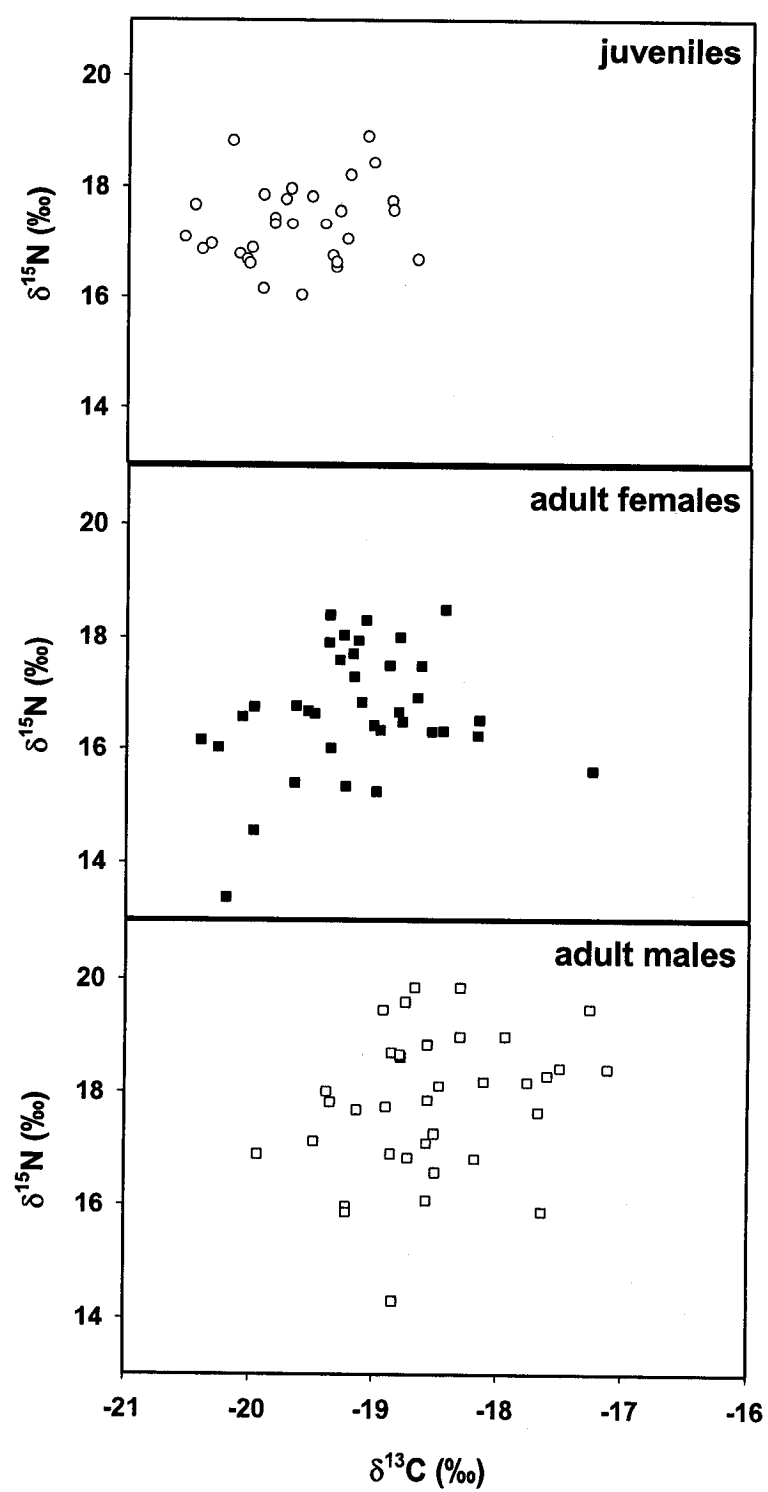
Figure 3.5: δ^{13}C and δ^{15}N in individual juvenile, adult female and male grey seals from winter sampling period.

Figure 3.6: Panel A: Body mass (kg) and $\delta^{13}C$ in juvenile (closed circles), adult female (open triangles) and adult male (closed squares) grey seals from winter sampling period. Panel B: $\delta^{15}N$ and rate of fat gain ($kg \cdot d^{-1}$) in individual adult female (open circles) and male (filled circles) grey seals from fall to winter sampling period. Panel C: Change (recapture value-initial value) in $\delta^{13}C$ and $\delta^{15}N$ from individual adult male (filled circles) and female (open circles) grey seals.

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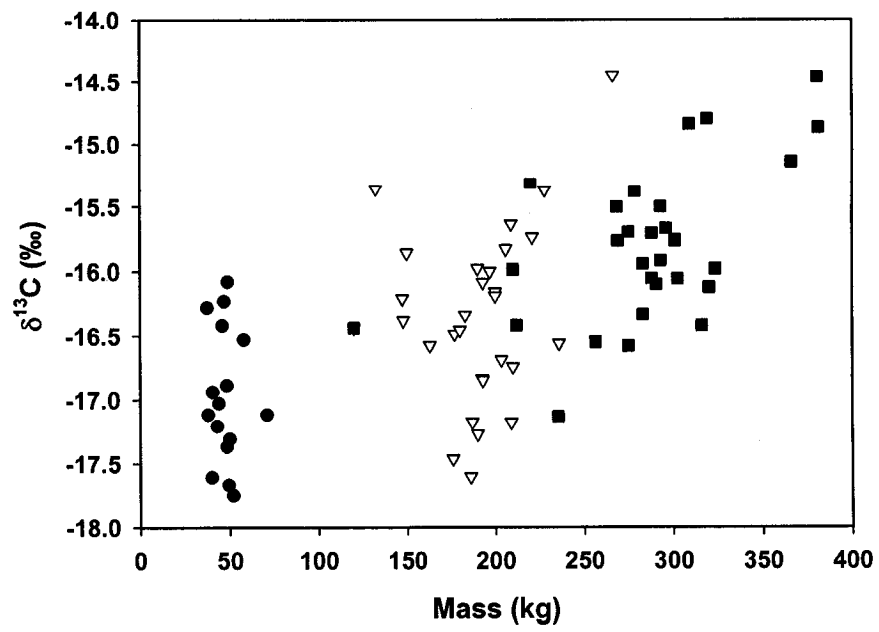
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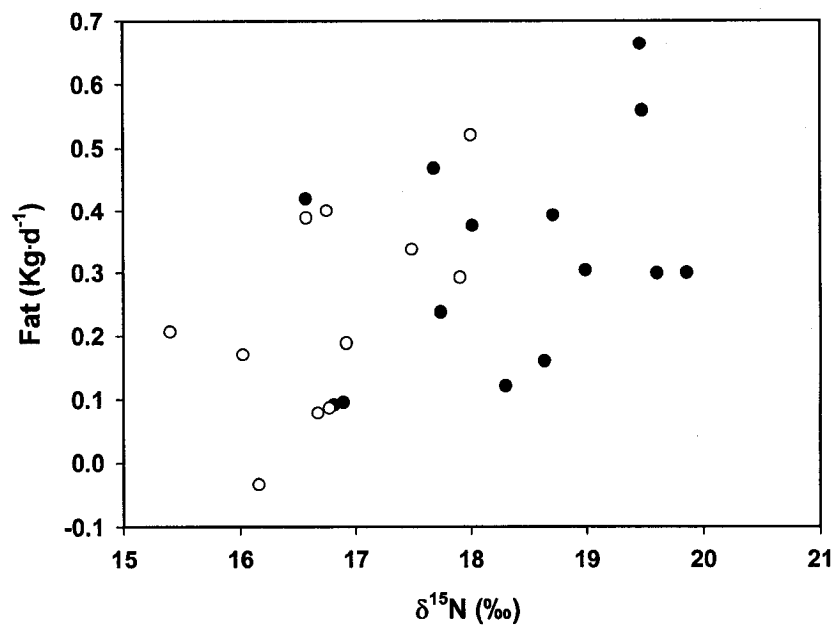
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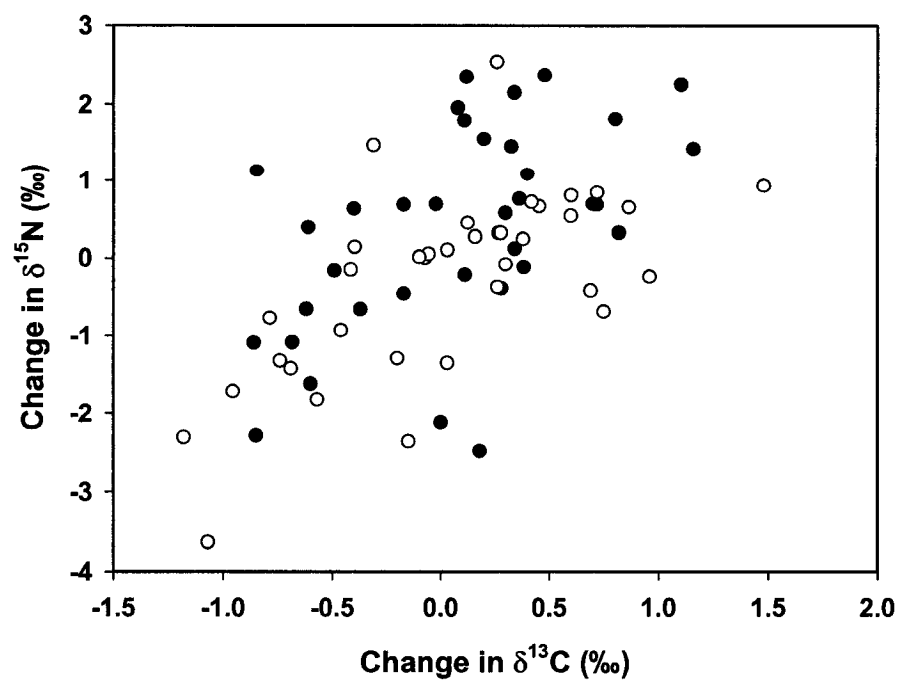
CHAPTER IV: CONVERGENCE OF DIET ESTIMATES DERIVED FROM FATTY ACIDS AND STABLE ISOTOPES; SUPPORT FOR LONG-TERM INTEGRATORS OF NATURAL DIETS WITHIN INDIVIDUAL GREY SEALS

INTRODUCTION

Accurate quantification of diet is a fundamental requirement for understanding the foraging ecology and energy budgets of free-ranging animals. Limitations of stomach content and fecal analyses (Jobling and Breiby 1986; Jobling 1987; Bowen and Siniff 1999) have led to the development of alternative biochemical methods. The two main approaches are fatty acid signature analysis and stable isotope analysis. Both of these methods provide inferences about or quantitative estimates of diet that are time-integrated and readily applied to many taxa (Kelly 2000; Iverson *et al.* 2004). In addition, sampling can be done non-lethally allowing for the study of small populations and of individuals over time. Both methods have been reviewed extensively (e.g., fatty acids: Iverson *et al.* 2004; Budge *et al.* 2006; stable isotopes: Kelly 2000; Post 2002). The two methods are independent; one examines the fatty acid composition of lipid stores, the other examines the isotope ratios of carbon and nitrogen in various tissues or whole body of a consumer, and often these samples are lipid extracted.

The concurrent analysis of stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes provides a two-dimensional picture of the dietary space occupied by a consumer relative to other consumers (Post 2002). Isotopes of nitrogen are enriched in consumers relative to diet by an average of 3-5 ‰ (Hobson and Welch 1992; Hobson *et al.* 1994) thereby providing a measure of trophic position. Carbon isotopes remain little changed with trophic transfer as they enrich by less than 1 ‰, and thus are more indicative of sources of primary

production (Hobson *et al.* 1994; France and Peters 1997; Kelly 2000). Carbon isotopes are known to reflect different sources of primary production and can be used to discriminate between carbon pools or habitats (e.g., terrestrial vs aquatic, benthic vs pelagic). For example in marine systems, the carbon signature increases from negative (depleted) values for pelagic species to more positive (enriched) values for benthic species, while $\delta^{15}N$ increases with trophic level within each system respectively (Davenport and Bax 2002; Sherwood and Rose 2005; Tucker *et al.* 2007; Chapter III). Analysis of stable isotopes does not easily permit individual prey species to be identified particularly in more complex food webs. However, stable isotopes allow for a standardized comparison among individuals or taxa and can provide temporal integration of diets over different timescales owing to the analysis of multiple tissues with different turnover times (Bearhop *et al.* 2004).

By contrast, fatty acid signature analysis can provide both a qualitative assessment of temporal or spatial changes in diet (e.g. Iverson *et al.* 1997a, 1997b; Smith *et al.* 1997) and a quantitative estimate of the species composition of the diet (Iverson *et al.* 2004, Bowen *et al.* 2006; Beck *et al.* 2007). I refer to the proportional distribution of all fatty acids measured in a consumer as its fatty acid signature. This is due to the fact that fatty acids are deposited in animal tissue in a predictable manner and there are limits on polyunsaturated fatty acid biosynthesis in higher order consumers (Iverson 1993). Proportional estimates of diet composition can be made at the level of the individual by statistically matching a consumer's fatty acid signature to an inclusive prey database (Iverson *et al.* 2004) known as quantitative fatty acid signature analysis (QFASA).

Both biochemical tracer methods have been validated through feeding experiments (e.g. Kelly 2000; Iverson *et al.* 2004) and are known to be long-term integrators of the assimilated portion of the diet. The strengths and limitations of the use of stable isotopes to study trophic interactions are rather well understood (Kelly 2000; Post 2002). However, feeding experiments on the use of fatty acids are fewer in number to date and have generally involved small number of animals, were short term and dealt with simple diets (typically < 5 different prey species). Of course, it is difficult to validate diet estimates from either of these methods in the field, particularly for wide-ranging aquatic predators such as a seal or seabird. However, if these two independent methods provide similar views of the diet then we would have greater confidence in the validity of those estimates.

In this Chapter, I compared proportional fatty acid signatures and stable isotope values of potential fish and invertebrate prey species of grey seals (*Halichoerus grypus*) from the Northwest Atlantic and those taken from individual grey seals. I hypothesized that fatty acid signatures characteristic of pelagic or benthic feeding would be correlated with the $\delta^{13}C$ in potential prey. For example, relatively high levels of 17:0, 18:1n-7 and 20:4n-6 are associated with benthic systems, and high levels of 14:0, 22:1n-11, 20:1n-9, 18:2n-6, 18:3n-3 and 18:4n-3 occur in pelagic systems (Budge *et al.* 2002; Käkelä *et al.* 2005). Likewise, I expected to see similar relationships in the fatty acid signatures of grey seals. I subsequently compared the proportional diet estimates derived from QFASA (Beck *et al.* 2007) with those from the stable isotope signatures (Tucker *et al.* 2007; Chapter III) of the same adult grey seals. First, I hypothesized that the proportion of pelagic prey species

estimated by QFASA would be correlated to $\delta^{13}C$. Second, I expected that the integrated

trophic position of the QFASA estimated diet would be correlated to $\delta^{15}N$. Grey seals are

known to consume complex, temporally and spatially variable diets. Over 60 prey items

have been identified in stomach contents (Bowen *et al.* 1993), although individual

animals generally consume only a small subset of these species (Beck *et al.* 2007).

METHODS

Grey seal sampling

The study was conducted on Sable Island (43°55′N, 60°00′W), a vegetated sandbar

approximately 45 km long, about 300 km SE of mainland Nova Scotia, Canada. Seals

breed on the island in January, return to moult in spring, and haul out on the Island

periodically at other times of the year (Beck *et al.* 2003). From 1996-2001, we sampled

adult grey seals in May-June (females=14; males=10), September-October (females=10;

males=14) and January (females=13; males=14) at the start of the breeding season.

Individuals were captured onshore using hand-held nets (see Bowen *et al.* 1992). Skin

samples (approximately 0.05-0.1g) were taken from the rear flipper. At the same time, a

blubber biopsy was taken of the full depth of the blubber layer from each animal on the

posterior flank (Beck *et al.* 2005; Beck *et al.* 2007).

Fish and invertebrate prey sampling

Fishes and invertebrates were collected and frozen during stratified, random, bottom-

trawl surveys conducted in the summer on the Scotian Shelf (Northwest Atlantic

Fisheries Organization sub areas 4V, 4W, and 4X) in 2000 and 2001 (see Budge *et al.*

2002). Three individuals each of 12 fish and 3 invertebrate species were thawed and fork

length or carapace width was measured to the nearest 0.1 cm and body mass to the

nearest 0.1 g. Each individual was then homogenized. Lipids were quantitatively

recovered in duplicate from sub-samples (approximately 1.5 g) of the homogenized tissue

using a modified Folch method (Iverson *et al.* 2001). Fatty acid profiles were compiled as

part of a larger prey database for the NW Atlantic (summarized in Budge *et al.* 2002). An

additional sub-sample (approximately 1.5 g) was subsequently analyzed for stable

isotopes of carbon and nitrogen.

Stable Isotope Analysis

Stable isotope analyses are presented in Chapter III. Briefly, seal, fish and invertebrate

samples were dried to constant weight (for 48 h at 80 °C in a drying oven) and crushed to

a fine powder using a mortar and pestle. Stable carbon and nitrogen isotope ratios of

these samples were determined by the analysis of CO_2 and N_2 produced by combustion in

a CE Elemental Analyzer followed by gas chromatograph separation and analysis with a

Delta plus isotope ratio mass spectrometer (G.G. Hatch Isotope Laboratories, University

of Ottawa, Ottawa, Ontario, Canada). Stable carbon and nitrogen ratios were expressed in

delta (δ) notation, defined as the parts per thousand (‰) deviation from a standard

material: $\delta^{13}C$ or $\delta^{15}N = ([R_{sample}/R_{standard}] - 1) \times 1000$; $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$). Standards

used were PDB limestone for $\delta^{13}C$ and N_2 in air for $\delta^{15}N$. A sub-sample (8%) was

analyzed in duplicate; the average standard error of the mean for replicates was 0.15 ‰

for $\delta^{13}C$ and 0.18 ‰ for $\delta^{15}N$.

Fatty Acid Analysis

Data for fatty acids of both potential prey (Budge *et al.* 2002) and seals (Beck *et al.* 2005)

have been previously published. Briefly, the lipid from blubber biopsies was

quantitatively extracted as described above. FA methyl esters (FAME) were prepared

from each extracted lipid sample using an acidic catalyst (the Hilditch method; see

Iverson *et al.* 2001; Budge *et al.* 2006). Duplicate analyses and identification of FAME

were performed using temperature-programmed gas–liquid chromatography (GLC)

(Iverson *et al.* 1997b, 2004; Budge *et al.* 2006). FAs were described by the standard

nomenclature of carbon chain length:number of double bonds and location (n-x) of the

double bond nearest the terminal methyl group. Individual FAs were expressed as a

percentage of total fatty acids. To improve normality, the proportional data were

normalized using a log transformation according to the following equation: $x$trans =

$\ln(x_i/c_r)$, where $x$trans is the transformed data, x_i is a FA expressed as percent of total

FAs, and c_r is the percentage of a reference FA, in this case 18:0 (Budge *et al.* 2002)

Diet Estimates

Diet estimates are presented in Beck *et al.* (2007). Thirteen species were identified in

grey seal diet estimates occurring at >1% on average (Table 4.5). The proportional diet

data were normalized using a log transformation. Fishes and invertebrates appearing in

QFASA estimates were classified as pelagic or benthic based on previous knowledge of

feeding habits (Scott and Scott 1988, Sherwood and Rose 2005). Trophic positions of fish

and invertebrate prey that comprised grey seal diet estimates were also derived form the

literature and an online database (FishBase; Froese and Pauly 2007). For individual grey

seals, I summed the proportions of each pelagic species (Table 4.2) estimated in the diet

to obtain the total percentage of pelagic prey. The trophic position of each seal was

calculated by taking the weighted average of the proportion of a particular prey item in

the diet, multiplied by the average trophic position of that prey as determined

independently from the literature.

Statistical Analysis

For both prey and seals, I only used FA's measured at >0.5 mass % of total fatty acids.

Transformed fatty acid data were subjected to principal component analyses (PCA) to

reduce multi-colinearity and generate independent principal components that could be

used as independent variables in subsequent regression analyses to evaluate their

relationship with $\delta^{13}C$. Only components having eigenvalues >1 or accounting for at least

5% of the total variance were retained. To generate PCA scores for prey, sample size was

augmented (n=579) by including additional individuals of the same species from the

Scotian Shelf Prey Base, sampled from the same areas and from the same time period

(data from Budge *et al.* 2002). Similarly, grey seal sample size was augmented (n=529)

by including additional individuals (data from Beck *et al.* 2005). Increasing the sample

sizes for both prey and grey seals ensured homogeneity of the correlation matrices. I also

fit a linear regression to evaluate the relationship between $\delta^{13}C$ and total percentage of

pelagic prey species estimated in the diet. Because sex-specific seasonal differences have

been found in stable isotope levels, fatty acid signatures and diets, I conducted separate

analyses for males and females using a GLM to test for the effect of sampling time on the

relationship between $\delta^{13}C$ and total percentage of pelagics estimated in the diet.

I also fit a linear regression to evaluate the relationship between $\delta^{15}N$ and the estimated trophic position of the diet. It is known that baseline values of $\delta^{15}N$ vary between benthic and pelagic systems such that organisms at equivalent trophic positions have different signatures (Sherwood et al. 2005; Tucker et al. 2007; Chapter III). Therefore I attempted to control for these differences with the $\delta^{13}C$ signature, by taking the $\delta^{15}N$: $\delta^{13}C$ ratio. I then fit a regression to evaluate the relationship between estimated trophic position and the $\delta^{15}N$: $\delta^{13}C$ ratio. PCA, regression and GLM models were fitted in S Plus version 6.2 (©1988, 2003 Insightful Corp.).

RESULTS

For fish and invertebrate prey, there were four significant principal components accounting for 80% of the variance in fatty acid signatures. Three of these components accounting for 72% of the variance (components 1, 2 and 4; Table 4.1 and 4.3; Figure 4.1) were significant predictors of $\delta^{13}C$ ($F_{3,44} = 33.98$; p<0.001).

There also were four significant principal components accounting for 85% of the variance in grey seal fatty acid signatures (Table 4.2). The first two of those components, which explained 72% of the variance, were significant predictors of seal $\delta^{13}C$ (Table 4.2 and 4.4; Figure 4.2).

I found a significant negative relationship between grey seal carbon signature and the proportion of pelagic prey in the diet (Figure 4.3; $F_{1,74} = 38.81$; p < 0.001). There was no effect of sampling time (males: $F_{2,37} = 0.89$; p = 0.42, females: $F_{2,36} = 0.92$; p = 0.41) for

either male or female seals. There was a significant correlation between the estimated

trophic position of the diet and $\delta^{15}N$ ($F_{1,74} = 12.89$; p = 0.001). Again, there was no effect

of sampling time (males: $F_{2,37} = 0.24$; p = 0.79, females: $F_{2,36} = 0.92$; p = 0.41) for either

male or female seals. There was also a significant correlation between trophic position

estimated from fatty acid signatures and the $\delta^{15}N$: $\delta^{13}C$ ratio (Figure 4.4; $F_{1,74} = 26.79$; p

< 0.001).

DISCUSSION

It is well established that both the fatty acid composition of lipid depots and stable

isotope values of lipid-free tissues are indicative of diet. Recently, Iverson *et al.* (2004)

developed a statistical model to estimate the proportions of prey species in the diet by

comparing the fatty acid signatures of predators with those of potential prey. This model

was validated in feeding experiments on captive animals and by comparison to prey

consumption by free-ranging harbour seals (*Phoca vitulina*) recorded with the use of an

animal-born video system (Crittercam) (Iverson *et al.* 2004). However, with any new

method further testing using field data is desirable. Concurrent sampling of individual

predators for both stable isotopes and fatty acids provide one such independent test.

Both fatty acids and stable isotopes are known to represent the assimilated portion of a

consumer's diet. Consequently, consumption of fish and invertebrates species are

independently identified by both their fatty acid profiles (Iverson *et al.* 1997a, 1997b;

Budge *et al.* 2002) and their stable isotope signatures (Lesage *et al.* 2001; Sherwood and

Rose 2005; Tucker *et al.* 2007; Chapter III). Moreover, I have demonstrated that both in a

number of prey species and in grey seals, there are significant correlations between fatty

acid signatures and carbon isotope values. $\delta^{13}C$ is indicative of carbon source due to

various physical and biological processes at the base of the food web (Post 2002) while

certain fatty acids are found in greater abundance in particular organisms and systems

(Budge *et al.* 2002, 2006). Components from PCA scores are weighted heavily by fatty

acids that are know to be strongly associated with both pelagic and benthic systems. For

example, there are negative relationships between $\delta^{13}C$ and the first principle component

for both fish and seals. Both of the first components are weighted by 14:0, 22:1n-11,

20:1n-9, 18:2n-6, 18:3n-3 and 18:4n-3 (Tables 3.3 and 3.4). These fatty acids are found

in elevated proportions in zooplankton, specifically copepod lipids (Graeve *et al.* 1994),

and variation in levels of these fatty acids, particularly 22:1n-11and 20:1n-9 likely

reflects high amounts of zooplankton in the diets of pelagic species such as herring and

capelin (Budge *et al.* 2002). Recall that the carbon signature becomes more positive from

pelagic to benthic species. Both of the second components are positively correlated with

$\delta^{13}C$ and are weighted by 18.1n-7 and 20:4n-6 (Tables 4.3 and 4.4). These fatty acids are

found in high concentrations in benthic diatoms and subsequently benthic invertebrates

and fish (Käkelä *et al.*, 2005; Budge *et al.* 2002).

Although I found significant correlations between FAs and $\delta^{13}C$, those relationships

explained a relatively small amount of the observed variability. PCA reduced the number

of FA variables from 39 to 4 for each of the prey species and grey seals. These new

variables accounted for most of the variance in the data. However, one characteristic of

PCA in this context is that the mixture of FA identified as a principal component is

constructed using only covariate information without regard to the relationship between FA's and their dietary origin. This may then be contributing to error in regressions with $\delta^{13}C$ since component scores may not be maximized along the same diet dimension represented by $\delta^{13}C$. Significant component scores were weighted by specific FA's characteristic of benthic/pelagic sources, suggesting that they are likely similar but not necessarily equivalent to $\delta^{13}C$. Nevertheless, I did find strong significant correlations (Pearson's Correlation: range 0.31-0.74) between $\delta^{13}C$ and individual fatty acid biomarkers (Table 4.6) strengthening our conclusion about the convergence between these two independent methods of inferring diet.

$\delta^{15}N$ is indicative of relative trophic position given that an organism's signature becomes enriched with every transfer up the food chain. This is due to selective retention of the heavier isotope relative to the lighter isotope within consumers. There is no analogous stepwise trophic pattern for fatty acids. This is because consumers, with little to no capacity for *de novo* biosynthesis, assimilate fatty acids roughly in proportion to their presence in the diet (Iverson *et al.* 2004; Budge *et al.* 2006). The trophic position of a consumer represents the weighted average of the trophic positions of its prey. Therefore it follows that the trophic position derived from an independent estimate of diet is known to match the $\delta^{15}N$ signature of a consumer (Vander Zanden *et al.* 1997).

Stable isotopes (Tucker *et al.* 2007; Chapter III) and qualitative analysis of fatty acid signatures (Beck *et al.* 2005) of grey seals reveal similar qualitative patterns in diet. Both approaches have found evidence for sex, ontogenetic and temporal variation in diets, as

well as a high degree of individual specialization. I found significant correlations between diet composition estimated from blubber fatty acids (Beck *et al.* 2007) and the carbon and nitrogen isotope signatures generated from a skin sample from the same animal (Tucker *et al.* 2007; Chapter III). This was in terms of both main carbon source of the diet and trophic position. I found no effect of season suggesting that there are no temporal effects influencing diet interpretation by either method or the relationship between them. Nevertheless, the correlations explained a relatively small amount of the observed variability.

I think there are several reasons for this. First, the temporal scale that each biochemical approach represents is somewhat unclear and this undoubtedly contributes to the strength of the correlation. Turnover of stable isotopes varies with the metabolic activity of the tissue sampled (Tieszen *et al.* 1983; Hobson and Clark 1992; Hobson 1993). Therefore, tissues with high turnover rates will provide dietary information assimilated from recent feeding events, while tissues with slower turnover rates will indicate feeding from more distant time periods. Thus changes in diet can take anywhere from a few days to many weeks to appear in an animal's tissue. The isotopic measurement of several tissues from the same individual can provide short-, intermediate-, and long-term dietary information (e.g., Hobson 1993). In addition, it is thought that the isotopic analysis of metabolically inactive tissues (e.g. hair, skin, whiskers, claws, feathers, and baleen) will reflect the diet of individuals only during the period of growth (Schell *et al.* 1989; Hobson *et al.* 1996). There is very little information on isotopic turnover rates for mammalian tissues. However, by coupling literature values of protein synthesis rates and carbon isotope

turnover rates in various mammal tissues, Kurle and Worthy (2002) estimated the time in which dietary information became incorporated into fur seal skin was on the order of 3-4 months prior to sampling. Thus, if a similar time scale applies to grey seals, the isotope signatures mainly reflect the prey consumed 3 months previous to sampling.

Similarly, FA analyses of different tissues (e.g., adipose tissue, blubber, milk, and blood) provide insights into diet over different temporal scales (reviewed in Budge *et al.* 2006). I analyzed the FA composition of grey seal blubber. Grey seals undergo two periods of fasting and subsequent replenishment over an annual cycle (*e.g.*, Beck *et al.* 2003). Seals deplete their blubber reserves during reproduction and again during the moult months later. Thus, the FA composition of grey seal blubber sampled early in the breeding season are thought to mainly reflect feeding over the course of several months (Beck *et al.* 2005), with little contribution from feeding earlier in the year. In feeding experiments on seals, it has been noted that the appearance of new dietary FA is evident within 1–2 wk of a switch in diet (Kirsch *et al.* 2000; Cooper 2004; Iverson *et al.* 2004). Therefore, it is assumed that FA signatures of seal blubber represent a dynamic integration of the diet over weeks to months.

Although there is undoubtedly overlap in the timescales of assimilation of the diet of the tissues sampled for FA and stable isotopes, it is also likely that they are not equivalent and thus we should expect them to both reflect previous diets in the same manner. Furthermore, individual variation in fractionation (the relationship between predator and diet signatures) has been noted for both stable isotopes (e.g., Hobson *et al.* 1996) and fatty acids (e.g., Iverson *et al.* 2004) and is likely also contributing to error. These two

approaches represent the assimilated signature from multiple dietary sources. Prey

species with more similar diets have more similar isotope signatures, making it difficult

to tease apart specific contributions to a consumer's diet. On the other hand, because of

the large number of FA's analyzed, FA signatures are far more powerful in defining and

identifying inter-specific differences, despite similarities in respective diets (Budge *et al.*

2002). The difference in precision between these two methods is also likely another

source of error.

I have shown two lines of evidence for the convergence of stable isotope and fatty acid

estimates of diet. First, in fish, invertebrates and grey seals principal components derived

from fatty acid signatures are correlated to the carbon isotope signature of the same

species. Second, both the estimated portion of pelagic prey and the trophic level of the

diet derived from the quantitative analysis of fatty acid signatures of individual seals are

positively correlated with the $\delta^{13}C$ and $\delta^{15}N$ signatures in those same individuals. The

application of stable isotopes mixing models (Phillips *et al.* 2005) might improve the

correspondence between the two types of tracers. However, this would require a

considerably larger isotope prey base. In addition, because the measurement of several

tissues for stable isotopes can provide a range of temporal dietary information (e.g.,

Hobson 1993; Hobson *et al* 1996) this could result in greater overlap in the timescales of

assimilated dietary information of these two biochemical methods.

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TABLES

Table 4.1: Significant principal components for fatty acid signatures of fish and invertebrate species, and the coefficients from a multiple regression with $\delta^{13}C$.

Component	Eigen value	Variance explained (%)	Cumulative variance	Coefficient B	t	p
1	9.05	45.25	45.25	-0.71	-6.31	0.000
2	3.89	19.42	64.68	0.67	6.71	0.000
3	1.66	8.31	72.99	0.03	0.35	0.694
4	1.31	6.56	79.55	0.54	4.30	0.000

Table 4.2: Significant principal components for fatty acid signatures of grey seals, and the coefficients from a multiple regression with $\delta^{13}C$.

Component	Eigen value	Variance explained (%)	Cumulative variance	Coefficient B	t	p
1	13.95	55.79	55.79	-0.395	-4.57	0.000
2	3.96	15.83	71.62	0.245	2.89	0.006
3	2.23	8.90	80.53	0.058	0.76	0.454
4	1.20	4.80	85.33	0.159	1.83	0.074

Table 4.3: Weightings of individual fatty acids in PCA components for fish and invertebrates which were significantly correlated with $\delta^{13}C$.

Fatty Acid	Component		
	1	2	4
14:0	0.900	-0.204	-0.186
16:0	0.824	-0.185	0.247
16:1n-7	0.871	0.302	-0.218
18:1n-11	0.513	-0.349	0.083
18:1n-9	0.757	0.119	0.230
18:1n-7	0.534	0.711	0.245
18:1n-5	0.723	0.452	0.083
18:2n-6	0.890	0.048	0.107
18:3n-3	0.749	-0.108	0.020
18:4n-3	0.737	-0.249	-0.460
20:1n-11	0.556	0.256	0.117
20:1n-9	0.827	-0.401	0.022
20:1n-7	0.526	0.710	-0.199
20:4n-6	-0.283	0.770	0.443
20:5n-3	0.524	0.624	0.103
22:1n-11	0.840	-0.363	0.121
22:1n-9	0.855	-0.138	0.050
22:5n-3	0.276	0.365	-0.494
22:6n-3	0.121	-0.589	0.545
24:1n-9	0.331	-0.674	-0.018

Table 4.4: Weightings of individual fatty acids in PCA components for grey seals which were significantly correlated with $\delta^{13}C$.

Fatty Acid	Component	
	1	2
14:0	0.880	-0.375
14:1n-5	0.814	0.469
16:0	0.598	-0.366
16:1n-11	0.898	0.071
16:1n-7	0.867	0.256
16:3n-6	0.884	-0.307
16:4n-1	0.771	-0.519
18:1n-11	0.823	0.124
18:1n-9	0.465	0.812
18:1n-7	0.478	0.696
18:1n-5	0.899	0.042
18:2n-6	0.779	0.385
18:3n-3	0.739	0.193
18:4n-3	0.800	-0.354
20:1n-11	0.740	0.139
20:1n-9	0.839	-0.223
20:1n-7	0.468	0.178
20:4n-6	-0.002	0.694
20:4n-3	0.876	0.048
20:5n-3	0.764	-0.332
22:1n-11	0.609	-0.663
22:1n-9	0.680	-0.411
21:5n-3	0.887	-0.064
22:5n-3	0.826	0.314
22:6n-3	0.613	0.389

Table 4.5: Main system (benthic/pelagic) and trophic levels derived from literature and online resources for main constituents (>1% on average) of grey seal diets estimated by QFASA.

Diet item	Average contribution (%)	System	Trophic level
Capelin	1.2	Pelagic	3.2
Herring	2.4	Pelagic	3.3
Lumpfish	1.6	Pelagic	3.5
Redfish small	12.8	Pelagic	3.5
Sandlance large	36.9	Pelagic	3.2
Sandlance small	5.1	Pelagic	3.0
Pollock large	1.1	Benthic	4.5
Pollock small	12.7	Benthic	4.0
Redfish large	17.3	Benthic	4.5
Snakeblenny	1.1	Benthic	4.0
Thorny skate	1.1	Benthic	4.5
Turbot	2.2	Benthic	4.5
Witchflounder	3.7	Benthic	3.5

Table 4.6: Pearson's Correlation for $\delta^{13}C$ and indicator fatty acids of pelagic and benthic systems from fish and invertebrates.

	Fatty Acids	Pearson's Correlation	Significance
Pelagic (n=45)	14:0	-0.739	0.000
	18:2n-6	-0.421	0.011
	18:3n-3	-0.353	0.018
	18:4n-3	-0.722	0.000
	20:1n-9	-0.700	0.000
	22:1n-11	-0.739	0.000
	22:1n-9	-0.694	0.000
Benthic (n=45)	16:4n-3	0.454	0.002
	17:0	0.515	0.000
	18:1n-7	0.485	0.001
	20:4n-6	0.700	0.000
	20:1n-11	0.309	0.039
	20:1n-7	0.342	0.022
	20:5n-3	0.586	0.000

FIGURES
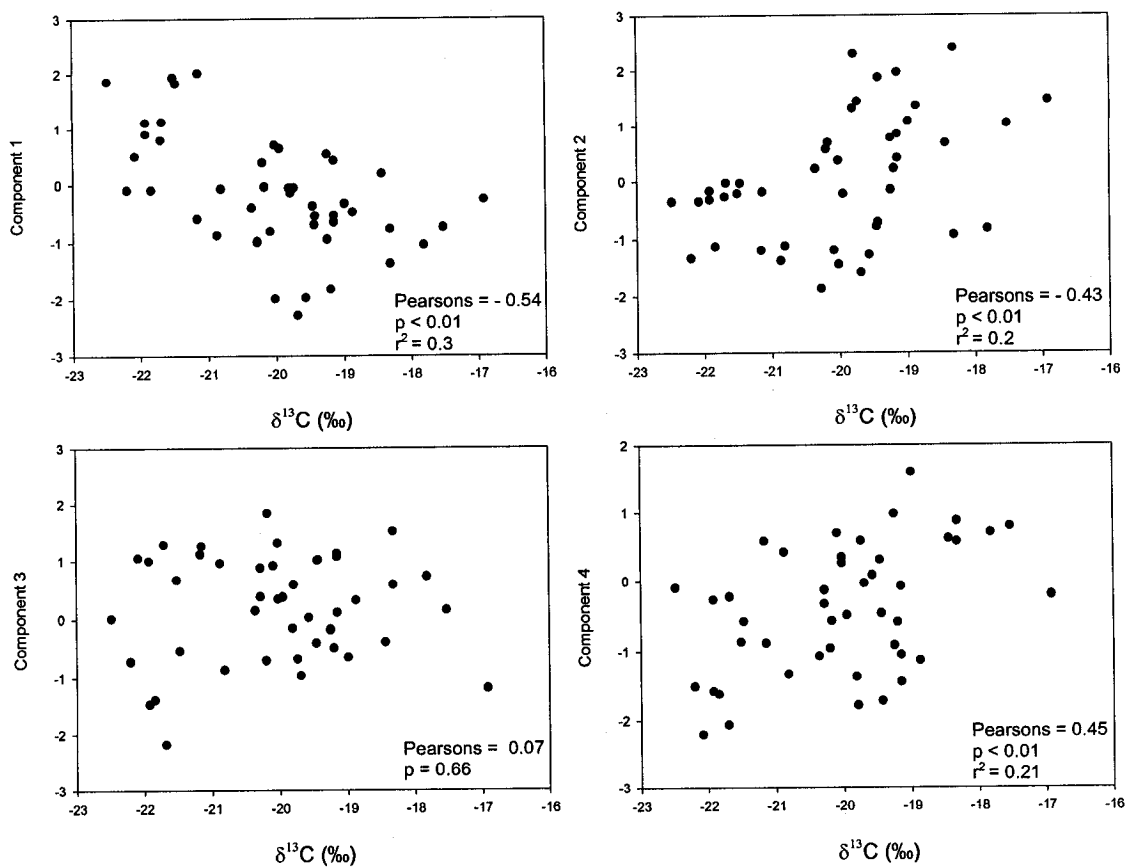
Figure 4.1: PCA components of fatty acids and $\delta^{13}C$ for fish and invertebrates.
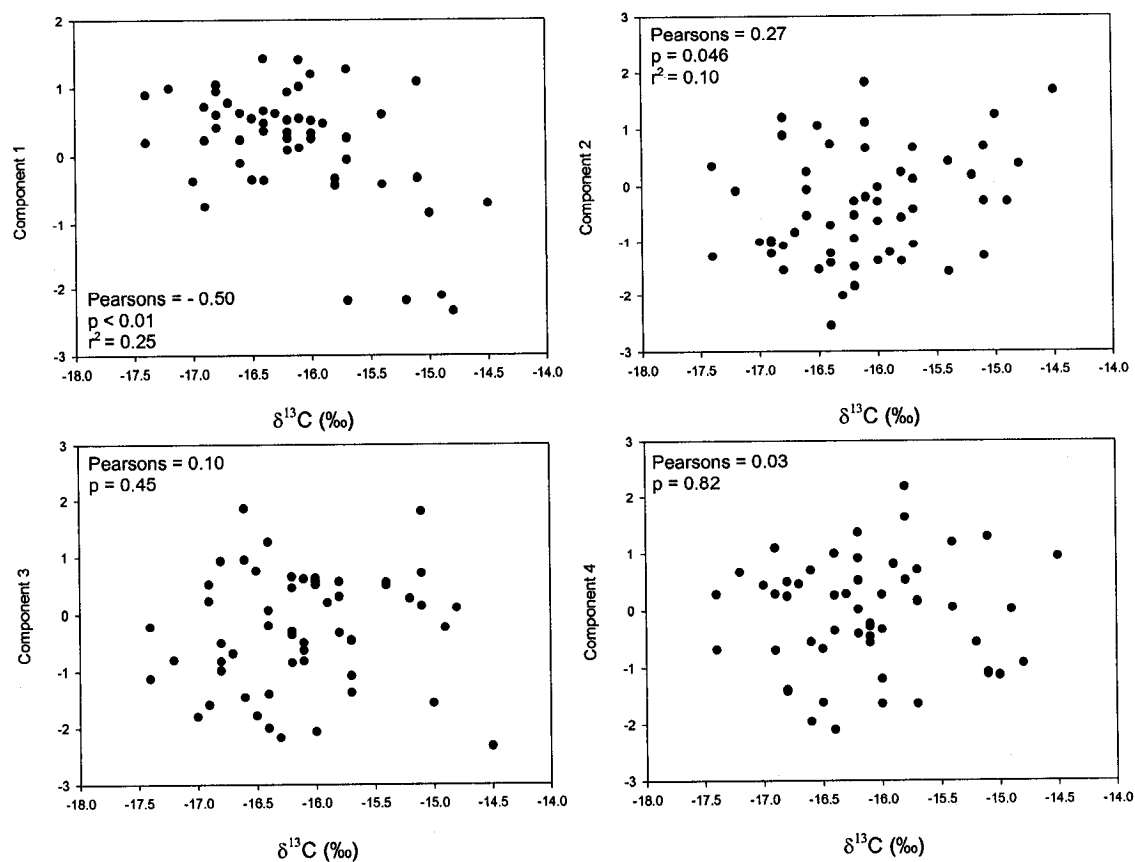
Figure 4.2: PCA components of fatty acids and $\delta^{13}C$ for grey seals.
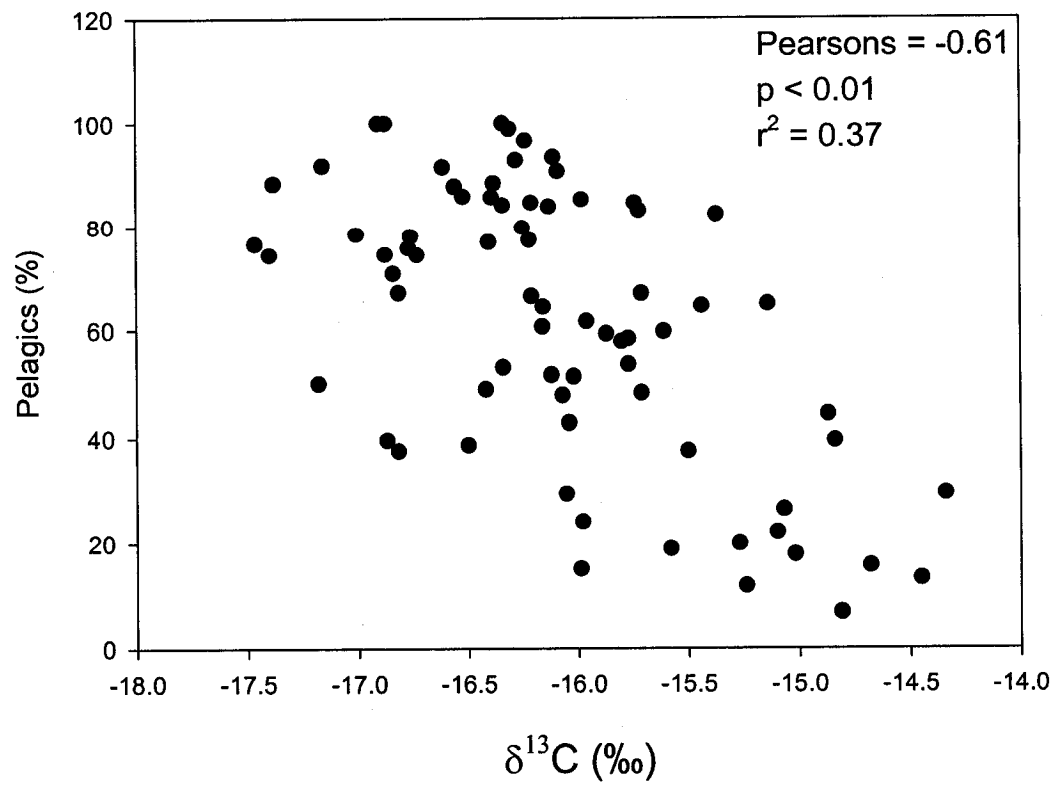
Figure 4.3: $\delta^{13}C$ and total pelagics in the diet (%).
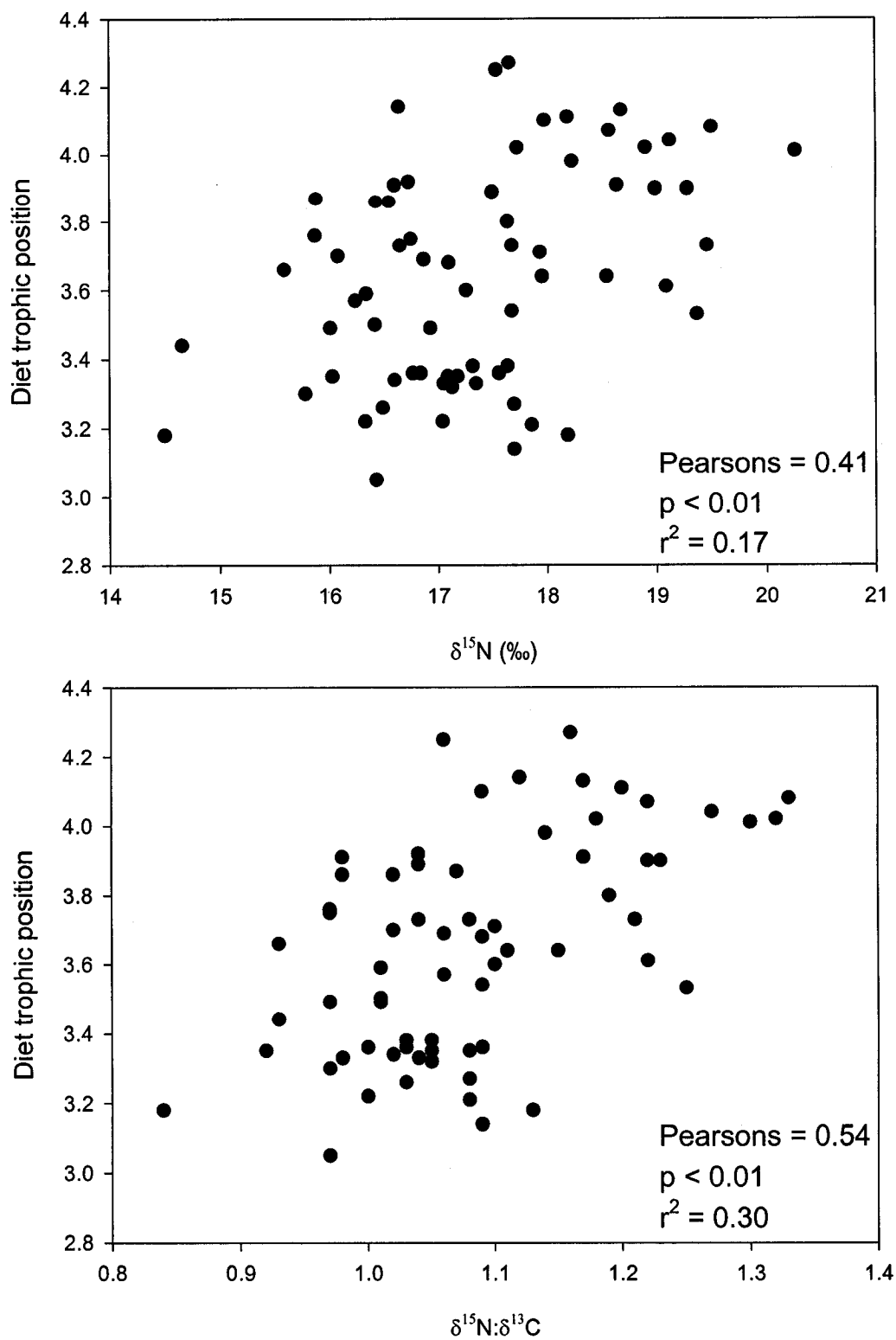
Figure 4.4: $\delta^{15}N$, $\delta^{15}N:\delta^{13}C$ ratio and trophic position of the diet (%).

CHAPTER V: INTER- AND INTRA-SPECIFIC DIFFERENCES IN DIETS OF HARP (*PHOCA GROENLANDICA*) AND HOODED (*CYSTOPHORA CRISTATA*) SEALS REVEALED THROUGH FATTY ACID SIGNATURES

INTRODUCTION

Diet has fundamental consequences with respect to gross energy intake, foraging costs

and exposure to foraging-specific risk factors such as predation and competition (Bolnick

et al. 2003). Inter-specific competition for prey has traditionally been viewed as

fundamental to the structure of ecological communities and species niche breadth (Pianka

1981; Polis 1984). Increasingly, intra-specific competition has been identified as a

significant component in the evolution of a species' overall niche width (Polis 1984;

Williams and Martinez 2000; Bolnick *et al.* 2003). Both inter- and intra-species

competition can be mitigated through resource partitioning over varying spatial and

temporal scales (e.g. Kato *et al.* 2000; Wikelski and Wrege 2000; Bradshaw *et al.* 2003;

Field *et al.* 2005). Within species, diets often diverge as a function of body size, age, sex,

condition and reproductive status (e.g. Clarke *et al.* 1998). Various hypotheses have been

proposed to explain this variation in diet such as niche divergence where competition is

minimized between male and females by the selection of different prey or by

spatial/temporal segregation in feeding. Alternatively, but not exclusively, variable sex-

specific costs of reproduction may result in differential resource use (Ginnett and

Demment 1997). Differential resource use by the sexes has been observed in both size

dimorphic (e.g. Clarke *et al.* 1998) and monomorphic (e.g. Lewis *et al.* 2002) species.

Also, differences in diet could simply be due to different energetic costs associated with

body size (e.g. Barbosa *et al.* 2000) due to either age and growth or size dimorphism.

Greater absolute energy requirements of larger animals may require differential use of

resources that can result in segregation in foraging. Moreover, predator size generally determines inter-specific dietary overlap (Sinclair *et al.* 2003), as ontogenetic shifts in diet often outweigh the variation in diets across similarly sized species (Woodward and Hildrew 2002). These various hypotheses could also be invoked to explain diet differences between closely related and/or sympatric species as well.

Although many studies have documented the degree of dietary specialization in terrestrial mammals, much less is known about prey selection in marine mammals. It is often assumed that classes of marine mammals differ in their diets based on the observed diversity of morphological, physiological and behavioural adaptations (Bowen *et al.* 2002). For example, many species of cetaceans display very specialized adaptations of feeding apparatus. Alternatively, pinnipeds are assumed to be generalist predators given their wide-ranging foraging behaviour and the number of different prey species identified from stomachs. There are of course exceptions within pinnipeds, and it is often found that relatively few prey species account for the majority of ingested energy (e.g. Bowen and Harrison 1994; Lawson and Stenson 1995; Lawson *et al.* 1995; Beck *et al.* 2007). Within species, there is evidence for sex differences in foraging behaviour and diet of different size-dimorphic pinnipeds where males are significantly larger than females, such as northern and southern elephant seals as well as grey seals (Beck *et al.* 2003a, b; Le Boeuf *et al.* 1993, 2000; Field *et al.* 2005). There is also evidence for ontogenetic shifts in foraging behaviour and diets (Beck *et al.* 2005) in pinnipeds as large changes in physiology and behavior have been documented between juveniles and adults (Le Boeuf *et al.* 2000; Field *et al.* 2005; Noren *et al.* 2005). However, overall differences and the

factors influencing dietary specialization have not been fully evaluated given the difficulty of studying marine mammals at sea (Bowen *et al.* 2002).

Harp (*Phoca groenlandica*) and hooded (*Cystophora cristata*) seals are abundant pinnipeds in the North Atlantic Ocean (Stenson *et al.* 1997, 2002, 2003). However, these two species typically partition foraging ranges and pupping habitats, and also exhibit differences in body size, degree of sexual body-size dimporphism, diving behaviour, migratory routes, and the time and energy invested in reproduction (Lydersen and Kovacs 1999). Harp seals are only slightly dimorphic with an average adult mass of 130kg and males being 10% larger than females (Hammill *et al.* 1995). Hooded seals are more size-dimorphic with adult males approximately 1.5 times larger than females and 2.3 times larger than adult harps. Although they are both wide ranging and exhibit long-distance seasonal migrations, harp seals mainly inhabit the continental shelf (Stenson and Sjare 1997; Folkow *et al.* 2004), while hooded seals are more associated with the continental shelf edge and deep ocean (Folkow and Blix 1999). These species also differ in their diving behaviour with most harp seal dives being <50m, although there are a number of dives to depths up to 200m (Stenson and Sjare 1997; Folkow *et al.* 2004). By contrast, hooded seals regularly dive deeper with a large portion of the dives to depths >300m and often exceeding 1000m (Folkow and Blix 1999). In contrast to sex differences in diving behaviour for other size-dimorphic pinnipeds (Le Boeuf *et al.* 1993, 2000; Beck *et al.* 2003a, b; Field *et al.* 2005; Breed *et al.* 2006), Folkow and Blix (1999) found no individual, sex or size-related differences in dive parameters for mature hoods, although

sample size was small. Harps have also been known to segregate by sex and age classes across their foraging range (Sergeant 1965, 1991).

These species differences in diving patterns are reflected in average diets estimated from stomach content analyses. However, diet estimates derived from stomach content analysis are often biased by a number of factors (Jobling and Breiby 1986; Jobling 1987). Stomach content analysis indicates that harp seals consume a mixed diet of capelin (*Mallotus villosus*), Arctic cod (*Boregadus saida*) and herring (*Clupea harengus*) among many other fish species, and invertebrates such as euphausiids (Lawson *et al.* 1995; Lawson and Stenson 1995, 1997). Data on hooded seals are relatively scarce, but they are presumed to mostly feed on a variety of deep-water fish such as halibut (*Hippoglossus hippoglossus*), redfish (*Sebastes sp.*) and squid as well as capelin, Atlantic cod (*Gadus morhua*) and Arctic cod (Ross 1993; Kapel 1995; Hammill and Stenson 2000; Potelov *et al.* 2000; Haug *et al.* 2006). Sex differences in diet have not been evaluated for either species, but age differences are evident in harp seals (Lawson and Stenson 1995).

Given their broad geographic and seasonal distribution, we should expect to find differences in the diet over time and space. To date, most samples have been collected in their winter ranges either before or after the breeding season and most of these from relatively nearshore locations. These data indicate geographical, seasonal and annual variation in harp and hooded seal diets (e.g. Lawson *et al.* 1995; Lawson and Stenson 1995; Lawson and Stenson 1997; Lawson *et al.* 1998).

There have been large changes in the fish assemblage of the North Atlantic with the collapse of groundfish stocks in the early 90's (e.g. Hutchings and Myers 1994; Rose 2004) and the coincidental changes in pelagic forage fish abundance and distribution (Frank *et al.* 1994; Carscadden *et al.* 2001) as well as that of seals (Lacoste and Stenson 2000; Sjare *et al.* 2004). Given our current lack of understanding factors influencing diet selection and implications for growth and condition (Sjare *et al.* 2004), it is unclear how species of seals should respond to such dramatic changes in the prey base.

Limitations of stomach content analysis have led to the development of alternative biochemical methods for estimating diets of predators. For several species of marine mammals, seabirds and terrestrial carnivores, fatty acid signature analysis has provided both a qualitative assessment of temporal or spatial changes in diet (e.g. Iverson *et al.* 1997a, 1997b; Smith *et al.* 1997; Beck *et al.* 2005) and a quantitative estimate of the species composition of the diet (Iverson *et al.* 2004; Beck *et al.* 2007). Fatty acids are deposited in animal tissue in a predictable manner and there are limits on polyunsaturated fatty acid biosynthesis in higher order consumers such that many fatty acids found in pinniped blubber can arise only from dietary sources (Iverson 1993). Fatty acids provide estimates of the diet of individuals that integrate consumption over periods of weeks to months and thus sampling locations of wide-ranging species are less likely to bias our understanding of what is eaten.

In this study I used fatty acid signature analysis to examine the sources of variation in the diets of these two phocid seal species that seem to partition space by both ranging and

organizing foraging behaviour in different ways. One species, the hooded seal, also exhibits a degree of sexual-size dimorphism that in other species (i.e., grey seal – Beck *et al.* 2005) has lead to sex-specific difference in diet. Given broad evidence for their importance in other taxa, I tested for the effects of three intrinsic factors (age, sex and body size) and three extrinsic factors (season and year effects and geographic location) on the diets of these species.

METHODS

Sampling

Seals were sampled along the Northeast coast of Newfoundland and Southern Labrador between November and May from 1994-2004 by experienced seals hunters and scientific personnel from the Department of Fisheries and Oceans (Sjare *et al.* 2004). Samples were similarly obtained during offshore cruises in the winters of 1994, 2002 and 2004 (Figure 5.1; Table 5.1). Seals were weighed to the nearest 0.5 kg and a blubber sample (approximately 0.5 kg) was taken from the posterior flank, placed in whirlpak® and frozen. Seal ages were determined to the nearest year by sectioning a lower canine tooth and then counting dentine annuli (Bowen *et al.* 1983; Lawson *et al.* 1992). In addition to the samples from killed seals, biopsy samples were taken from both live-captured harp (n =33) and hooded (n =12) seals during an offshore cruise to the whelping patch in March 2004. Adults were captured using a hand held net. Hooded seal biopsy samples also were taken during a cruise to the moulting patch off eastern Greenland during the spring of 2005 (n =17).

Fatty Acid Analysis

In the laboratory, a 0.5 g core of blubber representing the entire depth of the field-collected sample (i.e., from skin to underlying muscle) was taken. Lipids were quantitatively extracted from all blubber samples using a modified Folch method (Iverson *et al.* 2001.) FA methyl esters (FAME) were prepared using an acidic catalyst (the Hilditch method; see Iverson *et al.* 2001; Budge *et al.* 2006). Duplicate analyses and identification of FAME were performed using temperature-programmed gas–liquid chromatography (GLC) (Iverson *et al.* 1997b, 2004; Budge *et al.* 2006). Fatty acids (FA) were described by the standard nomenclature of carbon chain length: number of double bonds and location (n-x) of the double bond nearest the terminal methyl group. Individual FA's were expressed as a percent mass of total fatty acids. Although 67 fatty acids are routinely identified, I used 39 fatty acids of dietary or primarily dietary origin in our analysis (Iverson *et al.* 2004; Beck *et al.* 2005; Budge *et al.* 2006) which accounted for approximately 93% of total FA by mass.

Statistical Analysis

Harp seals were classified as juvenile (1-4years) and adults (4+ years) (Sjare *et al.* 2004) and into two seasons - pre-breeding (November to March reproduction period) and post-breeding (April-May). No harp seals were sampled during summer months. Given that FA represent an integration of the diet over periods of weeks to perhaps months (Iverson *et al.* 2004), I assumed that samples represent the assimilated diet from previous months. For example, our pre-breeding samples likely represent some feeding that occurred in early winter as well as the month sampled. Seals were also classified into 2 geographical

areas based on sampling location: inshore (defined as < 30 km from shore; Lawson *et al.* 1995), and offshore including the Labrador Banks and Grand Banks.

Hooded seals were similarly classified into juveniles (≤5 years) and adults (>5 years). I coded 2 seasons; pre- and post-breeding (where breeding occurred in mid March). I also classified the hooded seals samples into 3 geographic groups: Greenland, Northeastern Newfoundland (NE NFLD) and Northern Newfoundland and Labrador (NNL).

General Linear Model (GLM) multivariate analysis and discriminant function analysis (DFA) were used to examine the effects of sex, age-class, season, year, geographic area and body size on FA profiles (SPSS® version 10.1; SPSS Inc. 2000). These multivariate methods require that the number of samples exceeds the number of variables to provide reasonable assurance that covariance matrices are homogeneous (Budge *et al.* 2006). I used the largest subset of FA for each analysis, selecting those that exhibited the greatest average variance across samples to maximize the amount of information retained. To test for intrinsic (sex, age class, body size) and extrinsic (season, year, sampling area) effects in harp seals, I ran an overall GLM using 31 FAs which accounted for 92% of total FAs by mass. Animals that were biopsied from the whelping patch were dropped from analysis examining spatial effects because I had no knowledge of where they might have fed. To evaluate intrinsic effects in hooded seals, I used a subset of 37 FA (92.5% of total FAs) in an overall GLM. Because the number of animals sampled varied among sampling periods and areas, I constructed a second GLM using a subset of 17 FA (89% of total FAs) which had season, year and area as well as sex, age class and mass as main effects. To compare species, I pooled all harp and hooded seals, using the entire 39 FA set. All

two-way interactions were also evaluated for significance. To improve normality, the proportional data were normalized using a log transformation according to the following equation: $x\text{trans} = \ln(xi/cr)$, where $x\text{trans}$ is the transformed data, xi is a FA expressed as percent of total FAs, and cr is the percentage of a reference FA, in this case 18:0 (Budge *et al.* 2002).

RESULTS

Over the 10 year period, blubber samples were analyzed from 294 adult and 232 juvenile harp seals and 115 adult and 38 juvenile hooded seals (Table 5.1). Roughly equal numbers of males and females were sampled at each time period. The average FA compositions of each species and age class blubber are shown in Table 5.2. Seven FA, each > 5% of total FAs by mass, (16:0, 16:1*n*–7, 18:1*n*–9, 20:1*n*–9, 20:5*n*–3, 22:1*n*–11, and 22:6*n*–3) accounted for approximately 68% of the total FA. Overall, saturated, monounsaturated, and polyunsaturated FAs accounted for 15.9%, 56.8%, and 27.3% on average of total FA by mass, respectively (Table 5.2).

Harp seals

Intrinsic factors

I found a significant effect of sex ($F_{30,427}=1.85$; p=0.005), age class ($F_{30,427}=3.41$; p<0.001) and body mass ($F_{30,427}=1.79$; p=0.007) on harp seal fatty acid signatures. I then conducted separate analyses for adults and juveniles because of the large differences in sample size between age classes. This revealed evidence for sex differences in adults ($F_{30,263}=2.95$; p<0.001), but not in juveniles ($F_{30,241}=1.28$; p=0.137; Figure 5.2). Overall,

69.4% of age classes were correctly classified in a DFA with a cross validation error of 8.2% (Figure 5.3). The first discriminant function juveniles from adults due primarily to variation in 22:1n-11 and 18:4n-3. The 2nd discriminant function separated adult males from adult females due primarily to variation in 22:5n-3 and 20:1n-7. Most misclassified cases (approximately 30%) were between adults. There were also significant interactions between sex and body mass ($F_{30,427}$=2.15; p=0.001) and age class and body mass ($F_{30,427}$=3.36; p<0.001) suggesting that diets change differently for age classes of males and females as body size increases.

Temporal and spatial factors

I found a significant effect of season ($F_{30,427}$=3.02; p<0.001) and geographic sampling area ($F_{30,427}$=1.79; p=0.007) on harp seal fatty acid signatures. To control for age class effects, I separated juvenile samples from adults. DFA on adult samples suggested that diets varied seasonally in both the inshore and offshore (Figure 5.4). The first discriminant function separated pre-breeding samples from post-breeding offshore samples due to variation in 16:4n-1, 18:4n-1 and 21:5n-3. The second function spread post-breeding inshore and offshore samples due to variation in 16:4n-1 and 22:1n-7. Overall, 76% of individuals were correctly classified to season and area with a cross validation error of 10.4%. Most misclassified cases (24%) were between inshore samples as diets were more similar in the inshore and varied seasonally to a greater extent in the offshore. An analogous result was found for the DFA on juveniles samples (Figure 5.4). The first discriminant function separated pre-breeding samples from post-breeding offshore samples due to variation in 16:3n-6, 18:1n-7 and 22:6n-3. The second function

spread post-breeding inshore and offshore samples due to variation in 16:1n-7 and 20:5n-3. Overall, 76.3% of individuals were correctly classified to season and area with a cross validation error of 13.6%.

I tested for sex differences in adults within sampling season. The first discriminant function separated post- and pre-breeding animals, while the second function separated males from females (Figure 5.5). Misclassifications were primarily between sexes (25%) and were low between seasons (<7%). The difference between males and females were more pronounced in the pre-breeding period.

There was also a year effect on the FA composition of harps seal blubber ($F_{180,2592}=2.19$; $p<0.001$), and a significant interaction between season and year ($F_{90,1287}=1.59$; $p=0.001$) suggesting diets changed differently among seasons between years. There were also significant interactions between sex and year ($F_{180,2592}=1.28$; $p=0.008$) as well as age class and year ($F_{180,2592}=1.30$; $p=0.001$) suggesting diets of males and females, and adults and juveniles, varied differently among years. There was also a significant interaction between area and year ($F_{60,856}=2.09$; $p<0.001$) suggesting that diets changed differently in each area between years. Subsequently, to control for confounding effects, I separated juveniles from adults and examined animals from the pre-breeding period in which I had the greatest number of samples. In juveniles, 74.4% of years were correctly classified by DFA with cross validation error of 20.3% (Figure 5.6). The first discriminant function separated 1994 from 1995 and from the remaining years which formed a cluster due to large variation in 16:2n-6 and 22:1n-9. The second function separated 1994 and 1995 due

to variation in 16:1n-6, 22:5n-3. Again a similar result was found for adult harps. The first discriminant function separated 1994 from 1995 and from the remaining years which formed a cluster due to large variation in 16:2n-6 and 22:1n-9 and 18:4n-1. The second function separated 1994 and 1995 due to variation in 18:4n-3, 22:1n-7. 75.8% of years were correctly classified by DFA with cross validation error of 31% (Figure 5.6).

Hooded seals

Intrinsic factors

There was a significant effect of sex ($F_{36,108}=1.98$; $p=0.004$), age class ($F_{36,108}=3.00$; $p<0.001$) and body mass ($F_{36,108}=1.76$; $p=0.014$) across all hoods. Within juveniles, there was no effect of sex ($F_{13,23}=1.23$; $p=0.32$), but a significant effect of mass ($F_{13,23}=3.66$; $p=0.003$). Within adults, there was a significant effect of sex ($F_{36,70}=2.84$; $p=0.00$) and body mass ($F_{36,70}=2.54$; $p=0.00$). DFA on all samples of hoods indicated that juveniles differed from adults along the 1st discriminant function mainly because of variation in 16:1n-7, 18:1n-9, 20:5n-3 and 14:0, while the second discriminant function separated adult males and females due to variation in 18:4n-1, 20:4n-6 and 22:1n-9 (Figure 5.7). Overall, DFA classified 87.6% of the grouped cases with a cross validation error of 19.4%.

Temporal and spatial factors

I constructed a second GLM using 17 FA (accounting for 88.9% of FAs) to evaluate temporal and spatial effects. Pre- and post-breeding seals had significantly different FA signatures ($F_{16,122}=3.34$; $p=0.00$). In adults, sex differences persisted in each season with

DFA correctly classifying 72.2% of original cases with a cross validation error of 23% (Figure 5.8). Pre- and post-breeding animals were separated along the first discriminant function due to variation in 16:1n-7, 22:1n-11 and 22:1n-9, while the sexes were separated along the second function due to 18:1n-7, 20:1n-7. Misclassifications were mostly between sexes as opposed to between seasons (approximately 20% and 10%, respectively).

I was unable to test for individual year effects due to small sample sizes so I pooled years into 3 groups as follows: <1999, 2000-2003 and 2004 -2005. These groups contained approximately equal numbers of males and females. This analysis suggested longer-term temporal variation in diets ($F_{32,246}$=2.74; p=0.00). DFA on all samples correctly classified 75.2% of grouped cases with a cross validation error of 10.5%. The first function separated the 1999 and 2004 groups due to variation in 16:1n-7, 20:1n-9 and 22:1n-11, while the second function separated 2000 from the other groups primarily due to variation in 18:1n-9, 18:4n-3 and 22:6n-3 (Figure 5.9).

Finally, I found a significant effect of sampling area ($F_{32,246}$=5.25; p=0.00). DFA on all samples correctly classified 70% of cases with a cross validation error of 12.9%. The first function separated the Greenland samples from the other 2 areas due primarily to variation in 22:1n-9 and 22:1n-11, while the second function separated NE NFLD from NNL due to variation in 16:1n-7 (Figure 5.10). However, as Greenland animals were sampled in the summer, this conclusion may be confounded by a seasonal effect.

Misclassification of individuals occurred primarily between NE NFLD and NNL samples.

Species Differences

I found a significant effect of species ($F_{38,634}$=21.11; p<0.001) and significant interaction terms between species and all other variables: sex ($F_{38,634}$=2.271; p<0.001), age class ($F_{76,1270}$=8.54; p<0.001) and mass ($F_{38,634}$=2.98; p<0.001). These significant interaction terms suggest that the effects of each of these independent variables on FA profiles are different between the two species. DFA suggested no overlap in fatty acid signatures between any age class of harp and hooded seals (Figure 5.11). These species were identified along the first discriminant function (91.3% of the variance) which was primarily due to variation in 22:5n-3, 18:4n-3 and 18:1n-7. Age classes were identified along the second discriminant function (6.8% of the variance) due primarily to differences in 20:5n-3, 18:4n-1 and 18:3n-3. Overall, 83.4 % of the grouped cases were correctly classified with a cross validation error of 3.6 %. All misclassifications were solely between age classes within each species respectively.

DISCUSSION

Individuals of different age, sex and morphology are expected to exhibit differences in dietary niches largely due to sexual dimorphism, ontogenetic niche shifts, and resource polymorphism, respectively (Bolnick *et al.* 2003; Estes *et al.* 2003). Inter- and intra-specific dietary segregation has rarely been assessed for sympatric species of marine mammals given the difficulty of studying animals at sea through traditional methods.

Analysis of fatty acid signatures facilitates such a comparative approach because time-integrated information can be generated for a large number of individuals belonging to various demographic groups (e.g. Iverson *et al.* 1997a; Beck *et al.* 2005; Thiemann *et al.* 2006). Differences in FA profiles between groups of individuals can arise from differences in the proportion of the same prey species being consumed or from a different mixture of prey species altogether (Iverson *et al.* 2004; Budge *et al.* 2006). It is not possible to distinguish between these two possibilities by simply examining the fatty acid signatures of consumers alone because it is not possible to attribute the proportion consumed of a specific prey based on the level of individual FA's (Iverson *et al.* 2004). To do so, predator signatures must be considered relative to a whole suite of potential prey. However, different fatty acid profiles do indeed imply differences in diets (Iverson *et al.* 2004; Budge *et al.* 2006).

Sex differences

Sex differences in foraging behaviour and diet are assumed to reflect differences in sex-specific costs of reproduction, or in the case of size dimorphism, effects of larger body size or intra-specific competition. Sex differences in diet have been noted in both monomorphic (e.g. Lewis *et al.* 2002) and dimorphic (e.g. Clarke *et al.* 1998) animal species including pinnipeds (e.g. Beck *et al.* 2007). I found differences in fatty acid signatures in adults of both harp and hooded seals, but not in juveniles of either species. The magnitude of sex differences found in harp seals is relatively small compared with hooded seals as well as with grey seals (Beck *et al.* 2005) which also display a larger degree of sexual size dimorphism. I hypothesize that sex differences in the diets of adult

harp seals in the pre-breeding period are related to sex-specific costs associated with reproduction. Although this may also be true for hooded seals, divergent diet of males and females may also be due to the costs associated with maintaining a larger body size in males. This is consistent with the lack of sex differences in the diets of juveniles which do not have reproductive costs and exhibit little body-size dimorphism.

Age class and body size differences

I found significant differences among age classes of both harp and hooded seals as the fatty acid profiles of juveniles differed from adults. Age-class effects may entail endogenous factors such as body size and energetic demand, physiological differences and behavioural development or simply differences in spatial distribution. Many studies on pinnipeds have documented that both the physiological and behavioral capacity of juveniles to dive and forage develops over the first year of life (Merrick and Loughlin 1997; Burns et al. 1999; Baker and Donohue 2000; Noren et al. 2005). Thus, I expect that juvenile seals would be limited in their foraging ability relative to adults and presumably have access to fewer or different types of prey, including smaller size classes of particular species, resulting in significant age-class differences in FA profiles. In addition, spatial differences in foraging range have been noted between juveniles and adults of different pinniped species (e.g. Field et al. 2005) including harp seals (Sergeant 1991) which may result in differences in available prey. Indeed, ontogenetic diet shifts have been demonstrated in harp seals, through the analysis of stomach contents, involving an increase in the proportion of forage fish at the expense of pelagic invertebrates (Lawson and Stenson 1995). Little is known about ontogenetic diet changes in hooded seals.

Although we can make general inferences based on age-class or sex, I found a significant effect of body size across individuals of both species, where overlap between age-class and sex groups is correlated with body size. This suggests that endogenous energetic constraints may underlie sex and ontogenetic diet shifts.

Increasingly, body-size is seen as a crucial determinant of food web structure in terrestrial systems (Warren 1996; Chase 1999; Memmott *et al.* 2000; Williams and Martinez 2000). In terrestrial predators, an increase in predator size is associated with increases in both mean prey size (Carbone *et al.* 1999, Radloff and du Toit 2004) and prey diversity (Gittleman 1985; Cohen *et al.* 1993). Consequently, predator size generally determines the degree of inter- and intra-specific dietary overlap, as ontogenetic shifts in diet are often greater than the variation in diets across similarly sized species (Woodward and Hildrew 2002; Sinclair *et al.* 2003).

Analogous to results presented here, Tucker *et al.* (2007) found that diets in grey seals were most dissimilar as body size diverged, while animals of similar body size overlapped with respect to diet, irrespective of sex. It was hypothesized that dietary shifts to a greater proportion of benthic prey were made with increasing body size to minimize foraging costs associated with more dynamic pelagic prey. Since explicit diets have not been estimated at this point, it is not possible to delineate a particular mechanism in this case. However, the influence of body size on FA signatures for harps and hoods suggests an underlying energetic basis to intra-specific diet variation.

Temporal and spatial differences

I noted significant variation in diets for both harps and hoods at two temporal scales;

season and year. Seasonal differences in diets have been noted for other pinniped species

are have been linked to seasonal changes in prey availability (e.g. Brown and Pierce

1998; Hall *et al.* 1998; Wathne *et al.* 2000). Without specific information on distribution

and abundance of prey, it is unclear if overall seasonal differences in FA profiles are

related to prey availability, or to specific prey selection. Adult harps seals have been

noted to display preference for particular prey of higher energy density despite their local

abundance (Lawson *et al.* 1998). However, the significant seasonal effect for immature

animals noted here would indicate that animals are responding to seasonal changes in the

availability of prey either due to changes in prey or seal distributions, or both. I did note

significant spatial differences in FA signatures for both species. This has also been found

in stomach content analysis (e.g. Lawson *et al.* 1995; Lawson and Stenson 1995; Lawson

and Stenson 1997; Lawson *et al.* 1998). Though there are some misclassifications in

DFA, the spatial effect suggests that both harp and hoods spend most of their time

feeding in one region. If animals were moving about from one area to another, the range

in variation would be less pronounced.

For harp seals there were pronounced annual differences in FA signatures between the

mid 1990' and the late 1990's-2000's. Because of small sample sizes in most years I was

not able to make the same assessment for hooded seals. However, analysis of

amalgamated year groups suggests overall large-scale temporal variation in diets. During

the last decade, The Northwest Atlantic has undergone large ecological change. The once

abundant Atlantic cod stocks off Newfoundland were decimated by the early 1990's due to over fishing (Rose 2004). As well, capelin, a former principle prey of seals, cod, whales and seabirds, has declined in northern areas since the 1990's (Carscadden *et al.* 2001; Rose 2004). Concurrently, Arctic cod distribution shifted southward from Labrador to coastal Newfoundland and the Grand Banks out to the shelf edge.

While it is not possible to attribute the influence of a particular prey type to changes in FA profiles, the trends in our data are coincident with large fluctuations in prey availability over the last decade. In harp seals, I found a significant interaction between sex and year suggesting that the sexes responded in a different manner to large-scale environmental variability. This is in contrast to results for grey seals over this same time period (Beck *et al.* 2005). However, the shift in primary forage prey in Newfoundland waters were generally from capelin to Arctic cod, while the Scotian Shelf saw an increase in capelin abundance. Capelin is considered an important resource because of its high energy content relative to other forage fish (Carscadden *et al.* 2001; Rose and O'Driscoll 2002). It is hypothesized that the loss of capelin as a primary prey item has had an effect on overall condition and reproductive potential of female harp seals (Hammill *et al.* 1995; Sjare *et al.* 2004) cod (Rose and O'Driscoll 2002) and seabirds (Carscadden *et al.* 2001; Davoren and Montevecchi 2003). Sex-specific reproductive costs and/or intra-specific competition may have mandated a compensatory response by female harp seals with respect to diet selection.

Species differences

The divergence among demographic groups lends support to the idea of intra-specific dietary segregation in both harp and hooded seals. However, I also found a large inter-specific effect on fatty acid signatures suggesting dietary segregation between these two predators. There was no overlap in fatty acid signatures for any age-class or body size of harp and hooded seals. Harps and hoods are known to organize diving behaviour very differently. Even in areas where they overlap, hooded seals routinely exceed mean dive depths of harps (Stenson, unpublished data). It has also been observed that within weeks of being weaned, young of the year hoods begin routinely diving to depths of 250m (Stenson, unpublished data). Thus inter-specific differences in foraging and diving behaviour are manifested almost immediately and maintained over the course of adult life. While differences in fatty acid signatures can arise from variation in the proportion consumed of specific prey, differences in diving behaviour between the species, would suggest this segregation in diet is a manifestation of spatial segregation within the water column and may act to reduce inter-specific competition. Similar results in spatial segregation and inferred dietary segregation have been found for other pinnipeds (Le Boeuf *et al.* 1993, 2000; Field *et al.* 2005; Breed *et al.* 2006), and seabirds (Weimerskirch *et al.* 1997; González-Solis *et al.* 2000).

Few studies have comparatively documented ontogenetic diet differences for sympatric marine predators. Interestingly, our results contrast with those of terrestrial carnivore counterparts as it is commonly found that predator size, irrespective of species, determines dietary overlap (Carbone *et al.* 1999). In studies of sympatric terrestrial

predator guilds, the dietary niche of smaller carnivores is often nested within that of

larger carnivores (Sinclair *et al.* 2003; Radloff and du Toit 2004). This is not due to a

function of increasing number of prey species but rather an increasing range of prey sizes

for a given set of prey species. However, it is not possible for terrestrial carnivores to

spatially segregate foraging within a third dimension thereby shifting the type of prey

encountered altogether.

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TABLES

Table 5.1: Mean body mass (± SE) in each season for different age-classes of harps and hoods. Numbers in parenthesis represent sample sizes.

Species	Age-class	Mass (Kg)				
		Pre-breeding			Post-breeding	
		Inshore	Offshore		Inshore	Offshore
Harp	Juvenile	43.5 ± 1.4 *(138)*	40.1 ± 2.3 *(41)*		42.5 ± 3.7 *(17)*	33.1 ± 1.2 *(36)*
	Adult female	113.3 ± 2.9 *(90)*	104.1 ± 5.3 *(25)*		87.3 ± 6.3 *(18)*	69.2 ± 3.2 *(25)*
	Adult male	101.1 ± 4.6 *(36)*	105.1 ± 3.5 *(90)*		93.0 ± 7.7 *(19)*	76.4 ± 4.6 *(11)*

		Pre-breeding		Post-breeding		
		NENFLD	LAB	NENFLD	LAB	GRNLD
Hooded	Juvenile	-	43.9 ± 1.7 *(9)*	37.9 ± 2.8 *(24)*	42.5 ± 8.5 *(2)*	-
	Adult female	205.5 ± 16.8 *(8)*	148.5 ± 7.6 *(28)*	-	182.6 ± 9.4 *(10)*	108.3 ± 6.5 *(10)*
	Adult male	206.9 ± 11.5 *(24)*	199.7 ± 11.1 *(18)*	-	184.9 ± 17.6 *(13)*	152.1 ± 15.7 *(7)*

Table 5.2: Mean FA (%) signatures (± SE) for age-classes of Harps and Hoods.

	Harp Seals			Hooded Seals		
	Juvenile	Adult		Juvenile	Adult	
		Female	Male		Female	Male
	(n=232)	(n=189)	(n=105)	(n=38)	(n=55)	(n=60)
Unsaturated FAs						
14:0	5.67 ± 0.06	5.32 ± 0.06	5.37 ± 0.08	5.39 ± 0.1	4.7 ± 0.1	4.58 ± 0.11
16:0	8.9 ± 0.11	8.37 ± 0.13	8.12 ± 0.18	10.6 ± 0.26	8.97 ± 0.22	8.7 ± 0.21
17:0	0.16 ± 0.004	0.14 ± 0.01	0.11 ± 0.01	0.19 ± 0.01	0.17 ± 0.01	0.15 ± 0.01
18:0	1.34 ± 0.02	1.27 ± 0.03	1.21 ± 0.03	1.72 ± 0.06	1.62 ± 0.05	1.72 ± 0.05
Monounsaturated FAs						
16:1n-7	12.44 ± 0.2	13.7 ± 0.23	13.67 ± 0.25	12.29 ± 0.35	10.73 ± 0.24	11.94 ± 0.25
18:1n-9	14.09 ± 0.19	12.8 ± 0.22	11.41 ± 0.34	19.08 ± 0.66	20.97 ± 0.56	20.02 ± 0.49
18:1n-7	3.51 ± 0.06	3.89 ± 0.08	3.55 ± 0.09	3.68 ± 0.11	4.15 ± 0.08	4.48 ± 0.08
18:1n-5	0.56 ± 0.01	0.55 ± 0.01	0.55 ± 0.01	0.48 ± 0.01	0.46 ± 0.01	0.52 ± 0.01
20:1n-11	1.92 ± 0.04	1.85 ± 0.05	2.08 ± 0.1	2.02 ± 0.08	2.48 ± 0.08	2.34 ± 0.08
20:1n-9	11.31 ± 0.21	12.92 ± 0.28	15.02 ± 0.41	10.82 ± 0.3	13.7 ± 0.38	14.05 ± 0.28
20:1n-7	0.63 ± 0.02	0.83 ± 0.02	1.09 ± 0.07	0.53 ± 0.03	0.71 ± 0.04	0.93 ± 0.03
22:1n-11	5.91 ± 0.18	6.69 ± 0.22	8.85 ± 0.33	5.67 ± 0.38	7.03 ± 0.34	6.78 ± 0.24
22:1n-9	0.83 ± 0.02	1.11 ± 0.03	1.5 ± 0.07	0.82 ± 0.05	1.25 ± 0.06	1.28 ± 0.04
22:1n-7	0.11 ± 0.005	0.15 ± 0.01	0.22 ± 0.01	0.1 ± 0.01	0.14 ± 0.01	0.15 ± 0.01
21:5n-3	0.47 ± 0.004	0.46 ± 0.005	0.42 ± 0.01	0.05 ± 0.002	0.04 ± 0.001	0.044 ± 0.001
Polyunsaturated FAs						
16:2n-6	0.08 ± 0.01	0.07 ± 0.002	0.081 ± 0.01	0.22 ± 0.01	0.19 ± 0.004	0.23 ± 0.01
16:2n-4	0.26 ± 0.01	0.24 ± 0.01	0.17 ± 0.01	0.37 ± 0.02	0.35 ± 0.01	0.35 ± 0.01
16:3n-6	0.5 ± 0.01	0.54 ± 0.01	0.64 ± 0.02	0.18 ± 0.01	0.17 ± 0.01	0.19 ± 0.01
16:3n-4	0.28 ± 0.01	0.33 ± 0.01	0.37 ± 0.01	0.32 ± 0.03	0.28 ± 0.02	0.26 ± 0.02
16:4n-1	0.48 ± 0.01	0.59 ± 0.02	0.64 ± 0.03	1.5 ± 0.03	1.51 ± 0.03	1.46 ± 0.03
18:2n-6	1.49 ± 0.02	1.4 ± 0.03	1.2 ± 0.03	0.09 ± 0.004	0.09 ± 0.003	0.11 ± 0.002
18:2n-4	0.11 ± 0.002	0.11 ± 0.002	0.11 ± 0.002	0.12 ± 0.003	0.11 ± 0.003	0.12 ± 0.003
18:3n-6	0.12 ± 0.002	0.13 ± 0.002	0.12 ± 0.003	0.11 ± 0.003	0.12 ± 0.003	0.11 ± 0.003
18:3n-4	0.13 ± 0.002	0.11 ± 0.002	0.12 ± 0.003	0.62 ± 0.02	0.5 ± 0.02	0.42 ± 0.02

	Harp Seals			Hooded Seals		
	Juvenile	Adult		Juvenile	Adult	
		Female	Male		Female	Male
	(n=232)	(n=189)	(n=105)	(n=38)	(n=55)	(n=60)
18:3n-3	0.69 ± 0.02	0.5 ± 0.01	0.45 ± 0.02	0.07 ± 0.004	0.07 ± 0.002	0.08 ± 0.004
18:3n-1	0.1 ± 0.01	0.07 ± 0.003	0.07 ± 0.003	1.47 ± 0.06	1.11 ± 0.05	0.98 ± 0.04
18:4n-3	1.82 ± 0.04	1.54 ± 0.04	1.39 ± 0.06	0.15 ± 0.007	0.13 ± 0.001	0.13 ± 0.01
18:4n-1	0.17 ± 0.004	0.18 ± 0.01	0.21 ± 0.01	0.29 ± 0.01	0.29 ± 0.01	0.32 ± 0.01
20:2n-6	0.25 ± 0.004	0.23 ± 0.003	0.21 ± 0.01	0.11 ± 0.01	0.11 ± 0.004	0.1 ± 0.004
20:3n-6	0.07 ± 0.001	0.07 ± 0.001	0.07 ± 0.002	0.37 ± 0.01	0.34 ± 0.01	0.37 ± 0.01
20:4n-6	0.33 ± 0.01	0.33 ± 0.01	0.29 ± 0.01	0.12 ± 0.01	0.1 ± 0.003	0.1 ± 0.003
20:3n-3	0.09 ± 0.003	0.06 ± 0.002	0.07 ± 0.01	0.78 ± 0.03	0.69 ± 0.021	0.61 ± 0.02
20:4n-3	0.68 ± 0.02	0.5 ± 0.01	0.48 ± 0.02	6.2 ± 0.17	4.69 ± 0.18	4.73 ± 0.14
20:5n-3	6.98 ± 0.11	7.28 ± 0.15	6.73 ± 0.16	0.42 ± 0.01	0.39 ± 0.01	0.36 ± 0.01
22:4n-6	0.07 ± 0.002	0.08 ± 0.003	0.06 ± 0.004	0.04 ± 0.002	0.05 ± 0.003	0.07 ± 0.004
22:5n-6	0.12 ± 0.003	0.1 ± 0.002	0.08 ± 0.003	0.11 ± 0.004	0.1 ± 0.01	0.1 ± 0.01
22:4n-3	0.12 ± 0.002	0.1 ± 0.002	0.09 ± 0.003	0.1 ± 0.002	0.11 ± 0.002	0.1 ± 0.003
22:5n-3	5.17 ± 0.06	5.23 ± 0.07	4.55 ± 0.11	2.5 ± 0.06	2.57 ± 0.06	2.63 ± 0.07
22:6n-3	12.05 ± 0.16	10.16 ± 0.18	8.66 ± 0.25	10.29 ± 0.24	8.82 ± 0.21	8.41 ± 0.22
Percentage of total FAs						
Saturated	16.07 ± 0.19	15.1 ± 0.22	14.8 ± 0.29	17.91 ± 0.42	15.45 ± 0.37	15.15 ± 0.37
Monounsaturated	51.31 ± 0.92	54.5 ± 1.13	57.95 ± 1.68	55.5 ± 1.97	61.61 ± 1.78	62.49 ± 1.5
Polyunsaturated	32.63 ± 0.51	30.4 ± 0.57	27.25 ± 0.77	26.59 ± 0.76	22.94 ± 0.67	22.36 ± 0.63

FIGURES
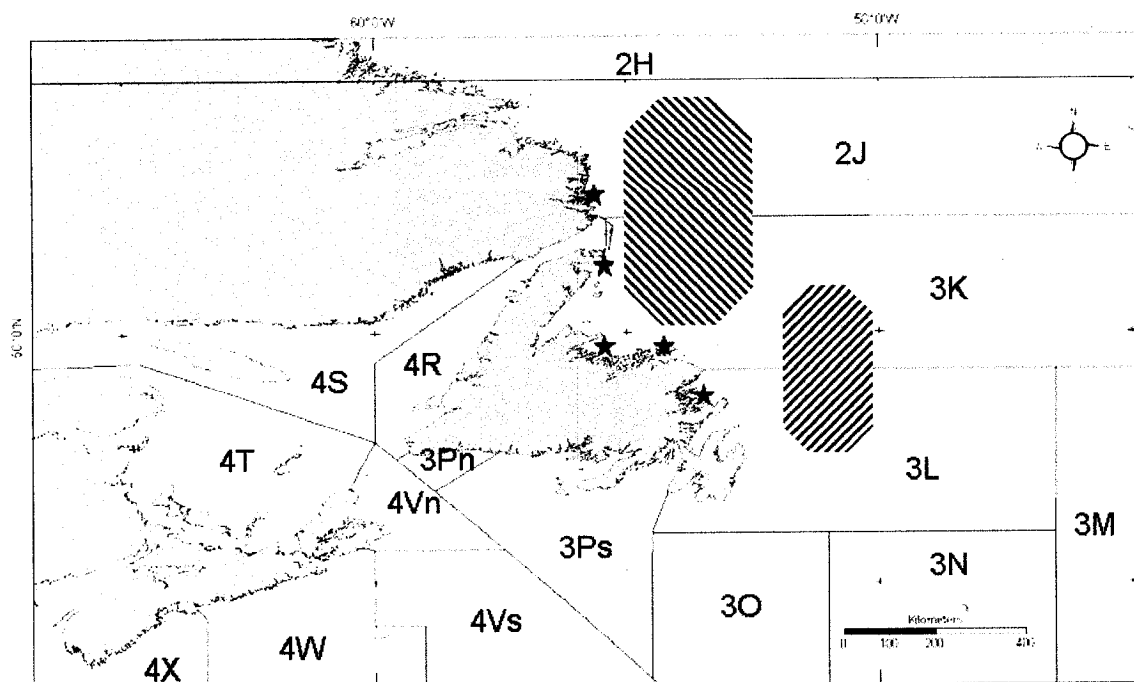
Figure 5.1: Map of NAFO subdivisions and sampling locations for harp and hooded seals (1994-2005). Stars denote nearshore areas and hatched marked rectangles denote offshore areas.
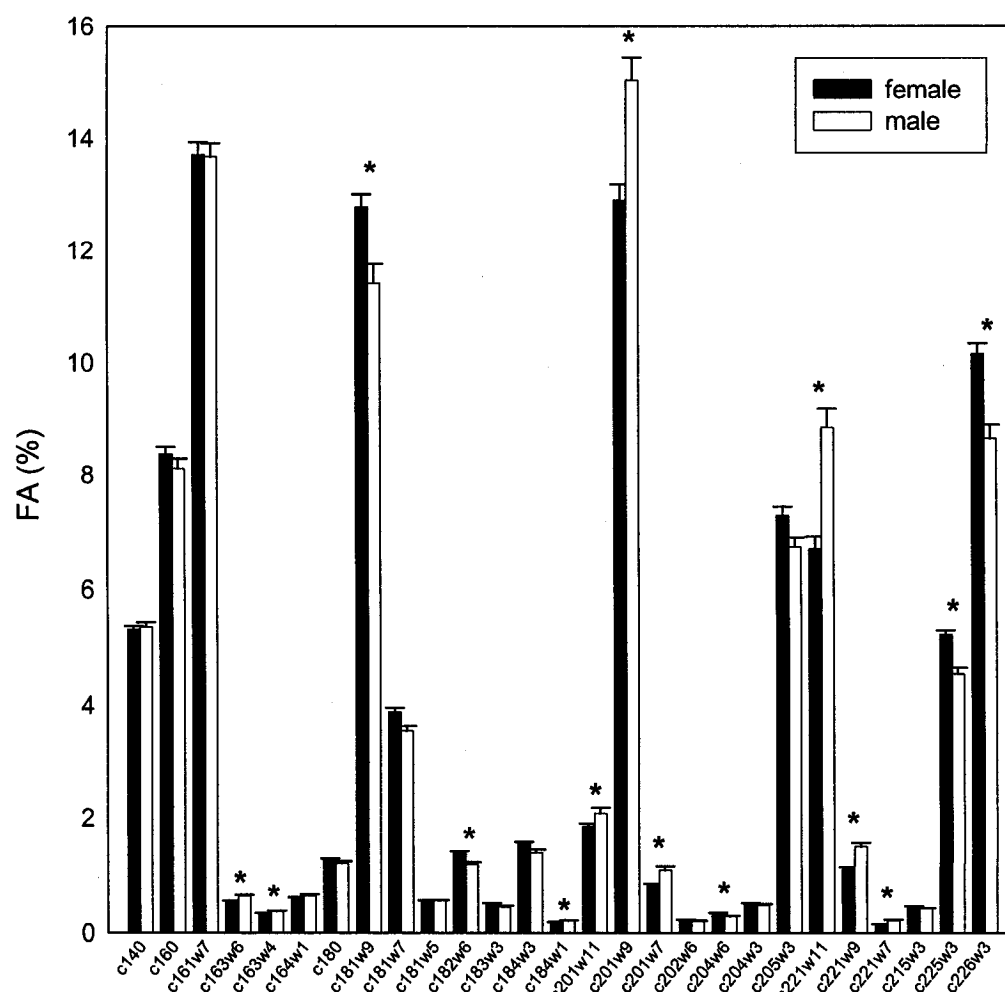
Figure 5.2: Sex differences in selected, abundant fatty acids of adult harps (error bars=1SE). * indicates significantly different at <0.05 significance.
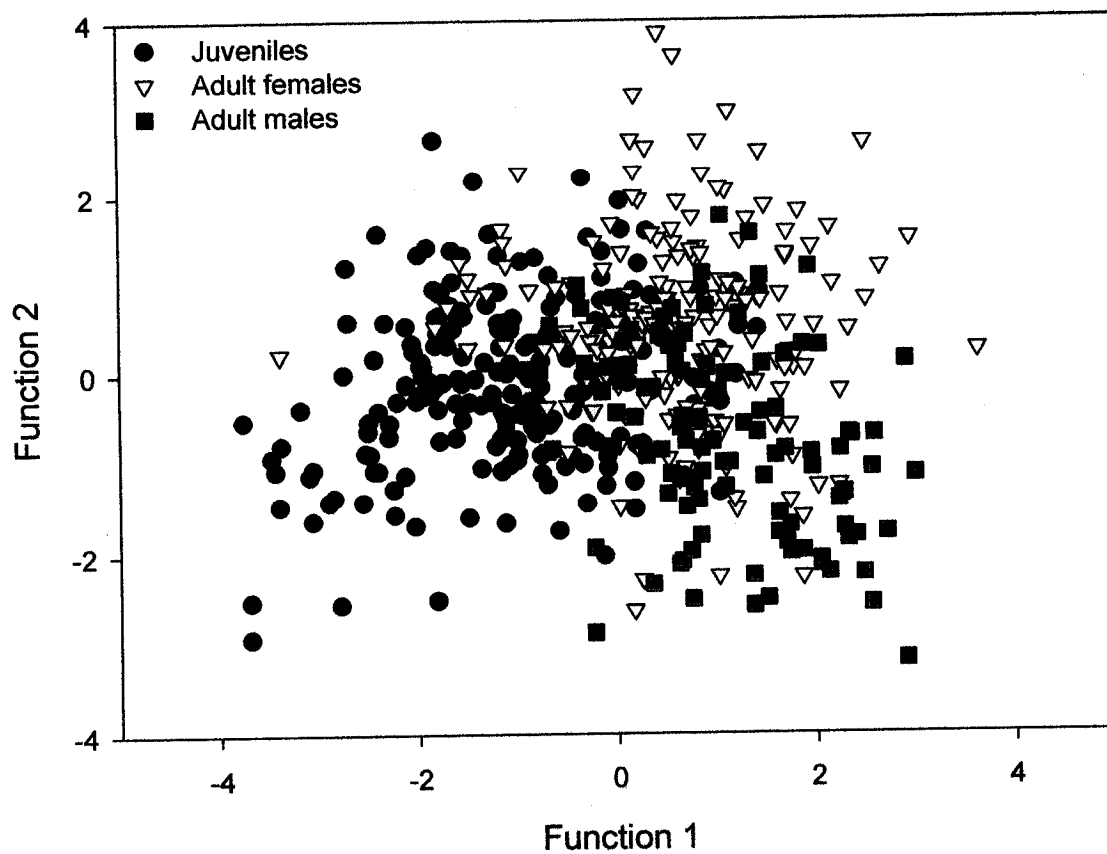
Figure 5.3: First two discriminant functions derived from fatty acid signatures for different age classes of harp seals.
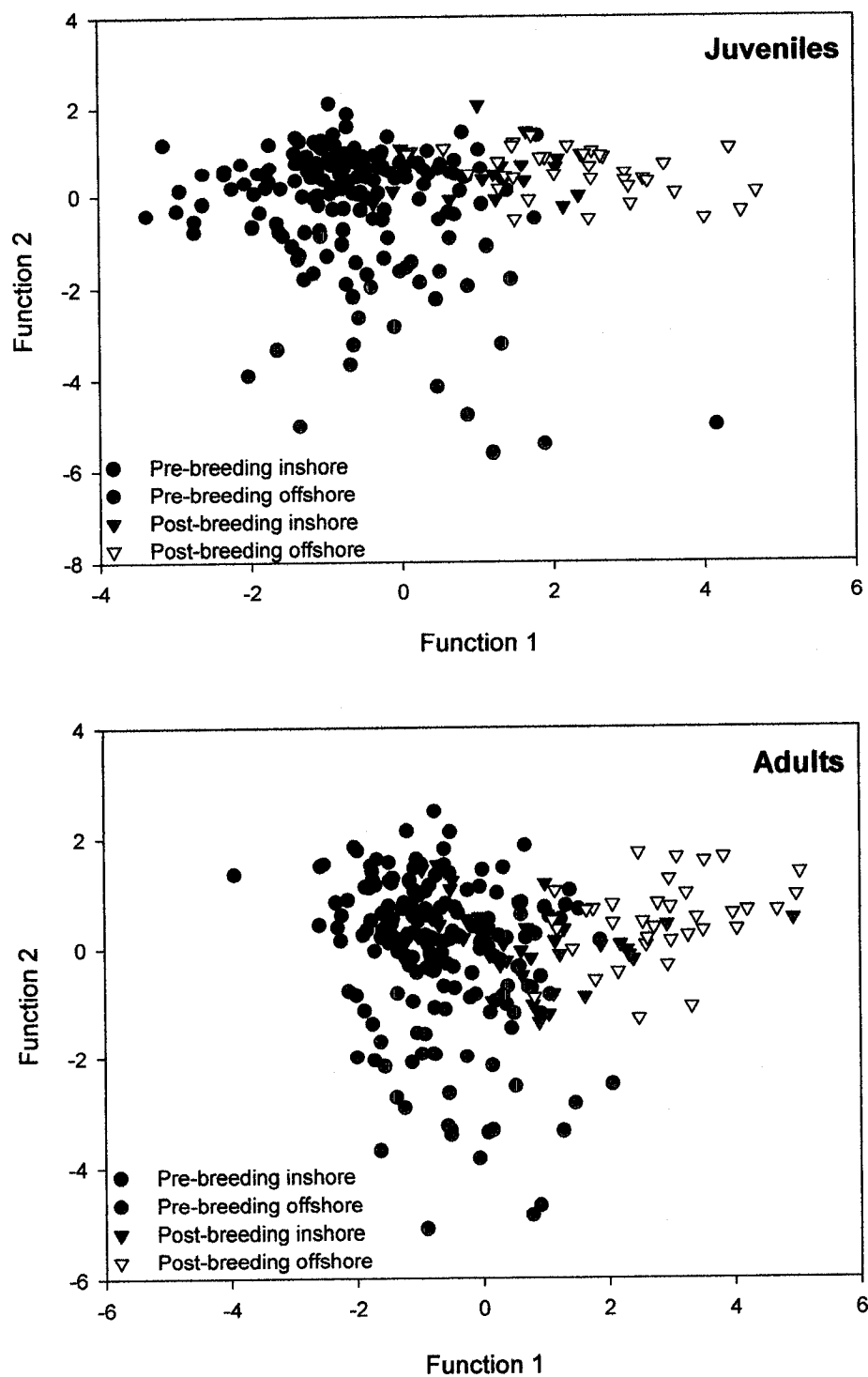
Figure 5.4: First two discriminant functions for juvenile and adult harps sampled in different seasons and areas.
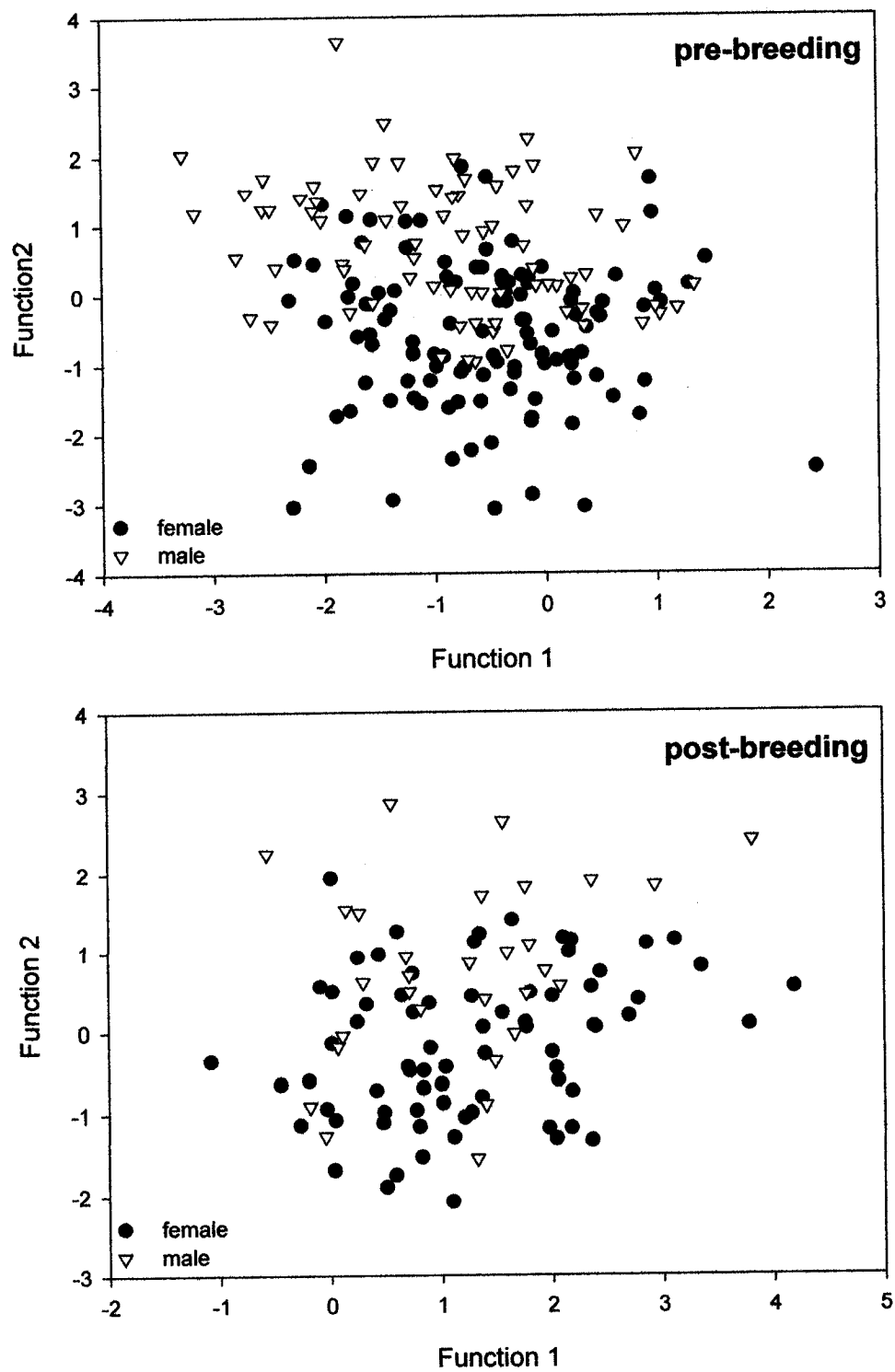
Figure 5.5: First two discriminant functions for adult male and female harps in pre- and post-breeding seasons.
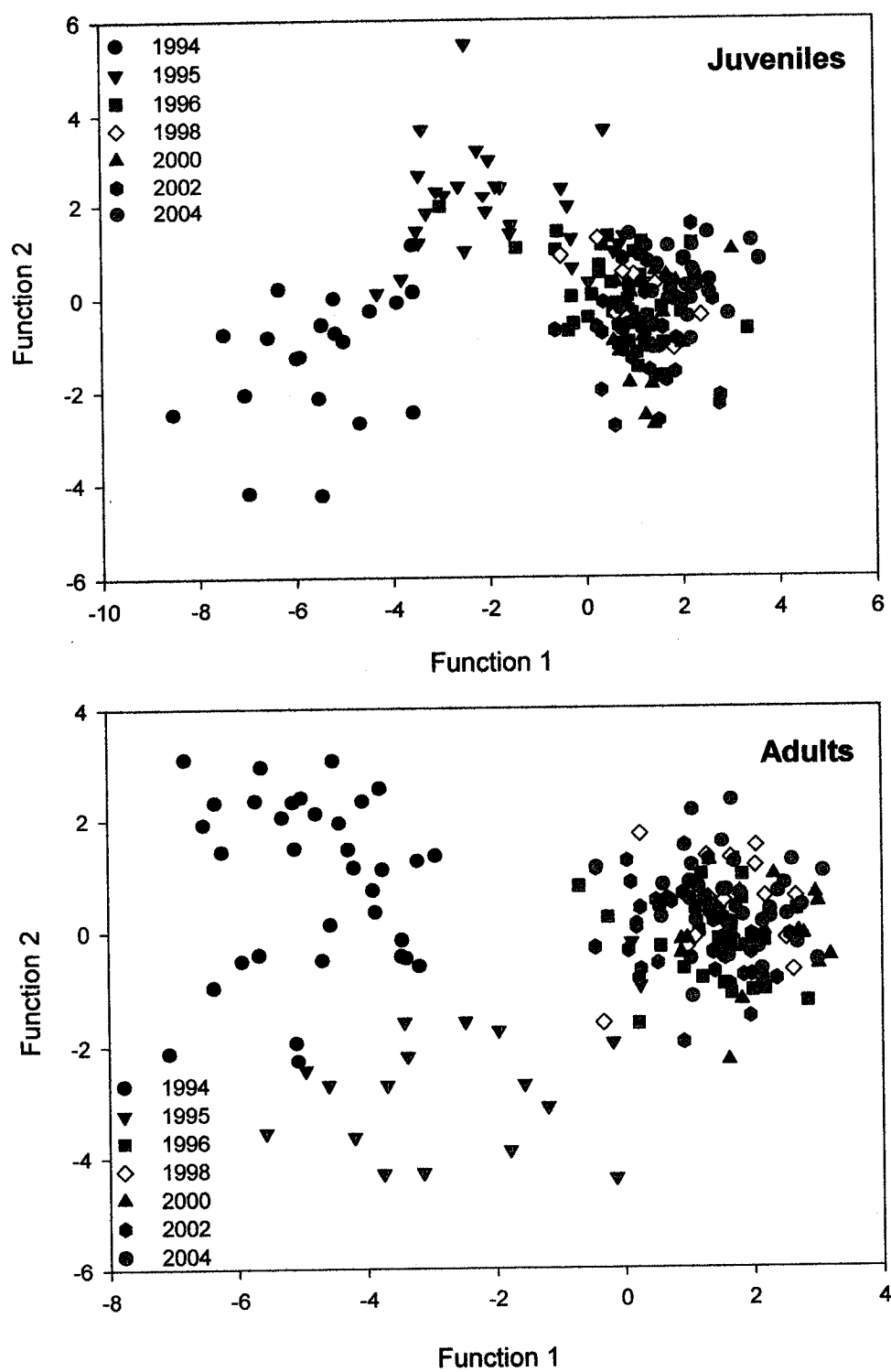
Figure 5.6: Discriminant plot of adult and juvenile harps sampled in different years from the winter sampling period.
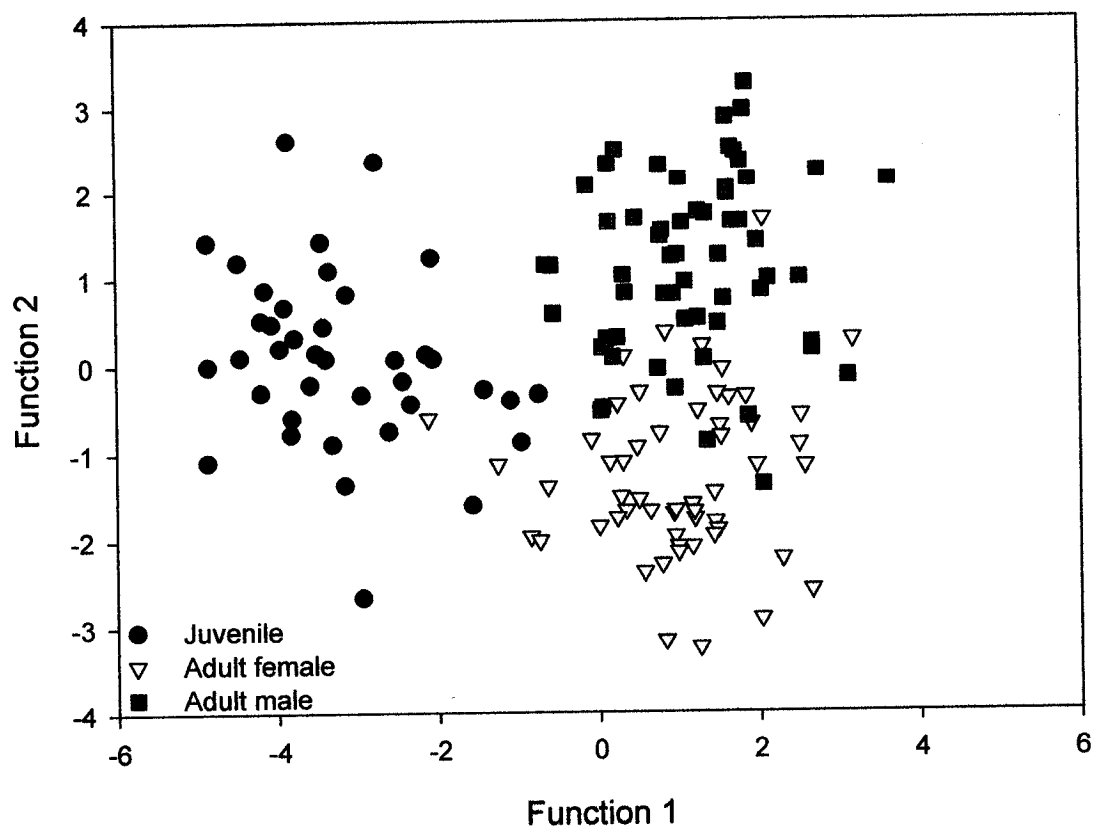
Figure 5.7: First two discriminant functions for juvenile and adult male and female hooded seals.
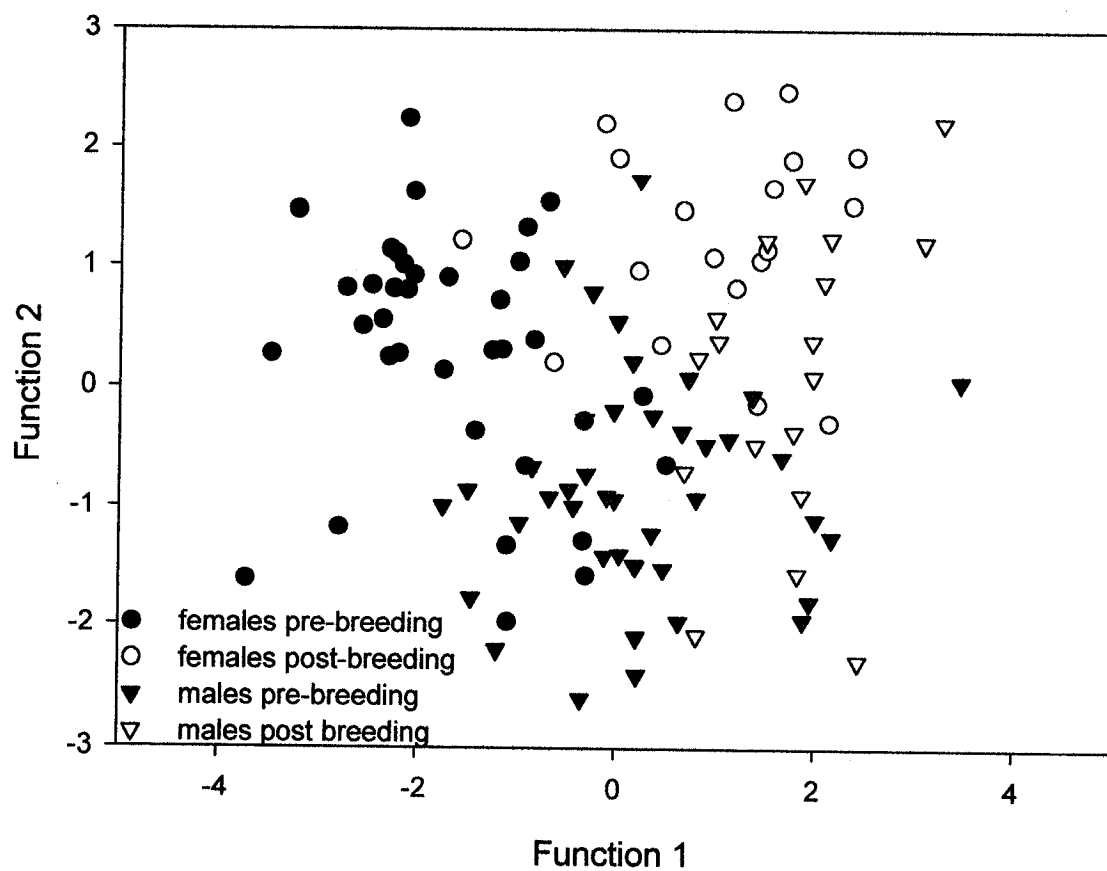
Figure 5.8: First two discriminant functions for adult male and female hoods in the pre- and post-breeding periods.
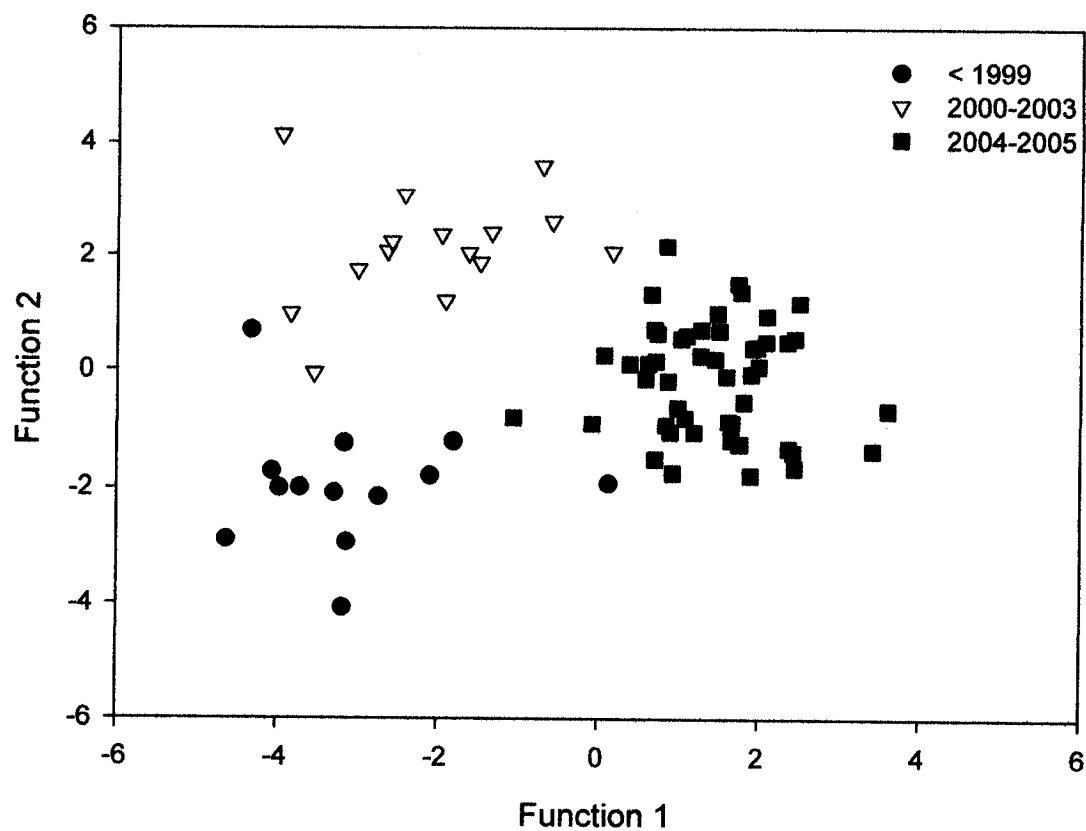
Figure 5.9: First two discriminant functions for adult hoods in different year groups sampled in the pre-breeding period.
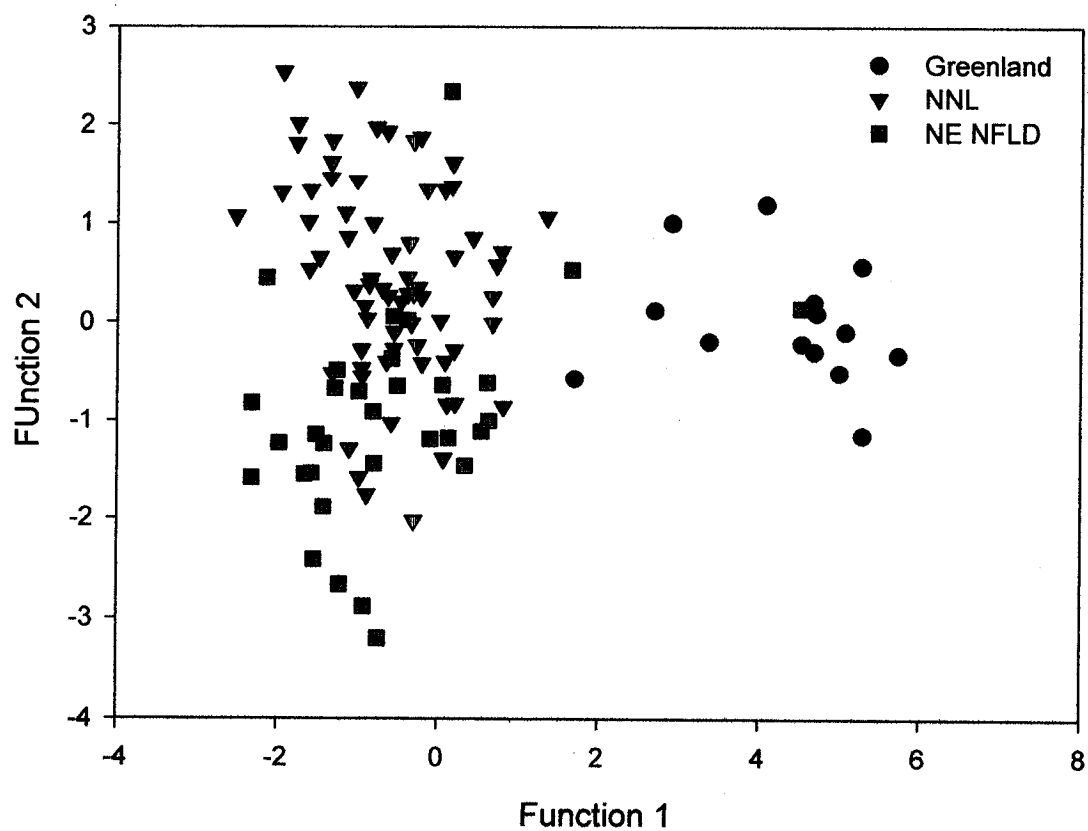
Figure 5.10: First two discriminant functions for adult hoods sampled in different areas (NNL=Northern Newfoundland and Labrador; NE NFLND = Northeastern Newfoundland).
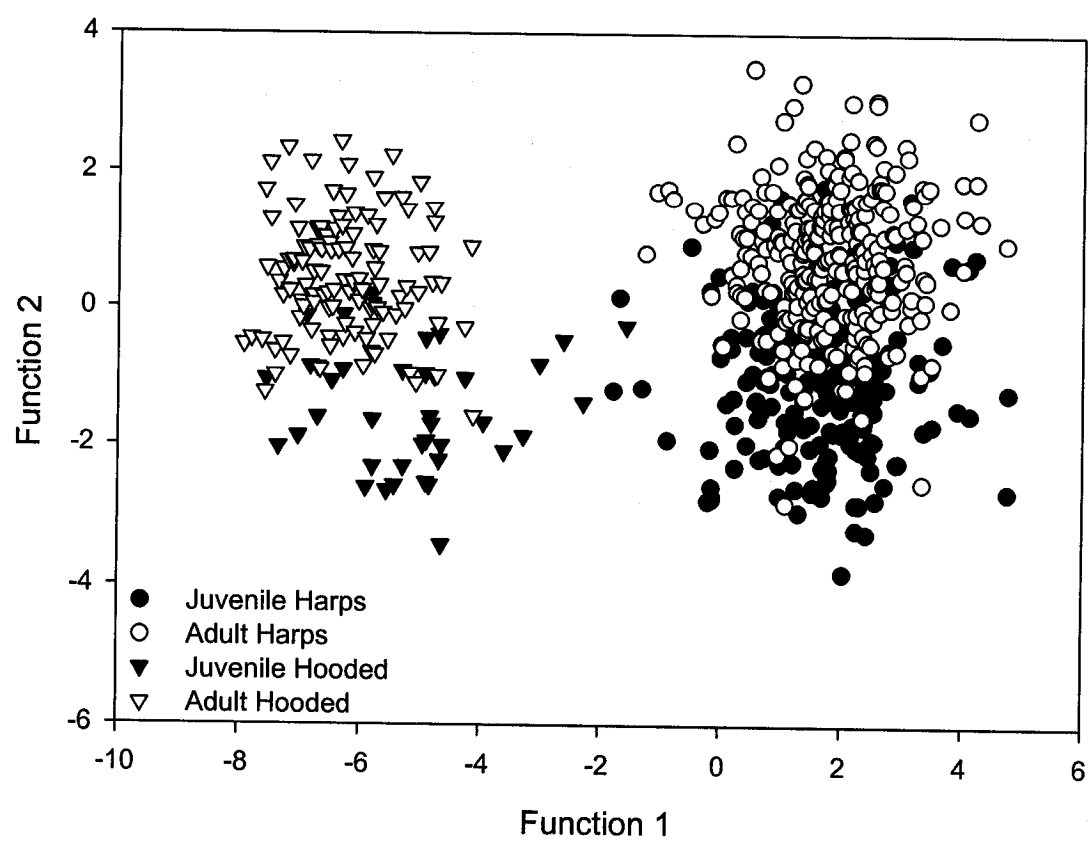
Figure 5.11: First two discriminant functions for juvenile and adult harp and hooded seals.

CHAPTER VI: SOURCES OF VARIATION IN DIETS OF HARP AND HOODED SEALS ESTIMATED FROM QUANTITATIVE FATTY ACID SIGNATURE ANALYSIS (QFASA)

INTRODUCTION

Harp (*Phoca groenlandica*) and hooded (*Cystophora cristata*) seals are numerous, wide-ranging piscivores in the North Atlantic Ocean (Stenson *et al.* 1997, 2002, 2003). As such they have been implicated in the decline of commercial fish stocks or in their failure to recover (see Sinclair and Murawski 1997). Estimating impact on fish stocks requires integrating predation pressure spatially and temporally (e.g. Hammill and Stenson 2000). Such models require information on predator consumption rates, abundance, spatial and temporal distribution, population structure, and, obviously, diet composition. However, not only do we lack this information across the entire range of these species, our understanding of factors influencing prey selection in these carnivores is deficient. Indeed, comparative analysis of diet segregation between sympatric species is rare. This is due to the difficulty of studying marine mammals at sea (Bowen *et al.* 2002). However, different age and sex classes of seals can vary in their spatial and temporal patterns of feeding (Hindell *et al.*1991; McConnell and Fedak 1996; Hindell *et al.* 1999; Field *et al.* 2001; Bradshaw *et al.* 2002; van den Hoff *et al.* 2002; Beck *et al.* 2003; Austin *et al.* 2004; Breed *et al.* 2006; Chapter V). Moreover, through the application of novel biochemical tracer techniques such as fatty acids (FA) and stable isotopes, there is emerging evidence for large intra-specific variation in diet amongst pinniped species related to ontogeny, sex, and body size (e.g. Lesage *et al.* 2001; Iverson *et al.* 1997; Thiemann *et al.* 2006; Beck *et al.* 2005, 2007; Tucker *et al.* 2007).

Inter-specific competition for prey has traditionally been viewed as fundamental to the structure of ecological communities and species niche breadth (Pianka 1981; Polis 1984). Within species, diets often diverge as a function of body size, age, sex, condition and reproductive status (e.g. Clarke *et al.* 1998). Various explanations have been proposed to account for diet divergences such as energetic requirements, sex-specific costs of reproduction, ontogenetic niche shift, resource polymorphism or minimizing inter-specific competition (reviewed in Bolnick *et al.* 2003). For example, differential resource use by the sexes, observed in both size dimorphic (e.g. Clarke *et al.* 1998) and monomorphic (e.g. Lewis *et al.* 2002) species has been linked to sex-specific reproductive costs. In addition, competition between the sexes may be minimized by the selection of different prey or by spatial/temporal segregation in feeding between males and females (e.g. Breed *et al.* 2006; Beck *et al.* 2007).

Apart from temporal or spatial segregation in resource use, these hypotheses do not make specific predictions about diet selection or the subsequent properties associated with that diet (i.e., the quality and costs related to capture, consumption and digestion). Beyond their perceived importance with respect to impact on commercial fish stocks, in a comparative manner, harp and hooded seals represent good model organisms to explore hypotheses about intrinsic and extrinsic factors influencing overall breadth and quality of the diet in marine carnivores. First, harp and hooded seals display distinct differences in life history, foraging behaviour and body size. Second, the North Atlantic ecosystems have undergone profound changes in species' abundance and distribution due to over fishing and environmental variability, such as trends in ocean temperature (Frank *et al.*

1994; Carscadden *et al.* 2001; Drinkwater 2002; Rice 2002; Rose 2004). This contrast in the extrinsic environment allows us to evaluate interactions with intrinsic factors influencing diet.

Harp seals are only slightly size-dimorphic with an average adult mass of 130kg and males being 10% larger than females (Hammill *et al.* 1995). Hooded seals are more size-dimorphic, with adult males being approximately 1.5 times larger than females and 2.3 times larger than adult harps. Although they are both wide ranging and exhibit long-distance seasonal migrations, harp seals mainly inhabit the continental shelf (Stenson and Sjare 1997; Folkow *et al.* 2004), while hooded seals are more strongly associated with the continental shelf edge and deep ocean (Folkow and Blix 1999). Harps and hooded seals also differ in their diving behaviour. Most harp seal dives are <50m, although there are a number of dives to depths up to 200m (Stenson and Sjare 1997; Folkow *et al.* 2004). By contrast, hooded seals regularly dive deeper with a large portion of the dives to depths >100m and often exceeding 1000m (Folkow and Blix 1999). Data from stomach content analysis suggest that harp seals consume a mixed diet of pelagic forage fish and invertebrates such as capelin (*Mallotus villosus*), arctic cod (*Boregadus saida*), herring (*Clupea harengus*), euphausiids, and amphipods (Lawson *et al.* 1995; Lawson and Stenson 1995, 1997). Data on hooded seals are relatively scarce, but they are presumed to mostly feed on a mix of pelagic and dermersal fish such as halibut (*Hippoglossus hippoglossus*), redfish (*Sebastes sp.*) and squid with smaller quantities of herring, capelin, Atlantic cod (*Gadus morhua*) and Arctic cod (*Boregadus saida*) (Ross 1993; Kapel 1995; Hammill and Stenson 2000; Potelov *et al.* 2000; Haug *et al.* 2006).

FA signature (FAS) analysis can provide both a qualitative assessment of temporal or spatial changes in diet (e.g. Iverson *et al.* 1997a, 1997b; Smith *et al.* 1997) and a quantitative estimate of the species composition of the diet (Iverson *et al.* 2004, Bowen *et al.* 2006; Beck *et al.* 2007). This is due to the fact that FA are deposited in animal tissue in a predictable manner and there are limits on polyunsaturated FA biosynthesis in higher order consumers (Iverson 1993). Proportional estimates of diet composition can be made at the level of the individual using quantitative fatty acid signature analysis (QFASA), which statistically matches a consumer's FA signature to an inclusive prey database, after accounting for predator metabolism effects in a mixing model (Iverson *et al.* 2004). Previously, I defined both intra- and inter-specific differences in diets for harp and hooded seals based on a qualitative assessment of FA profiles which coincided with general expectations based on stomach content analysis (Chapter V). Differences in FA profiles between groups of individuals can arise from differences in the proportion of the same prey species being consumed or from a different mixture of prey species altogether (Iverson *et al.* 2004; Budge *et al.* 2006). It is not possible to distinguish between these two possibilities by simply examining the fatty acid signatures of consumers alone because it is not possible to attribute the proportion consumed of a specific prey based on the level of individual FA's (Iverson *et al.* 2004). To do so, predator signatures must be considered relative to a whole suite of potential prey and as in other modeling exercise, entails a number of assumptions. However, different fatty acid profiles do indeed imply differences in diets (Iverson *et al.* 2004; Budge *et al.* 2006). Therefore, the objective of this study was to define specific sources of variation in diets of harp and hooded seals belonging to different demographic groups across various temporal and spatial scales, by

estimating diets of individuals using QFASA. Subsequently, I evaluated the quality of

diets with respect to overall energy density and niche breadth.

METHODS

Sampling of Seals

Seals (harp n=502; hooded n=124; Table 5.2, Chapter V) were sampled along the

Northeast coast of Newfoundland and Southern Labrador between November and May

from 1994-2004 by experienced seal hunters and scientific personnel from the

Department of Fisheries and Oceans (Sjare *et al.* 2004). Samples were similarly obtained

during offshore cruises in the winters of 1994, 2002 and 2004. Seals were weighed to the

nearest 0.5 kg and a blubber sample (approximately 0.5 kg) was taken from the posterior

flank, placed in whirlpak® and frozen. Seal ages were determined to the nearest year by

sectioning a lower canine tooth and then counting dentine annuli (Bowen *et al.* 1983;

Lawson *et al.* 1992). In addition to the samples taken from seals postmortem, biopsy

samples were taken from both live-captured harp (n =24) and hooded (n =12) seals

during an offshore cruise to the whelping patch in March 2004. Adults were captured

using a hand held net. Hooded seal biopsy samples also were taken during a cruise to the

moulting patch off Eastern Greenland during the spring of 2005 (n =17). In the

laboratory, a 0.5 g core of blubber representing the entire depth of each field-collected

sample (i.e., from skin to underlying muscle) was taken. Lipids were quantitatively

extracted from all blubber samples using a modified Folch method (Iverson 2002).

Harp seals were grouped into two age classes; juveniles (1-4 years) and adults (4+ years) (Sjare *et al.* 2004) and two seasons – pre- and post-breeding (where March is the breeding period). No harp seals were sampled during summer months. Given that FA represent an integration of the diet over periods of weeks to months (Iverson *et al.* 2004), I assumed that our samples represent the assimilated diet from previous months. Seals were also classified into two geographical areas based on sampling location: inshore (defined as < 30 km from shore; Lawson *et al.* 1995), and offshore, including the Labrador Banks and Grand Banks. Hooded seals were similarly classified as juveniles (<5 years) and adults (>5 years) and grouped into two seasons; pre- and post-breeding (breeding also occurs in mid March). Hooded seal samples were also assigned to one of three geographic groups: Greenland, Northeastern Newfoundland (NE NFLD), and Northern Newfoundland and Labrador (NNL). These groups contained approximately equal numbers of males and females.

Sampling of Prey

Fishes and invertebrates were collected and frozen during stratified, random, bottom-trawl surveys conducted in the summer in the Northwest Atlantic (Northwest Atlantic Fisheries Organization sub areas 2J, 3K, 3L, 4T, and 4V) between 1993 and 2002 (see Budge *et al.* 2002). In addition, I obtained supplementary samples from deep water trawl surveys of the Davis Strait (NAFO sub areas 0A and 1A) in the fall of 2004. Specimens were thawed and fork length or carapace width was measured to the nearest 0.1 cm and body mass to the nearest 0.1 g. Each individual was then homogenized and lipids were

quantitatively recovered in duplicate from a sub-sample of homogenate (approximately

1.5 g) as above.

Fatty Acid Analysis

FA methyl esters (FAME) were prepared using an acidic catalyst (the Hilditch method;

see Iverson 1993; Budge *et al.* 2006). Duplicate analyses and identification of FAME

were performed using temperature-programmed gas–liquid chromatography (GLC)

(Iverson *et al.* 1997, 2004; Budge *et al.* 2006). FA were described by the standard

nomenclature of carbon chain length: number of double bonds and location (n-x) of the

double bond nearest the terminal methyl group. Individual FA were expressed as a mass

percent of total fatty acids. Although 67 FA are routinely identified, I used 39 FA of

dietary or primarily dietary origin in our analysis (Iverson *et al.* 2004; Beck *et al.* 2005;

Budge *et al.* 2006), which accounted for approximately 93% of total FA by mass.

Prey Library

I used a prey base comprised of 2039 individuals representing 24 species to estimate the

diets of harp seals; 2289 individuals representing 29 species were used to estimate the

diets of hooded seals. Among these species were those known to be consumed based on

stomach content analysis, or which were fairly abundant and found at depths that harp or

hooded seals are known to forage. Naturally, diets and therefore FA signatures (FAS) of

fish vary with ontogeny (Budge *et al.* 2002). Therefore, sample size permitting, I split

species into small and large size classes and evaluated differences in FAS by MANOVA.

Size class splits were based on either median length or a length reported in the literature

at which significant changes in diet have been noted. Size splits for species were retained in subsequent modeling procedures if there were significant differences in FAS and were differentiated well in simulations (see Appendix 1). Diet simulations and prey on prey modeling (Iverson *et al.* 2004) were conducted on each prey library to evaluate the robustness of QFASA to differentiate individual prey species or size categories (see Appendix 1 for details). I also evaluated the effect of different calibration coefficients and FA sets on diet estimates (see Appendix 1 for details).

Diet Estimation

The diet of individual seals was estimated using QFASA (Iverson *et al.* 2004). First, the statistical model was used to estimate what mixture of prey FAS minimized the Kullback-Leibler distance between the prey FA and the adjusted FA composition of each seal (see below). Second, the estimated mixture of prey was converted to an estimate of diet by weighting each prey species by its mean fat content. Standard errors of the estimated diet included both variability within and between seals. Within seal standard errors were estimated using a bootstrapping procedure which includes within prey-species variability in FA composition and fat content (Beck *et al.* 2007). Briefly, new mean FAS_p and mean fat contents were created by re-sampling with replacement within species. Subsequently, bootstrapped mean FAS_p were then used to estimate the mixture of prey that most closely matched the FA profile of the individual seal. These signatures where then converted to proportional diet estimates by weighting each prey species by its new fat content. Bootstrapping procedures were performed 1000 times (Iverson *et al.* 2004). Average within-seal standard error for each prey species was calculated as:

$$SE_{wj} = \sqrt{\sum_{i=1}^{n}\left(SE_{wji}^{2}\right)/n}$$

where SE_{wj} is the average within-seal standard error for prey type j, n is the number of

seals, and SE_{wji} is the within standard error for prey type j for seal i using the

bootstrapping procedure. Total SE for each prey (SE_j) was calculated as follows:

$$SE_j = \sqrt{\left(SE_{wj}^{2} + SE_{bj}^{2}\right)/n}$$

where SE_{bj} is the standard error of the mean percent composition in the diet of prey type j

between individual seals.

Due to predator metabolism, the FA composition of the predator will never match that of

its prey (Iverson et al. 2004). However, individual FA are deposited and/or modified in

predator lipid stores in a predictable fashion (Cooper 2004; Iverson et al. 2004) such that

corrections can be applied to account for this effect of metabolism; that is, proportions of

individual predator FA are 'calibrated' to account for differences. Calibration coefficients

(CCs) have been determined for a number of different phocid and marine bird species

through controlled, captive feeding experiments (i.e. Iverson et al. 2004). While the

effect of metabolism is remarkably similar for individual FA across diverse species (i.e.

FA consistently higher or lower in predator than prey: Iverson et al. 2004, 2006, 2007)

the magnitude of CCs can vary, which can effect overall diet estimates (see Appendix 1).

I used the average CCs derived for juvenile and pup grey seals as well as juvenile harp

seals (see Iverson *et al.* 2004 for details). For harp seals, I averaged diet estimates across three model iterations that used different calibration coefficients (average harp *CC*s, average of grey-harp *CC*s, average of grey-harp-pup *CC*s). Therefore, for each iteration of the bootstrapping procedure outlined above, three estimates were derived and subsequently averaged. Similarly for hooded seals, I averaged estimates across two model iterations that used the grey-harp *CC*s and the grey-harp-pup *CC*s.

Diet diversity or niche breadth was calculated for each seal's diet using the standardized Shannon-Weiner Index (*H'*; Krebs 1999):

$$H' = \left(-\sum_{s}^{j} p_j \ln p_j \right) / \ln S$$

where p_j is the proportion of prey species *j* in the diet, and *S* is the total number of prey consumed across all individuals (*S*= 24 for harps; *S*=26 for hoods). Energy density (*E_d*; kJ·g^{-1}) of diets were calculated using the lipid composition of prey species (e.g. Trudel *et al.* 2005).

Dietary overlap was calculated between each age-class group and between species using the Morisita-Horn index (C*_H*; Krebs 1999):

$$C_H = \left[2 \left(\sum_{j}^{n} p_{jk} p_{jl} \right) \right] / \left[\left(\sum_{j}^{n} p^2{}_{jk} \right) + \left(\sum_{j}^{n} p^2{}_{jl} \right) \right]$$

where p_{jk} is the mean proportion of prey type j in the diet of group k, p_{jl} is the mean

proportion of prey type j in the diet of group l, and n is the total number of prey

consumed by both groups. Degree of dietary overlap is small when C_H is between 0-

0.29, medium when C_H is between $0.30 - 0.59$, and large when C_H is > 0.60.

Statistical Analysis

To evaluate the effects of sex, age-class, season, year and sampling area on diet

composition for harp and hooded seals, I used a randomization procedure (Efron and

Tibshirani 1998). Briefly, a 2-way MANOVA (R® version 2.3.1; The R Development

Core Team 2006) was performed to generate test statistics for main effects and

interactions in pair wise comparisons. I randomly permuted the factor labels 10 000 times

to build a permutation distribution rather than compare test statistics to the normal theory

distributions. Significance levels were then computed by determining the number of

times the reference distribution gave a test statistic equal or greater than the observed

value. Post hoc univariate and multivariate t-test's, were also compared to reference

distributions to determine where the significant differences occurred. I also tested for

main effects of sex, age class, season, area and species on E_d and H' by MANOVA

(SPSS® version 10.1; SPSS Inc. 2000).

RESULTS

Harp seals

I identified 24 prey items in harp seal diets, 6 of which were present at proportions >5%

and together accounted for 89% of total overall average diet (Table 6.1). These included

amphipods (24.3% ± 1.1), arctic cod (8.6% ± 0.7), capelin (14.6% ± 0.7), herring (7.7% ± 0.7), sand lance (*Ammodytes dubius*) (23.0% ± 0.9) and large redfish (10.3% ± 0.8). Individuals consumed between 1 and 14 items, with a mean of 5.1 ± 2.0. Overall, dominant prey species differed by sex (p=0.002), age-class (p<0.001), season (p<0.001), area (p<0.001) and year (p<0.001). Juveniles consumed a greater proportion of American plaice (*Hippoglossoides platessoides*) (p=0.039), herring (p<0.001), northern sand lance (p<0.001), polar cod (*Arctogadus glacialis*) (p=0.005), pollock (*Pollachius virens*) (p=0.025) and squid (p=0.002), while adults consumed greater proportions of amphipods (p<0.001), euphausiids (p=0.001) and both small (p=0.019) and large (p<0.001) redfish. To control for age class effects, I separated juveniles from adults in subsequent analyses.

Adult harp seals

In adults, both sexes consumed equally high proportions of capelin and redfish (Figures 6.1, 6.2), however diet composition varied significantly between males and females (p<0.001) in other components. Males consumed approximately twice the proportion of amphipods (p<0.001), while females consumed higher proportions of arctic cod (p=0.014), snake blenny (p=0.019), and sand lance (p<0.001). There were significant seasonal (p<0.001) differences in diet composition (Figures 6.1, 6.2), but no significant interaction between sex and season (p=0.25). Differences were due primarily to higher proportions of amphipods (p<0.001) in the pre-breeding period, while polar cod (p=0.007) and large redfish (p<0.001) were higher in the post-breeding period. Significant differences were also noted for large Atlantic salmon (*Salmo salar*) (p=0.007), lumpfish (*Cyclopterus lumpus*) (p<0.001) and plaice (p=0.045), which were

all higher, albeit in small proportions, in the post-breeding period. There was a significant effect of sampling area (p<0.001) although no significant interaction between sex and area (p=0.24). Differences between areas were due primarily to higher proportions of amphipods (p<0.001) and large redfish (p=0.006) consumed in the offshore, while higher proportions of pelagic forage fish, namely arctic cod (p<0.001), capelin (p=0.035) and sand lance (p<0.001), were consumed in the inshore. Although proportions were small, differences were also noted in the level of arctic eelpout (*Lycodes lavalaei*) (p=0.036) and snake blenny (*Enchelypus cimbrius*) (p=0.025), which were higher in inshore diets, while large salmon (p<0.001) and polar cod (p=0.035) were higher in the offshore. There was a significant interaction between area and season (p<0.001). The inshore-offshore differences noted above remained generally consistent within seasons, however there were significant differences between seasons for both inshore (p=0.005) and offshore samples (p<0.001). Most notably, in the inshore, the proportion of large redfish (p=0.01) was higher in the post-breeding period. In the offshore, amphipods (p<0.001) were almost double the level in the pre-breeding period, while herring (p=0.016), polar cod (p<0.001) and large redfish (p<0.001) were consumed in greater proportions in the post breeding period.

Diet composition varied significantly by year (p<0.001) but there were no significant interactions with any other main effects (all p's >0.16). Post hoc analysis suggested that both 1994 and 1995 differed from all other years in diet composition (Figure 6.3), while 1996, 2000, 2002 and 2004 were all similar (p's > 0.14); 1998 differed from 2002 (p=0.036) and 2004 (p=0.027). In 1994, there were elevated proportions of amphipods

(p's <0.001) and decreased proportions of capelin (p's< 0.001) and sand lance (p's <0.03) relative to other years. Similarly, in 1995 there were elevated proportions of arctic cod (p's <0.001) and lower levels of capelin (p's <0.004). Increased proportions of American plaice, Atlantic cod (*Gadus morhua*), lumpfish and Greenland halibut (*Reinhardtius hippoglossoides*) (p's <0.025) in the diet were estimated in 1998.

Juvenile Harp seals

There were no significant sex differences among juvenile male and female harp seals (p=0.54), although diets did vary by season (p<0.001), year (p<0.001) and area (p<0.001). Seasonal variation in diet composition was primarily due to elevated levels of sand lance (p=0.031) in the pre-breeding period, and elevated levels of redfish (p<0.001) in the post-breeding period. Significant differences were also noted for more minor dietary components such as plaice (p=0.018) and pollock (p<0.001): both were higher in the post breeding period. Offshore diets were characterized by a higher proportion of redfish (p<0.001) and polar cod (p<0.0086), while inshore diets had higher proportions of sand lance (p=0.016). There was no significant interaction between season and area (p=0.19).

A similar pattern was observed in annual differences for juveniles. Post hoc analysis suggests that 1994 differed from all years except 1998, while 1995 in turn differed from all other years. With the exception of differences between 1996 and 2004 (p=0.013), diet composition was similar from 1996-2004. In 1994, there were elevated proportions of amphipods (p's <0.001) and decreased proportions of capelin (p's< 0.02) and redfish (p's

<0.04) relative to other years. Similarly, in 1995 there were elevated proportions of arctic cod (p's <0.001) and sand lance (p's<0.04) and lower levels of capelin (p's <0.001) in the diet.

Energy density and niche breadth

Overall, energy density (E_d) of harp seal diets ranged between 4.5 and 6.5 kJ·g^{-1} (Figure 6.4), and, although energy density did not differ greatly in magnitude among demographic groups, there was a significant effect of sex ($F_{1,525}=25.95$, p<0.001), age class ($F_{1,525}=31.11$, p<0.001), area ($F_{1,525}=28.06$, p<0.001) and season ($F_{1,525}=16.13$, p<0.001). In adults, which had higher E_d overall, energy densities were significantly greater in males than females ($F_{1,293}=4.75$, p=0.033). For both adults and juveniles, offshore diets had higher E_d and E_d's were higher in the pre-breeding period.

Overall niche breadth (H') for harp seals ranged between 0 and 0.66 (Figure 6.5) and there were significant effects of age class ($F_{1,525}=13.76$, p<0.001), season ($F_{1,525}=36.59$, p<0.001) and area ($F_{1,525}=28.06$, p<0.001). In adults, females had a significantly higher H' than males ($F_{1,525}=8.1$, p=0.005). H''s were all higher in juveniles, in offshore, and in post-breeding diets. In addition, there was a significant negative correlation between E_d and H' (Pearson's = -0.59, p<0.001).

Hooded seals

I identified 26 prey items in hooded seal diets overall, 5 of which were present at proportions of >5% and together accounted for 80% of total overall average diet (Table

6.2). These included amphipods (11.2% ± 1.2), Atlantic argentine (*Argentina silus*)

(13.2% ± 1.1), capelin (16.3% ± 1.2), euphausiids (5.0% ± 0.7) and large redfish (34.5%

± 2.5). Individuals consumed between 1 and 13 items, with a mean of 5.7 ± 2.5. Overall,

the dominant prey species in hooded seal diets differed by sex (p=0.04), age-class

(p<0.001), season (p<0.001), area (p<0.001), and amalgamated year (p=0.002). Diets for

adults were characterized by higher proportions of large redfish (p<0.001), while

juveniles consumed higher proportions of arctic cod (p=0.003), herring (p=0.011), sand

lance (p<0.001), eelpout (p=0.003) and white baraccudine (*Notolepsis rissoi*) (p<0.001)

(Figure 6.6). Again, I separated adults from juveniles to control for age class effects.

There were no sex differences between male and female juvenile hooded seals (p=0.55).

Sample sizes for juveniles were not large enough across other main effects to adequately

evaluate significance.

Adult hooded seals

Diets for adult hooded seals were comprised mainly of large redfish, Atlantic argentine,

capelin, amphipods, herring, euphausiids and longfin hake (*Urophycis chesteri*) (Figure

6.6). However, I found significant differences in diet composition between males and

females (p=0.011) as males consumed significantly greater proportions of large redfish

(p=0.0314) and Greenland halibut (p=0.039) and females consumed greater proportions

of blue hake (p<0.001) and white baraccudine (p=0.002). There was a significant effect

of season on diet composition (p<0.001), but no significant interaction between sex and

season (p=0.619). Differences were due primarily to higher proportions of argentine

(p<0.004) and capelin (p<0.001) in the pre-breeding period, while the proportion of large

redfish (p<0.001) was 2-fold higher in the post-breeding period. There was a significant effect of sampling area on diet composition (p<0.001), but no significant interaction between sex and area (p=0.10). Animals sampled in Greenland varied significantly from the other two areas for many species, but differences were primarily due to elevated proportions of longfin hake (p<0.001) and polar cod (p<0.001) and decreased levels of argentine (p=0.003). There were significant differences between Labrador (LAB) and NE Newfoundland (NENFLD) with respect to the proportion of capelin (higher in NENFLD; p<0.001) and redfish (higher in LAB; p=0.021).

There were significant differences between year groups (p<0.001). Post hoc analysis suggested that 2000 and 2004 were the most divergent years, due to large decreases in the proportions of capelin (p<0.001) and euphausiids (p=0.0015) and a large increase in the proportion of large redfish (p<0.001).

Energy density and niche breadth

Overall, energy density (E_d) of hooded seal diets ranged between 4.9 and 6.0 kJ·g^{-1} (Figure 6.4), and there was a significant effect of season ($F_{1,152}$=5.90, p<0.016) where E_d was higher in pre-breeding, and of area ($F_{1,152}$=12.49, p<0.001). Energy densities were equivalent in juveniles and adults ($F_{1,152}$=0.04, p=0.84) and in males and females ($F_{1,152}$=0.053, p=0.82).

Overall, niche breadth (H') for hooded seals ranged between 0.36 and 0.68 (Figure 6.5) and there were significant effects of season ($F_{1,152}$=18.37, p<0.001), age class

($F_{1,152}$=14.95, p<0.001), and area ($F_{1,525}$=14.24, p<0.001). Niche breadth was higher in both juveniles and in the pre-breeding season, as well as greater in NENFLD. There was no significant difference between adult males and females ($F_{1,152}$=2.69, p=0.10).

Harp seals vs. hooded seals

Overall, the energy density (E_d) of harp seal diets was significantly higher than hooded seal diets ($F_{1,678}$=16.78, p<0.001). Conversely, hooded seals had marginally greater niche breadths ($F_{1,678}$=4.0, p=0.046). Dietary overlap, as measured by the Morisita-Horn index (C_H), between harp seals and hooded seals was moderate for adults and high for juveniles (Table 6.3).

DISCUSSION

Through the application of QFASA (Iverson *et al.* 2004) I have defined diets for individual harp and hooded seals belonging to different demographic groups and over various temporal and spatial scales. The approach of QFASA estimates the proportional contribution of assimilated prey integrated over a time period of weeks to months (Iverson *et al.* 2004; Beck *et al.* 2007). The average harp seal diet was estimated to be comprised predominantly of amphipods, arctic cod, capelin, herring, sand lance and large redfish. Hooded seal diets were composed primarily of amphipods, Atlantic argentine, capelin, euphausiids and redfish. Harp seals consumed two times the proportion of amphipods (24%), while hooded seals consumed three times the proportion of redfish (34%); proportions of capelin (15%) were generally equivalent overall. Atlantic cod were

found in trace levels on average in harp seal diets (range 0.07-0.91%); no Atlantic cod were reported in hooded seals.

Our results are generally consistent with previous estimates based on stomach content analysis. Studies applying this more traditional approach have indicated that harp seals consume a mixed diet dominated by pelagic forage fish such as capelin, arctic cod and herring, and invertebrates such as amphipods and euphausiids (Lawson *et al.* 1995; Lawson and Stenson 1995, 1997). Data on hooded seals are scarce, but they have been found to mostly feed on a variety of deep-water fish such as halibut, redfish and squid as well as capelin, Atlantic cod and arctic cod (Ross 1993; Kapel 1995; Hammill and Stenson 2000; Potelov *et al.* 2000; Haug *et al.* 2006). Perhaps the most surprising result reported here was the high proportion of amphipods in both harp and hooded seal diets. Amphipods have always been reported in high frequencies in stomach contents of both seal species (e.g. Lawson *et al.* 1995; Haug *et al.* 2006), however it has always been difficult to assess the relative proportional contribution to diets. Other pinnipeds are known to regularly consume pelagic amphipods or euphausiids, although some species posses specific adaptations for filter-feeding on these prey (i.e. crabeater seals). Amphipods have elevated lipid contents (this study: mean 8.4%, range 3.0-19.5%) and foraging and handling costs are likely relatively minimal if animals are feeding within dense aggregations of plankton. Another interesting result was the large fraction of Atlantic argentine in hooded seal diets. Information on argentine is scare, although they can be found in abundance on the Continental shelf (Scott and Scott 1988), likely in

aggregations, and at depths of 140-1440 m (Froese and Pauly 2007); which are well within the diving range for these predators (Follow and Blix 1999).

Dietary overlap between harp and hooded seals was medium for adults and high for juveniles (Table 6.3). However, given what is known about the differences in foraging behaviour and distribution of these two species (Follow and Blix 1999; Folkow *et al.* 2004), it is difficult to assess how this overlap might be manifested over broad temporal and spatial scales. Recent data from satellite tagging indicate that both species may co-occur outside of the breeding period (Folkow *et al.* 1996, 2004). Data from stomach contents in the Greenland Sea suggest that although both co-occurred, diets varied significantly between species (Haug *et al.* 2004). It has been postulated that differences in prey selection were related to different foraging depths as hooded seals dive to deeper depths than harp seals (Folkow and Blix 1999; Folkow *et al.* 2004). E_d was higher in harp seal diets because their diets tended to be comprised of greater proportions of pelagic forage fish and invertebrates with high energy and lipid contents (mean lipid content for main diet constituents: 5.7% ± 0.1). In contrast, hooded seals tended to have larger niche breadths. In sympatric terrestrial carnivores, larger species tend to have larger niche breadths, although the diets of smaller predators are often nested within those of larger predators (i.e. Sinclair *et al.* 2003; Radloff and du Toit 2004), resulting in a fairly large degree of dietary overlap.

Age class effects

I found significant differences between juvenile and adult diets for both harp and hooded seals. In harp seals, although diets were dominated by pelagic species and significant dietary overlap was evident, juveniles consumed approximately double the proportions of pelagic forage fish, namely capelin, herring and sand lance, while adults consumed double the proportions of amphipods and redfish. In hooded seals, adult diets were dominated by redfish (44%), which comprised only 7% of the diet for juveniles. Juveniles consumed between 2-3 times the proportion of arctic cod, capelin, euphausiids, Greenland halibut, sand lance, Vahl's eelpout and white barracudine. Proportions of amphipods and argentine were equivalent. Indeed, ontogenetic diet shifts have been demonstrated in harp seals through the analysis of stomach contents. In harp seals, this shift is primarily due to increases in the proportion of pelagic invertebrates at the expense of forage fish (Lawson *et al.* 1995). Little is known about ontogenetic diet changes in hooded seals.

Ontogenetic diet differences have been noted for many animal taxa (reviewed in Bolnick *et al.* 2003; Estes *et al.* 2003). Ontogenetic diet shifts are thought to result from either differing energetic costs associated with body size or learning (Estes *et al.* 2003). In pinnipeds, it is known that juveniles undergo a period of physiological development related to dive capacity, and it is often hypothesized, a period of behavioural development (e.g. Baker and Donohue 2000; Field *et al.* 2005; Noren *et al.* 2005). However, it is difficult to partition effects with respect to diet selection; and of course these are not necessarily mutually exclusive hypotheses. For both harp and hooded seals

niche breadth was higher in juveniles, which may indicate more experimentation, or at least less specialization, by these naïve foragers. In harp seals, energy density was higher in adults, potentially mandated by overall higher energy costs related to maturation and body size. Analogous results have been found between juvenile and adult grey seals (Beck *et al.* 2007). I also found a negative correlation between E_d and H', suggesting that less diverse diets, focused around high energy-content prey, likely have greater returns. In harp seals, the proportion of pelagic invertebrates was greater in adults than in juveniles. This may be a function of differences in age class distributions (Sergeant 1965, 1991), resulting in different prey encounters rates, or particular prey selection. Although the energy return is great with respect to lipid content, I hypothesize that efficient, high consumption of amphipods may require larger gut capacity to process high volumes of indigestible, chitinous material (i.e. Martensson *et al.* 1994; Ginnett and Demment 1997; Lawson *et al.* 1997; Carbone *et al.* 1999).

Sex differences

I found significant differences in diet between adult males and females for both harp and hooded seals. In harp seals these differences were with respect to the proportional species composition, the energy content of the diet and the overall breadth of the diet. Adult male and female harp seals consumed equally high proportions of capelin (11%) and redfish (14%). Diets for males were dominated by amphipods (43%) although these also comprised a large fraction for females (25%). Females also consumed double the proportions of arctic cod (11%) and sand lance (21%). Females had greater diet diversity; however, E_d was higher in males due to the higher proportion of amphipods. For adult

hooded seals the primary difference between males and females was in the proportion of redfish (52% vs. 40% respectively). Females consumed marginally higher proportions of Atlantic argentine, blue hake, white barracudine, euphausiids and herring. I noted no sex differences in the E_d or niche breadth.

Sex differences in foraging behaviour of pinnipeds are assumed to reflect differences in sex- specific costs of reproduction, body size, or competitive abilities (i.e. Beck *et al.* 2003, 2007). It is likely that sex differences in diets in adult harp seals in the pre-breeding period are related to sex-specific costs associated with pregnancy, lactation and reproduction. Although this may also be true for adult hooded seals, divergent diets of males and females may also be due to the costs associated with maintaining larger body size in males. The lack of sex differences in the diets of juveniles is probably indicative of the lack of reproductive costs or, in the case of hoods at that age, lack of significant body-size dimorphism.

Spatial and Temporal differences

Data from stomach content analysis has previously indicated distinct differences in nearshore and offshore diets for harp seals (Lawson et al. 1995; Lawson and Stenson 1997; Lawson *et al.* 1998). In the nearshore, diets tended to be dominated by capelin, herring, arctic cod while in the offshore, diets tended to be dominated by invertebrates, capelin, sand lance and a mix of demersal species. For both adults and juveniles, I found similar differences in diets; amphipods (32%) and redfish (16%) were approximately 2-fold higher in offshore diets, while arctic cod (10%) and sand lance (26%) were

approximately 2-fold higher in nearshore diets. These former species are more associated with nearshore areas, while redfish are found on the shelf and shelf edges (Scott and Scott 1988; Froese and Pauly 2007). I found large-scale regional differences in hooded seal diets as well, confirming conclusions from stomach content analysis (e.g. Haug *et al.* 2006).

There were significant differences between pre- and post-breeding diets for both harp and hooded seals which resulted in higher E_d overall in the pre-breeding period. In adult harp seals, seasonal diet differences were primarily due to higher proportions of amphipods in the pre-breeding period, while polar cod and large redfish were higher in the post-breeding period. Polar cod, which are also bathypelagic like redfish, are generally found at higher latitudes, associated with ice, and found mainly in offshore waters at or beyond the edge of the continental shelf. Therefore, increased consumption may be linked to northern migration during post-breeding-pre-moulting feeding. In juvenile harp seals, seasonal variation in diet composition was primarily due to elevated levels of sand lance in the pre-breeding period, and again elevated levels of redfish in the post-breeding period. Differences in hooded seals were due primarily to higher proportions of argentine and capelin in the pre-breeding period, while the proportion of large redfish was higher in the post-breeding period. Following moulting in April, harp seals appear to gradually increase fat reserves over the summer and fall during the northerly migration (Hammill *et al.* 1995; Chabot and Stenson 2002). Both adult male and female NW Atlantic harp seals reach peak body mass in February just prior to breeding in February. In hooded seals, most energy stores are accumulated between September and March just prior to

reproduction (Chabot *et al.* 2006; Thordarson *et al.* 2007). Of course for these highly migratory species, it is unclear whether seasonal diet differences are due to particular prey selection during the period of pre-breeding fattening, to seasonal differences in prey availability, or even to seal distribution. However a relationship between higher energy diets and higher rates of fat accumulation occurring by chance seems highly coincidental. Although life histories are slightly different, in grey seals, for which there is more complete diet information over the annual cycle of fat deposition, females appear to select higher quality prey species during an important period of energy acquisition (Beck *et al.* 2007).

During the last decade, the Northwest Atlantic has undergone massive ecological change. The once abundant Atlantic cod stocks off Newfoundland were decimated by the early 90's due to over fishing (Rose 2004). However, changes in ocean climate appear to have amplified declines, or the ability of stocks to recover due to reduced recruitment and growth. Ocean conditions in the early 1990's were among the coldest ever recorded and were accompanied by many coincident changes in both biotic and abiotic conditions (Drinkwater 2002). In particular, capelin, a former principle prey of seals, cod, whales and seabirds, has declined in northern areas since the 1990's (Carscadden *et al.* 2001; Rose 2004). Capelin became scarce along the coast of Labrador and the Grand Banks while abundance increased on the Flemish Cap and the Scotian Shelf (Lilly and Simpson 2000; Carscadden *et al.* 2001). Concurrently, Arctic cod distribution shifted southward from Labrador to coastal Newfoundland and the Grand Banks out to the shelf edge. This

expansion in distribution and arctic cod biomass peaked in 1995 (Lilly and Simpson 2000).

Inter-annual variation in pinniped diets is assumed to reflect variation in prey abundance and subsequent encounter rates (Bowen & Siniff 1999). Indeed, during this same past decade there were notable changes in harp seal distribution and diet as indicated from stomach content analysis. From 1990-1995, Arctic cod became a significant prey species for seals in near shore areas in the spring (Lawson *et al.* 1995). Arctic cod had been the key prey species in winter diets since 1986 (Stenson and Perry 2001). Anecdotal reports have suggested an increase in harp seal abundance in inshore waters over this decadal time period (Lacoste and Stenson 2000; Sjare *et al.* 2004), although some portion of the population was continuing to consume capelin in offshore areas (Stenson and Perry 2001). In addition, since the late 1990's the amount of sand lance has increased in offshore diets, while herring has increased in inshore diets. Furthermore, changes in diets of other species, most notably seabirds, corroborate other sources of information indicating major changes in the distribution of fishes during the 90's (i.e. Montevecchi and Myers 1996, 1997; Rowe *et al.* 2000; Davoren and Montevecchi 2003).

Concurrent with these observations, over this decade I noted significant changes in harp seal diets derived from QFASA, which generally reflect the broad changes in prey distribution and abundance. In 1994, there were decreased proportions of capelin and sand lance relative to other years. Similarly, in 1995 there were elevated proportions of arctic cod and again lower levels of capelin. Changes in hooded seal diets were also noted

between amalgamated year groups, and broad changes in diets for grey seals have been documented for this time period as well (Beck *et al.* 2005).

Overall I noted broad inter-and intra-specific variation in diets, diet quality and diet breadth for these two pinniped species displaying different foraging tactics. Our results are consistent with previous, more general estimates based on traditional techniques. However, the powerful advantage of the QFASA approach is that estimates are made at the level of the individual thereby increasing our ability to understand and detect differences among demographic groups. Both inter-and intra-specific variation in diet, whether due to sex or ontogenetic differences, subsequently influenced by broad spatial and temporal effects, must be considered when determining the role of these top predators in ecosystem structure.

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TABLES

Table 6.1: Mean diet composition (% ± SE), energy density (E_d, kJ·kg⁻¹) and diet diversity (H') among age and sex classes of Harp seals.

| | Pre-breeding | | | | | | Post-breeding | | | | | |
| | Juvenile | | Adult Female | | Adult Male | | Juvenile | | Adult Female | | Adult Male | |
Prey	Inshore (n=138)	Offshore (n=41)	Inshore (n=90)	Offshore (n=25)	Inshore (n=36)	Offshore (n=39)	Inshore (n=17)	Offshore (n=36)	Inshore (n=49)	Offshore (n=25)	Inshore (n=19)	Offshore (n=11)
Pelagic Forage Fish												
Capelin	21.2 ± 1.55	15.3 ± 2.5	12.7 ± 1.6	6.6 ± 2.02	16.7 ± 2.97	6.8 ± 1.83	11.2 ± 2.3	17.4 ± 2.71	10.3 ± 1.62	13.2 ± 3.12	9.0 ± 2.29	10.6 ± 5.05
Fourline Snake blenny	1.1 ± 0.32	1.5 ± 0.91	2.2 ± 0.79	1.5 ± 0.84	1.0 ± 0.53	0.5 ± 0.37	2.0 ± 0.88	0.9 ± 0.33	4.1 ± 1.26	0.2 ± 0.2	0.6 ± 0.59	0.4 ± 0.37
Herring	11.0 ± 1.45	11.8 ± 3.53	4.4 ± 1.23	1.8 ± 1.25	8.7 ± 2.66	1.2 ± 0.84	14.2 ± 4.67	11.9 ± 2.61	5.7 ± 1.58	6.9 ± 3.07	2.4 ± 1.29	8.4 ± 4.48
Northern Sand lance	33.8 ± 1.8	27.8 ± 3.56	23.8 ± 2.12	20.1 ± 4.36	10.4 ± 2.35	9.3 ± 2.4	27.9 ± 5.59	23.6 ± 3.59	22.9 ± 2.64	10.4 ± 3.36	17.7 ± 4.11	7.6 ± 3.01
Gadidae												
Arctic Cod	8.3 ± 1.35	6.3 ± 1.61	14.5 ± 2.07	7.9 ± 3.01	9.9 ± 2.54	3.5 ± 1.37	7.8 ± 2.82	4.7 ± 1.86	12.1 ± 2.17	0.7 ± 0.42	7.2 ± 2.67	5.5 ± 2.86
Atlantic Cod	0.0 ± 0.01	NA	0.3 ± 0.2	NA	NA	NA	NA	NA	0.9 ± 0.74	NA	0.9 ± 0.91	NA
Atlantic Cod Large	NA	NA	0.1 ± 0.05	NA	NA	0.0 ± 0.02	NA	NA	0.1 ± 0.07	NA	NA	NA
Polar Cod	1.4 ± 0.44	2.5 ± 1.04	0.6 ± 0.46	0.4 ± 0.37	0.3 ± 0.2	0.5 ± 0.35	1.3 ± 0.67	4.5 ± 1.21	0.9 ± 0.45	2.6 ± 1.01	0.5 ± 0.45	5.9 ± 3.41
Pollock	0.2 ± 0.14	0.0 ± 0.01	0.0 ± 0.03	0.5 ± 0.47	NA	NA	0.7 ± 0.55	3.3 ± 1.52	0.1 ± 0.07	0.7 ± 0.7	0.5 ± 0.46	NA
Rock Cod	NA	NA	0.0 ± 0.01	NA	NA	NA	NA	NA	NA	NA	NA	NA
Other												
Atlantic Salmon	0.0 ± 0.01	0.1 ± 0.09	0.1 ± 0.09	NA	NA	NA	0.2 ± 0.2	0.1 ± 0.13	NA	NA	0.5 ± 0.53	NA
Atlantic Salmon Large	0.2 ± 0.06	0.6 ± 0.22	0.0 ± 0.02	0.2 ± 0.2	NA	0.1 ± 0.05	0.4 ± 0.19	0.9 ± 0.23	0.1 ± 0.05	0.6 ± 0.21	NA	0.3 ± 0.33
Arctic Eelpout	1.6 ± 0.54	3.0 ± 1.53	1.4 ± 0.83	NA	NA	NA	1.6 ± 1.56	0.7 ± 0.41	2.6 ± 1.06	0.0 ± 0.01	NA	0.1 ± 0.05
Common Lumpfish	0.2 ± 0.11	0.3 ± 0.24	0.0 ± 0.01	0.0 ± 0.04	NA	NA	0.4 ± 0.42	0.1 ± 0.08	0.2 ± 0.08	NA	0.7 ± 0.66	NA
Redfish	0.7 ± 0.18	0.4 ± 0.19	1.5 ± 0.37	2.7 ± 1.56	0.3 ± 0.29	1.3 ± 0.82	0.3 ± 0.33	0.6 ± 0.42	0.9 ± 0.36	1.1 ± 1.04	1.5 ± 0.64	0.7 ± 0.68
Redfish Large	2.7 ± 0.56	7.3 ± 2.7	7.7 ± 1.25	5.4 ± 2.57	12.7 ± 2.56	12.6 ± 2.78	13.9 ± 4.66	14.0 ± 3.36	15.0 ± 2.8	36.6 ± 4.79	17.7 ± 5.51	24.1 ± 7.46
Snailfish	NA	0.2 ± 0.15	0.2 ± 0.22	0.5 ± 0.43	NA	NA	NA	NA	NA	NA	NA	NA
Vahls Eelpout	0.0 ± 0.02	NA	0.0 ± 0.02	NA	NA	NA	NA	0.6 ± 0.34	0.0 ± 0.04	NA	0.3 ± 0.28	NA

	Pre-breeding						Post-breeding					
	Juvenile		Adult				Juvenile		Adult			
			Female		Male				Female		Male	
Prey	Inshore (n=138)	Offshore (n=41)	Inshore (n=90)	Offshore (n=25)	Inshore (n=36)	Offshore (n=39)	Inshore (n=17)	Offshore (n=36)	Inshore (n=49)	Offshore (n=25)	Inshore (n=19)	Offshore (n=11)
Pleuronectidae												
American Plaice	0.2 ± 0.08	0.5 ± 0.45	NA	NA	NA	0.1 ± 0.08	1.1 ± 0.77	1.0 ± 0.56	0.2 ± 0.21	0.1 ± 0.07	1.2 ± 1.17	NA
Winter Flounder	0.4 ± 0.15	0.4 ± 0.14	1.4 ± 0.38	0.5 ± 0.51	0.1 ± 0.05	0.8 ± 0.49	1.3 ± 0.68	0.8 ± 0.44	1.7 ± 0.55	0.3 ± 0.14	0.0 ± 0.01	0.8 ± 0.78
Greenland Halibut	0.3 ± 0.13	0.1 ± 0.04	0.1 ± 0.13	0.1 ± 0.11	NA	0.0 ± 0.01	0.3 ± 0.26	0.6 ± 0.33	0.4 ± 0.31	NA	0.3 ± 0.3	0.9 ± 0.9
Invertebrates												
Amphipods	14.3 ± 1.24	19.3 ± 4.33	23.4 ± 2.24	44.3 ± 7.05	33.8 ± 4.21	60.6 ± 5.64	14.7 ± 4.73	12.7 ± 2.52	17.1 ± 2.43	26.5 ± 3.51	34.0 ± 4.84	32.2 ± 6.24
Euphausiids	2.25 ± 0.51	2.4 ± 1.44	5.5 ± 1.17	7.4 ± 2.62	6.1 ± 2.46	2.9 ± 1.36	0.7 ± 0.53	1.1 ± 0.74	4.7 ± 1.66	0.1 ± 0.1	5.3 ± 3.83	2.6 ± 1.75
Squid	0.12 ± 0.08	0.4 ± 0.25	0.0 ± 0.02	0.0 ± 0.03	NA	NA	0.2 ± 0.16	0.4 ± 0.31	NA	0.2 ± 0.14	NA	0.0 ± 0.04
E_d (kJ·kg^{-1})	5.5 ± 0.02	5.5 ± 0.07	5.5 ± 0.04	5.7 ± 0.1	5.7 ± 0.06	6.0 ± 0.08	5.4 ± 0.07	5.4 ± 0.05	5.4 ± 0.05	5.6 ± 0.04	5.6 ± 0.09	5.7 ± 0.09
H'	0.37 ± 0.01	0.35 ± 0.02	0.38 ± 0.01	0.30 ± 0.03	0.35 ± 0.02	0.23 ± 0.03	0.41 ± 0.02	0.43 ± 0.02	0.42 ± 0.01	0.35 ± 0.02	0.37 ± 0.03	0.38 ± 0.03

Table 6.2: Mean diet composition (% ± SE), energy density (E_d, kJ·kg^{-1}) and diet diversity (H') among age and sex classes of Hooded seals.

	Pre-breeding						Post-breeding				
	Juvenile		Adult				Juvenile	Adult			
			Female		Male			Female		Male	
Prey	LAB (n=24)	NENFLD (n=9)	LAB (n=28)	NENFLD (n=8)	LAB (n=18)	NENFLD (n=24)	(n=5)	GRNLND (n=9)	LAB (n=10)	GRNLND (n=5)	LAB (n=13)
Pelagic forage fish											
Capelin	29.8±3.42	25.7±5.46	12.0±2.27	25.9±4.36	8.6±1.8	18.1±2.78	30.4±7.51	15.6±4.11	0.9±0.85	9.9±4.87	5.1±1.64
Common Lumpfish	NA	0.5±0.45	NA	NA	0.0±0.02	0.1±0.08	1.3±1.27	1.8±1.73	NA	0.4±0.4	NA
Herring	7.4±2.31	7.4±4.19	6.6±1.71	0.5±0.31	3.8±1.73	2.2±0.93	0.9±0.9	0.7±0.73	1.9±1.46	NA	0.4±0.41
Northern Sandlance	9.0±2.09	9.3±4.36	0.2±0.23	1.0±1.02	0.5±0.48	0.3±0.3	1.7±1.72	0.5±0.52	NA	NA	NA
Gadidae											
Arctic Cod	3.8±1.37	4.1±1.78	1.2±0.77	2.8±2.62	0.8±0.47	1.4±0.76	NA	0.1±0.14	0.3±0.28	NA	0.2±0.19
Blue Hake	0.1±0.07	0.7±0.7	2.2±0.8	1.9±1.57	NA	NA	1.3±0.91	3.9±2.15	0.2±0.21	2.8±2.77	NA
Longfin Hake	0.3±0.2	NA	2.9±0.97	0.6±0.48	1.1±0.71	3.3±2.35	NA	23.0±6.86	0.0±0.004	20.7±4	1.2±0.53
Polar Cod	1.9±0.97	5.0±2.82	0.3±0.16	3.2±2.07	1.8±1.04	2.3±0.91	6.9±4.84	7.1±2.44	NA	19.7±4.16	1.0±0.7
Pollock	NA	NA	NA	NA	NA	NA	10.3±5.07	1.4±0.96	NA	NA	NA
Pleuronectidae											
Greenland Halibut	2.5±1.78	7.0±3.21	NA	NA	NA	NA	2.3±2.32	NA	0.1±0.13	NA	0.3±0.34
Greenland HalibutLarge	0.4±0.41	0.5±0.47	NA	0.3±0.31	1.3±0.78	0.5±0.47	3.7±2.76	6.2±1.38	NA	9.2±3.33	0.5±0.31
Haddock	NA	NA	NA	NA	NA	0.2±0.17	NA	NA	NA	NA	NA
Halibut	NA	NA	NA	NA	0.1±0.06	0.1±0.11	NA	NA	NA	NA	NA
White Hake	NA	NA	NA	NA	NA	0.3±0.26	NA	NA	0.3±0.34	NA	0.8±0.61
Winter Flounder	NA	0.3±0.29	NA	NA	0.8±0.44	0.2±0.19	NA	NA	0.2±0.24	NA	NA
Other											
Arctic Eelpout	NA	NA	NA	NA	0.0±0.02	0.1±0.08	NA	1.6±1.58	NA	NA	NA
Atlantic Argentine	17.0±3.21	1.5±1.54	22.5±2.49	11.5±3.22	15.3±3.19	13.4±2.85	6.3±2.88	1.0±0.89	8.3±2.53	0.1±0.13	7.6±1.51
Redfish	0.8±0.43	7.8±2.79	0.1±0.09	1.1±1.14	0.4±0.36	0.3±0.25	1.0±0.97	0.8±0.57	NA	1.8±1.84	NA
Redfish Large	4.1±1.86	1.1±1.03	32.8±4.72	25.6±7.25	49.4±5.34	41.1±6.15	18.2±10.37	22.7±8.85	71.7±6.25	26.2±7.87	77.1±3.77
Vahls Eelpout	0.4±0.23	5.0±2.83	NA	NA	NA	NA	3.6±3.63	0.5±0.47	1.2±1.19	NA	0.0±0.04
White Barracudine	1.1±0.52	3.9±2.51	0.5±0.23	1.3±0.87	0.1±0.05	0.0±0.01	2.0±1.1	1.6±1.06	0.0±0.04	NA	NA
Common Grenadier	NA	3.5±1.86	NA	NA	NA	NA	NA	0.1±0.1	NA	NA	NA
Invertebrates											
Amphipods	8.4±2.89	12.9±6.6	13.9±3.37	13.4±4.03	13.8±3.35	12.1±3.56	6.4±2.83	10.2±4.47	12.2±2.75	9.2±2.74	5.6±2.05
Euphausiid	12.9±2.55	3.9±2.07	4.9±2.02	11.1±4.25	2.5±0.82	4.2±1.31	3.0±1.79	1.2±1.24	2.5±1.67	NA	0.1±0.14
Shrimp	NA	NA	NA	NA	0.0±0.02	NA	NA	NA	NA	NA	NA

	Pre-breeding						Post-breeding				
	Juvenile		Adult				Juvenile	Adult			
			Female		Male			Female		Male	
Prey	LAB (n=24)	NENFLD (n=9)	LAB (n=28)	NENFLD (n=8)	LAB (n=18)	NENFLD (n=24)	(n=5)	GRNLND (n=9)	LAB (n=10)	GRNLND (n=5)	LAB (n=13)
Squid	0.2 ± 0.13	NA	NA	NA	0.0 ± 0.01	0.0 ± 0.01	NA	NA	NA	NA	NA
E_d (kJ·kg^{-1})	5.4 ± 0.04	5.4 ± 0.09	5.4 ± 0.04	5.4 ± 0.06	5.4 ± 0.05	5.4 ± 0.05	5.5 ± 0.06	5.6 ± 0.06	5.3 ± 0.05	5.6 ± 0.12	5.3 ± 0.03
H	0.5 ± 0.02	0.5 ± 0.03	0.4 ± 0.02	0.5 ± 0.02	0.4 ± 0.03	0.4 ± 0.03	0.50 ± 0.03	0.46 ± 0.04	0.24 ± 0.05	0.48 ± 0.03	0.22 ± 0.04

Table 6.3: Morisita-Horn index (C_H) of dietary overlap.

| Species	Age class comparison	Season	C_H
Harps	Adults	Pre-VS Post-breeding	0.91
	Juveniles	Pre-VS Post-breeding	0.94
	Adults VS Juveniles	Pre-breeding	0.79
		Post-breeding	0.89
Hoods	Adults	Pre-VS Post-breeding	0.89
	Juveniles	Pre-VS Post-breeding	NA
	Adults VS Juveniles	Pre-breeding	0.57
		Post-breeding	NA
Harps VS Hoods	Adults	Pre-breeding	0.51
		Post-breeding	0.61
	Juveniles	Pre-breeding	0.70
		Post-breeding	NA

FIGURES
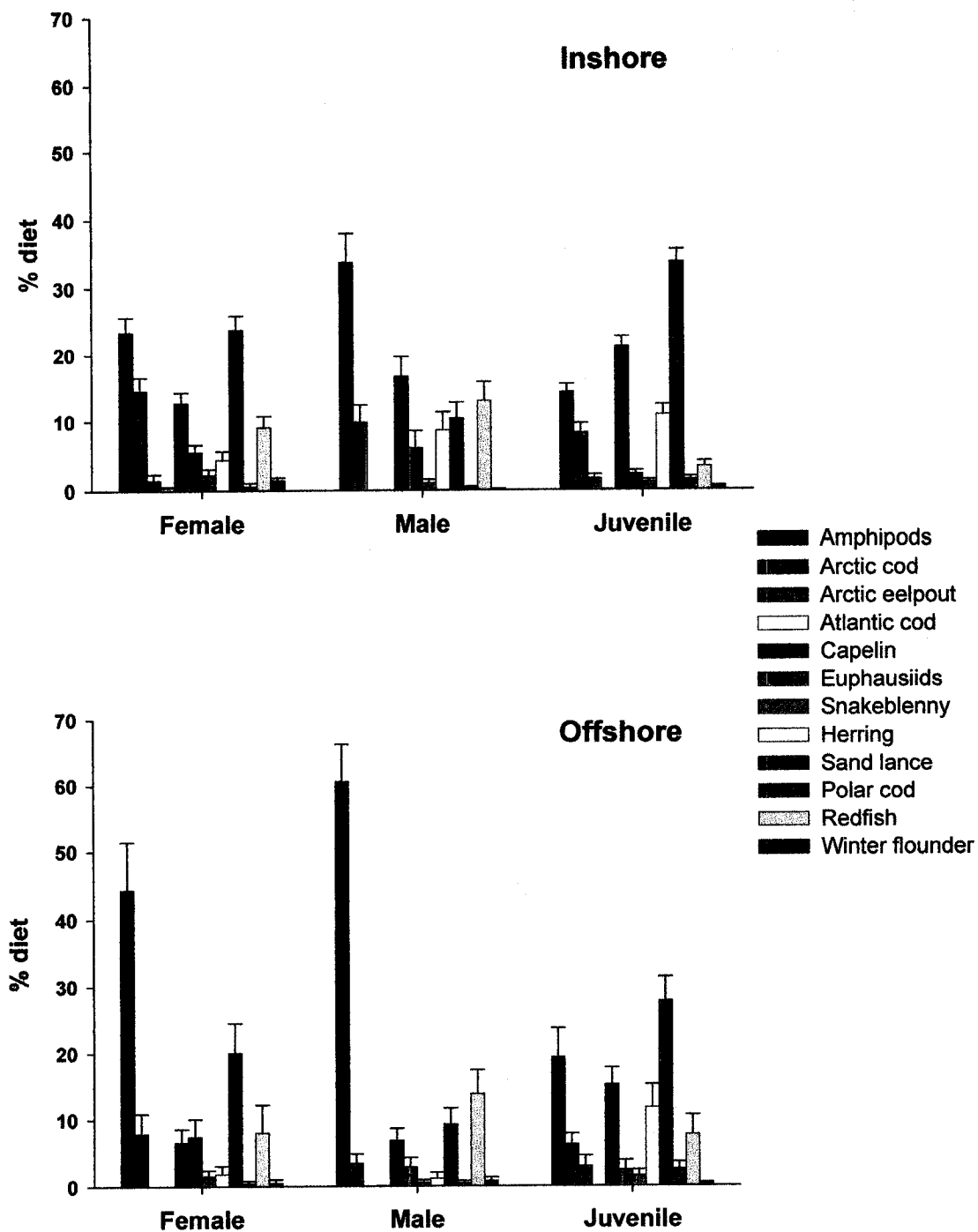
Figure 6.1: Mean diet composition (% ± SE) for adult female, adult male and juvenile harp seals from the Pre-breeding period sampled in inshore and offshore areas.
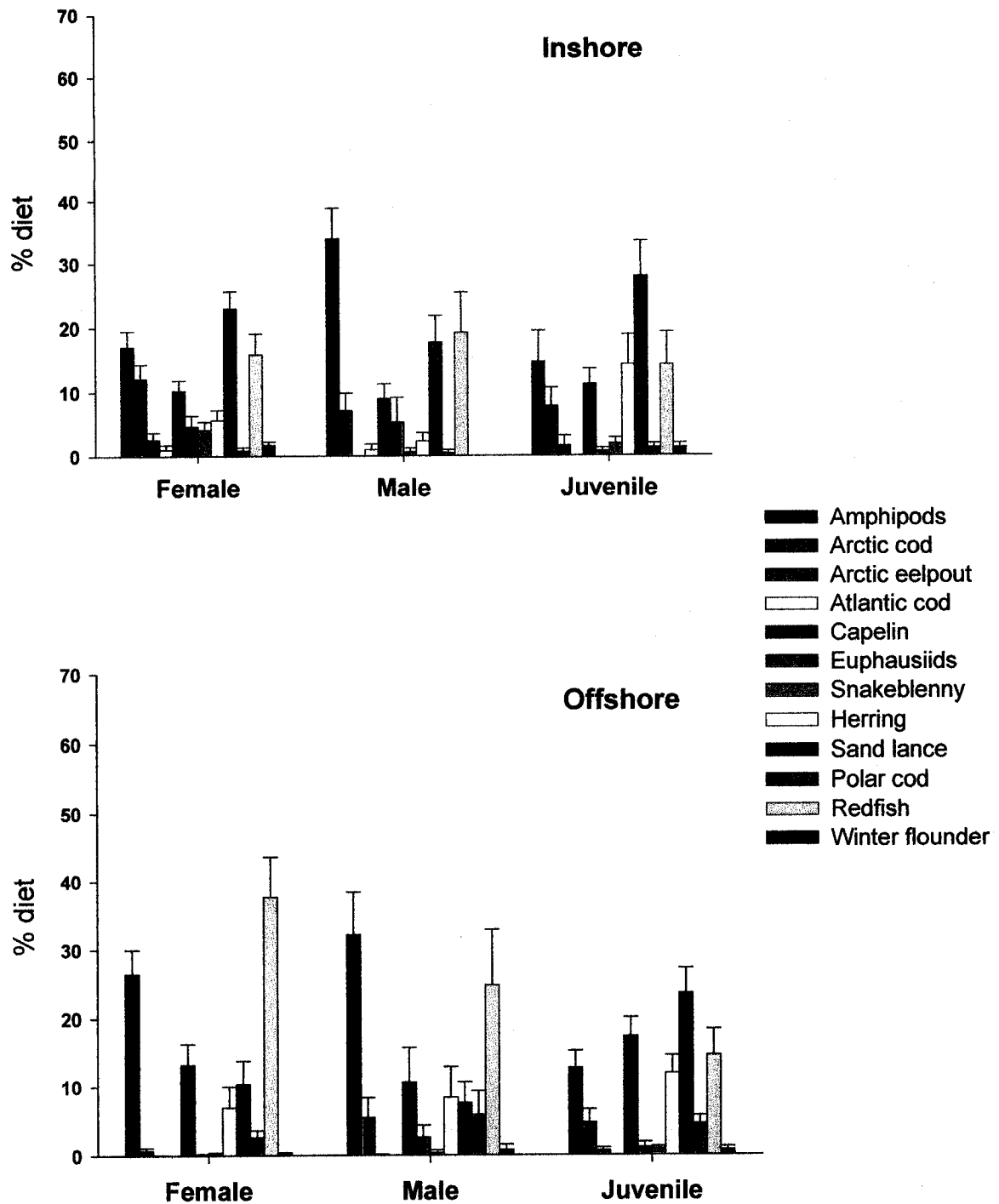
Figure 6.2: Mean diet composition (% ± SE) for adult female, adult male and juvenile harp seals from the Post-breeding period sampled in inshore and offshore areas.

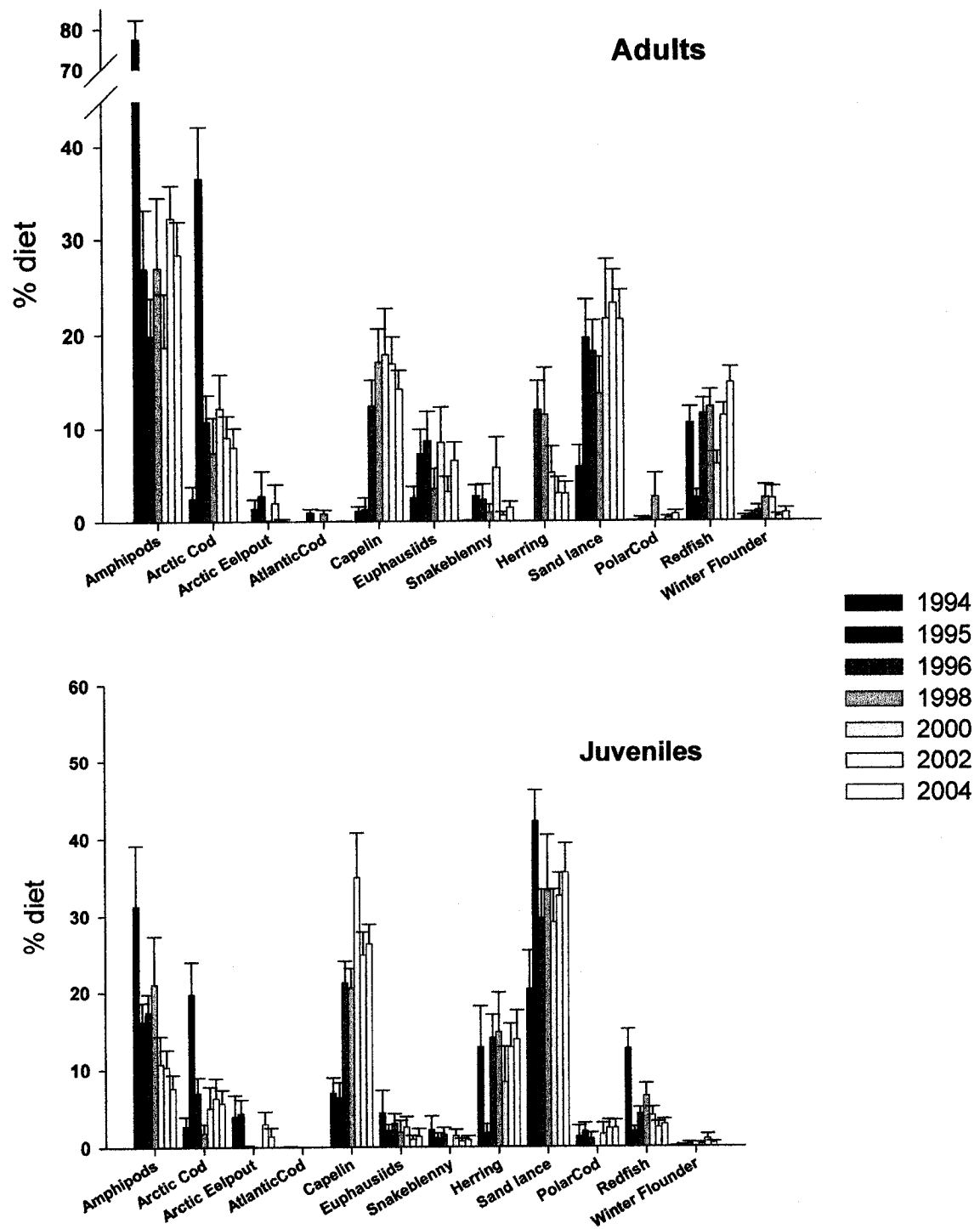Figure 6.3: Mean diet composition (% ± SE) for adult and juvenile harp seals from different years.

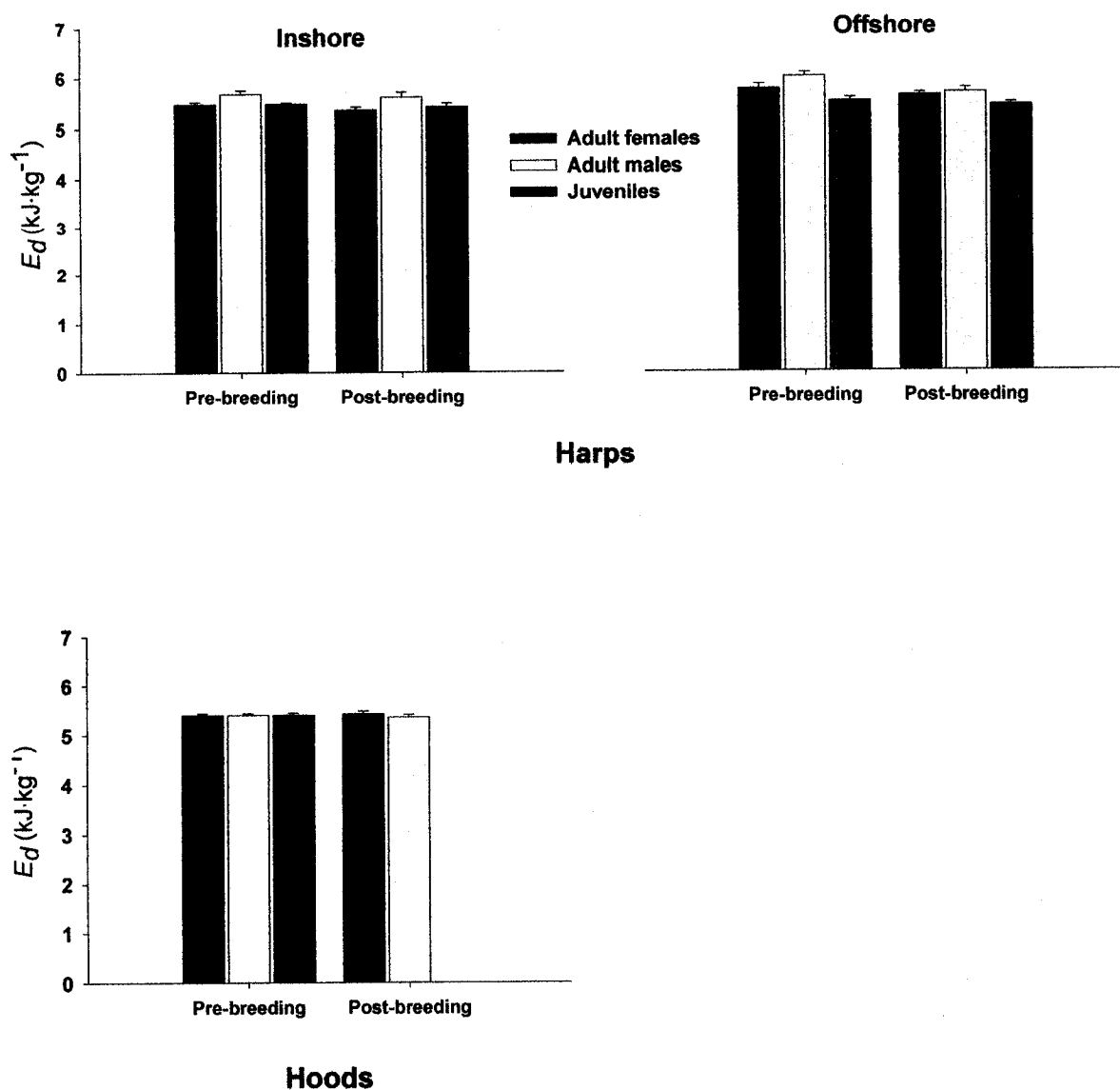Figure 6.4: Mean Energy Density of the diet (E_d; kJ·kg^{-1} ± SE) for adult female, adult male and juvenile harp and hooded seals from the pre- and post-breeding period. Harp seals are further divided into inshore and offshore samples.

Figure 6.5: Mean Shannon-Weiner index of diet diversity ($H' \pm$ SE) for adult female, adult male and juvenile harp and hooded seals from the pre- and post-breeding period. Harp seals are further divided into inshore and offshore samples.
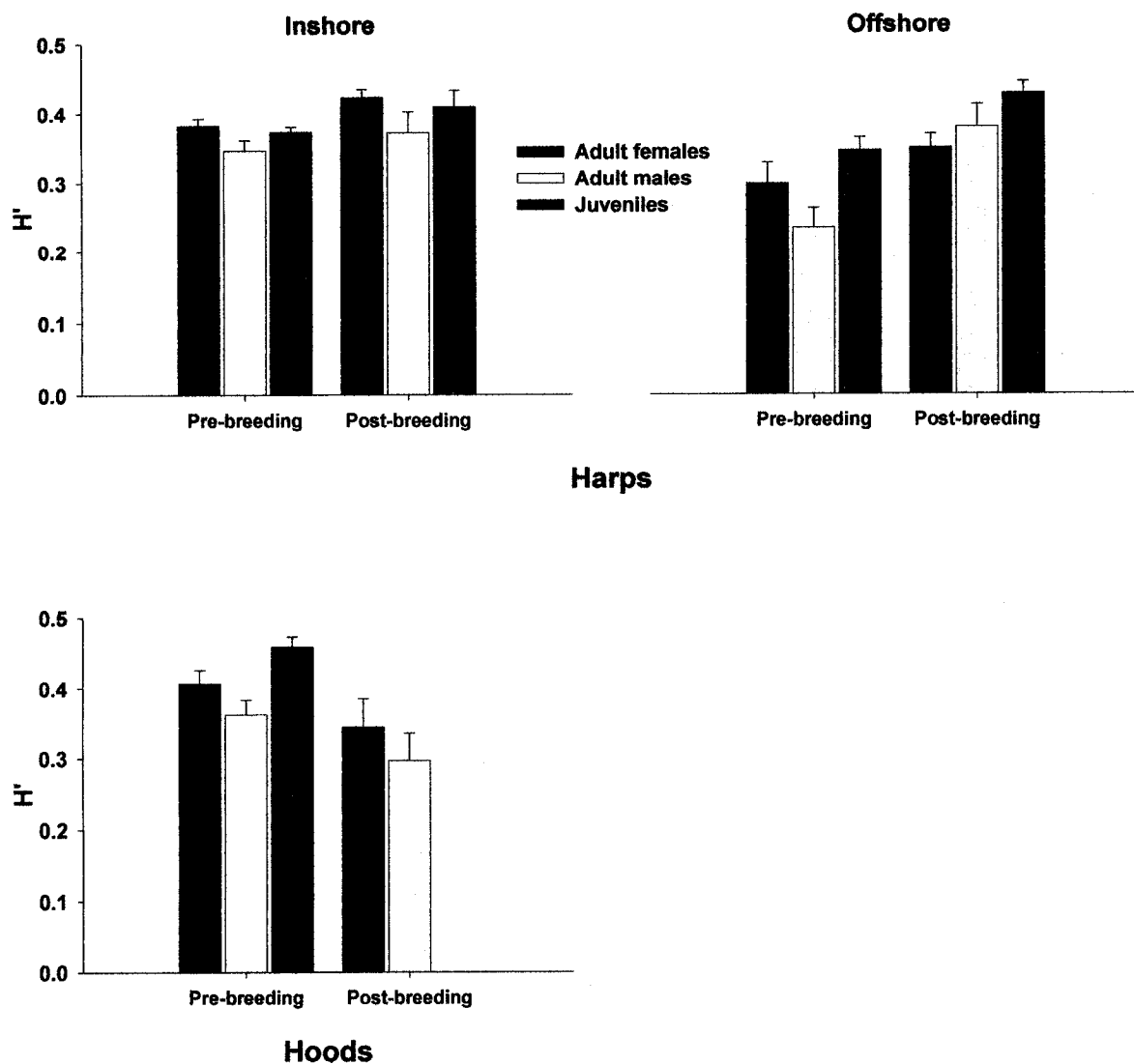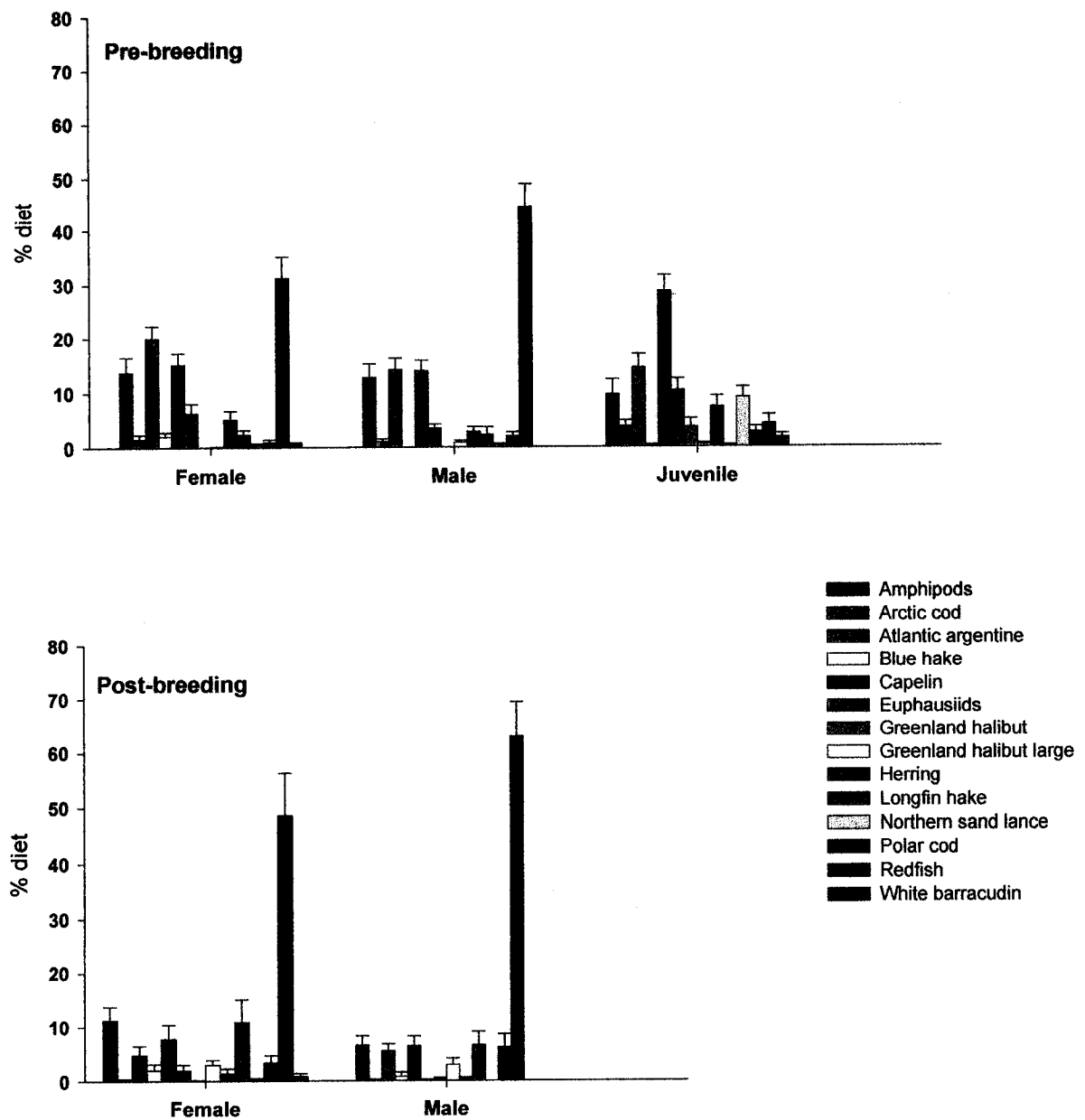
Figure 6.6: Mean diet composition (% ± SE) for adult female, adult male and juvenile hooded seals from the Pre- and Post-breeding period.

CHAPTER VII: CONCLUSION

Diet has important consequences with respect to energy intake, overall foraging costs and influences the degree of competitive interactions amongst organisms or exposure to predation thereby affecting an individual's fitness and survival. At the ecosystem level, understanding the diet of top predators is a first step in delineating predator prey interactions and their potential role in structuring or influencing food web structure. In the case of wide ranging top-level marine predators, such as whales, seals and seabirds, there is little information on diet with respect to individual, geographical and temporal variation of diet. This can lead to inaccurate predictions of predation effects on commercially harvested species.

The results generated in this thesis provide new insight into the basis of species, ontogenetic, sex and individual variation in diet of large marine carnivores. Overall I noted broad inter-and intra-specific variation in diets, diet quality and diet breadth for these three pinniped species displaying different foraging tactics. I applied two biochemical techniques to estimate diet and demonstrated convergence between them thereby strengthening my assertions of dietary differences. The powerful advantage of both the FA and stable isotope approaches is that estimates are made at the level of the individual thereby increasing our ability to understand and detect differences among demographic groups. Key findings demonstrate that seals show marked demographic and individual variation in feeding, thus individuals are achieving similar endpoints by exploiting different energy sources. These diet differences are generally consistent with known differences in foraging behaviour. I also noted broad spatial and temporal

variation in diets, although differences were maintained between demographic groups, suggesting that ecological segregation is preserved at multiple scales. These results lend further support for the idea of multiple foraging strategies with convergent success and underscore the need to account for such variability in developing predation models.

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# APPENDIX 1: DERIVATION OF HARP AND HOODED SEAL PREY LIBRARIES

HARP SEAL PREY LIBRARY

Prey library selection and FA sets

I evaluated the effects of main model parameters (prey library, FA subsets, calibration coefficients (CC)) by repeatedly estimating diets for all seals (n=526). First, I identified both primary and secondary prey libraries for diet estimation. The primary prey set was comprised of the most common prey found in stomach contents (e.g. Lawson *et al.* 1995; Lawson and Stenson 1995, 1997; Stenson, personal communication). The secondary set contained additional rare prey found in stomachs and species of special concern. These included species such as yellowtail flounder, wolffish and various skates. Thus the first step was to evaluate whether or not the addition of these species altered the interpretation of the diet and should be retained for the final modeling procedure. It is thought that limiting the prey library leads to fewer misclassifications and more accurate assessment of diet. Mean diet estimates are presented in Figure A.1 using the extended dietary FA set and the average of the harp-grey-pup CCs (results were similar for other FA and CC sets). On average, the proportions of main components are very similar (predominantly amphipods, capelin, arctic cod, northern sand lance and redfish) between the two prey libraries. The various size splits within prey species were evaluated by cluster analysis and their ability to be discriminated in QFASA was tested through subsequent modeling procedures. Splits were removed if poorly discriminated or the split resulted in other species being misclassified. In addition, closely related species (i.e. shrimps) were evaluated in a similar manner and pooled if poorly discriminated.

Figure A.1: Average diet estimates (n=526) using grey-harp-pup *CC*s and extended FA set for final prey library and secondary library. Dots represent outliers defined as being any value greater or less than 1.5 times the interquartile range (75th percentile–25th percentile) above the 75th (or below the 25th) percentile.

Final prey library
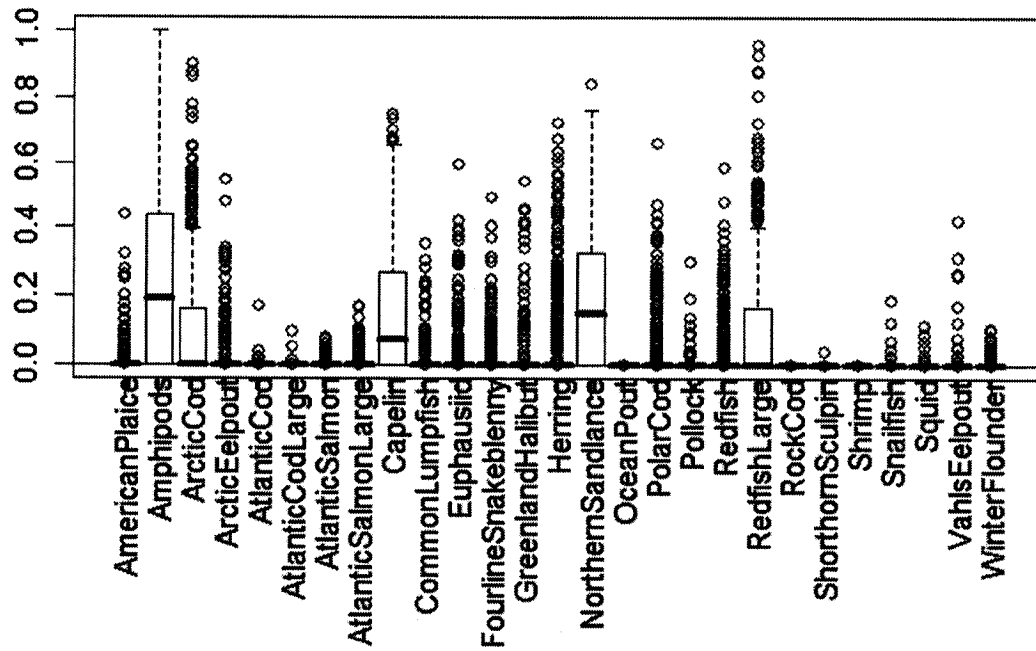
Secondary library
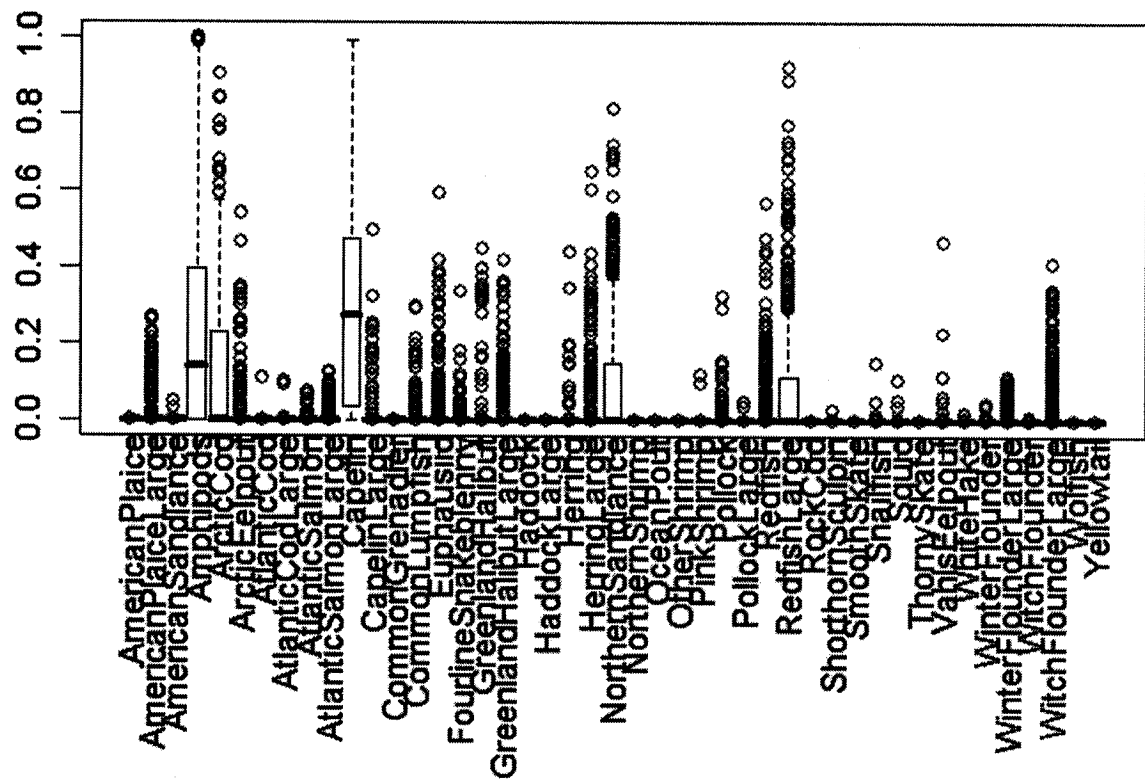
Next, I evaluated diet estimates based on the dietary (n=30 FA) and extended dietary (n=39) FA subsets. The extended fatty acid set includes an additional 9 fatty acids that arise from a combination of diet and biosynthesis. For example, although found in prey, in predators levels of 14:1n-5 are produced predominantly from biosynthesis, while some proportion of 22:5n-3 arises from modification (Ackman *et al.* 1988, Iverson 1993, Iverson *et al.* 1995). Fatty acids such as 16:0, 16:1n-7, 18:0 and 18:1n-9, can arise from biosynthesis in the predator, but are also highly indicative of differences in various prey (Iverson 1993, Iverson *et al.* 2001). The extended FA subset accounts for 95% of total FA, while the dietary set accounts for 51%. Again, I estimated diets for all seals using both FA sets. This was done for the different *CCs* and results are analogous. Relative to the extended FA set, the dietary subset underestimates proportions of amphipods, arctic cod, capelin and northern sand lance, and overestimates redfish and euphausiids (Figures A.2 & A.3). Amphipods, arctic cod, sand lance and capelin are all known to be important dietary items of harps based on stomach contents (see Chapters V and VI). Furthermore, redfish are known to be predators of capelin, sand lance and arctic cod, while euphausiids are prey of capelin, sand lance and arctic cod (Scott and Scott 1988; Froese and Pauly 2007). Thus the misclassifications are logical and it would appear that the extended dietary FA subset provides a more accurate assessment of diet likely because more information is retained to discriminate species. Furthermore, these additional FAs are clearly abundant in this system and considered important trophic indicators (Budge *et al.* 2002; Iverson *et al.* 2004), thus exclusion would clearly be inappropriate.
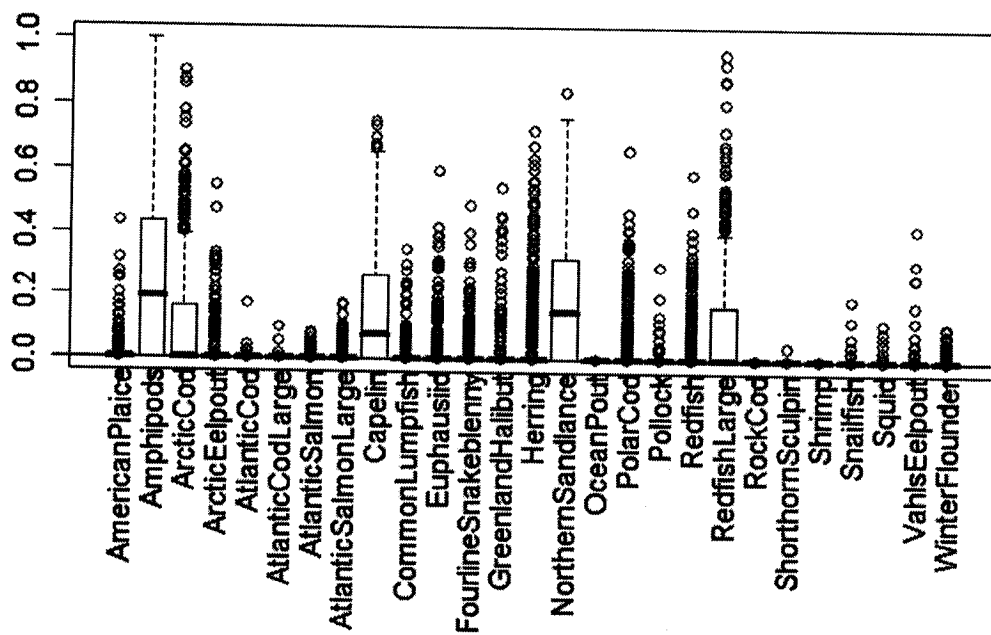
Figure A.2: Average diet estimates (n=526) using primary prey library, grey-harp-pup *CC*s and extended FA set. Dots represent outliers defined as being any value greater or less than 1.5 times the interquartile range (75th percentile–25th percentile) above the 75th (or below the 25th) percentile.
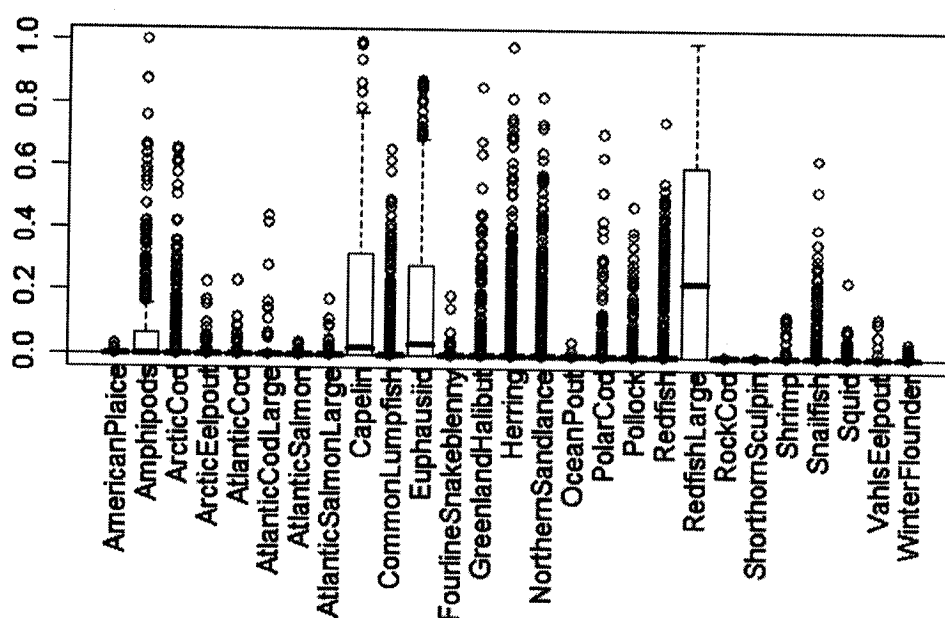
Figure A.3: Average diet estimates (n=526) using primary prey library grey-harp-pup
*CC*s and dietary FA set. Dots represent outliers defined as being any value greater or less
than 1.5 times the interquartile range (75th percentile–25th percentile) above the 75th (or
below the 25th) percentile.

Calibration Coefficients

It is well established that calibration coefficients are necessary for the accurate estimation of diet (Iverson *et al.* 2004). While the effect of metabolism is remarkably similar for individual FA across diverse species (i.e. FA consistently higher or lower in predator than prey: Iverson *et al.* 2004, 2006, 2007) the magnitude of *CC*s for individual FAs can vary (Table A.1), which can effect overall diet estimates. Therefore proceeding with the extended dietary FA subset, I evaluated different *CC*s as well as combinations of these different sets on diet interpretation. The harp (n=5), grey (n=8) and pup (n=17) *CC*'s are based on relatively small sample sizes and due to this fact, as outlined in Beck *et al.* (2007), it is preferable to use the average of these *CC*'s in combination.

There are discrepancies, but no large differences in diet assessment between the three main sets, or combinations of sets. In fact, the species composition of the diet estimates were all similar with amphipods, artic cod, capelin, sand lance and redfish as main components (Figure A.4). I had no *a priori* reason to select one calibration set over the other in the final modeling. Therefore, I opted to average the diet estimates derived using the three different coefficient sets to incorporate potential error. Specifically, I averaged diet estimates using the harp *CC*, the grey-harp *CC* average, and the grey-harp-pup *CC* average. The harp seal set is species specific; however sample size is small thus including the grey seal set (a related phocid species) likely incorporates potential variation. The pup calibration set is perhaps the best defined since a sub-sample of milk was measured in conjunction with the mom-pup pairs providing a direct link with ingested food and fat deposits in the 'predator'. These also represent the scenario of ingesting a high fat diet.

Table A.1: Calibration coefficients (*CC*) for FAs for juvenile grey seals, juvenile harp seals and grey seal pups. Data from Iverson *et al.* (2004).

| FA	Grey *CC*	Pup *CC*	Harp *CC*
14:00	0.86	0.95	0.94
16:00	0.74	0.83	0.63
16:1n-7	1.52	1.30	1.62
16:2n-6	0.76	0.81	0.74
16:2n-4	1.50	0.89	0.95
16:3n-6	0.86	1.00	1.12
17:00	1.40	0.78	0.91
16:3n-4	0.68	0.98	0.87
16:4n-1	0.59	0.97	0.77
18:00	0.84	0.64	0.79
18:1n-9	3.46	1.15	2.79
18:1n-7	1.41	1.04	1.44
18:1n-5	1.04	0.99	1.00
18:2n-6	2.02	1.04	1.57
18:2n-4	0.98	0.94	0.86
18:3n-6	1.08	0.78	0.94
18:3n-4	2.32	1.01	2.59
18:3n-3	2.27	1.07	1.48
18:3n-1	0.95	0.88	0.95
18:4n-3	0.96	0.96	0.99
18:4n-1	1.10	1.01	1.39
20:1n-11	3.42	0.97	2.84
20:1n-9	0.81	0.91	1.00
20:1n-7	0.71	0.82	1.06
20:2n-6	1.65	1.02	1.39
20:3n-6	1.07	0.91	1.00
20:4n-6	0.82	0.92	1.04
20:3n-3	1.16	0.98	0.98
20:4n-3	2.11	1.00	1.50
20:5n-3	0.65	0.82	0.80
22:1n-11	0.20	0.47	0.35
22:1n-9	0.27	0.49	0.59
22:1n-7	0.18	0.90	0.26
21:5n-3	1.37	1.02	1.45
22:4n-6	1.00	1.03	1.00
22:5n-6	1.04	0.96	0.76
22:4n-3	2.58	1.01	1.55
22:5n-3	4.64	1.09	3.91
22:6n-3	1.11	1.00	0.94
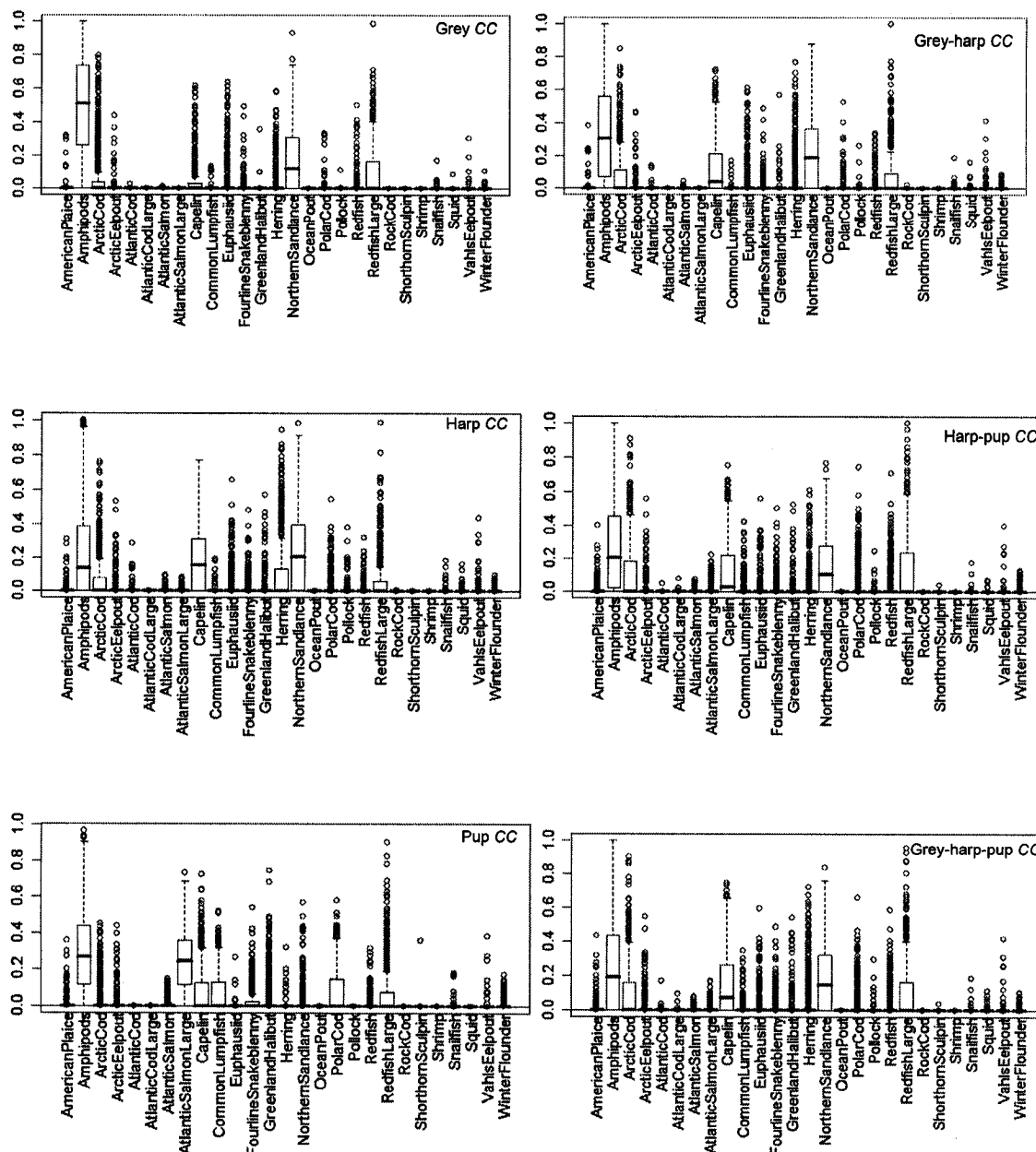
Figure A.4: Mean diet estimates (n=526) using grey, harp, pup *CC*s or combinations of those. Dots represent outliers defined as being any value greater or less than 1.5 times the interquartile range (75th percentile–25th percentile) above the 75th (or below the 25th) percentile.

Diet simulations and prey-on-prey modeling

Prey species occupying similar dietary niches have similar FAS (i.e. Budge *et al.* 2002). However, species of fish and invertebrates are typically well differentiated by their FA signatures (Budge *et al.* 2002) likely due in part to the fact that despite similarities, diets are rarely identical amongst species. Diets of seals often span multiple trophic levels where both fish and their prey, or even the prey of those prey, are consumed. For example harp seals are known to feed on redfish, capelin and amphipods in high proportions (e.g. Lawson *et al.* 1995; Lawson and Stenson 1995, 1997). For this predator species, this may pose an analytical limit to the application of a technique which traces the assimilated portions of unmodified FAs and attempts to find the closest statistical match between multiple potential prey and the predator. Thus, from the previous example, one might overestimate the proportion of redfish in the diet at the expense of capelin and amphipods because these in turn form the basis of redfish diets. Therefore modeling exercises allow us to test the performance limits and ability of QFASA to make differentiations in the specific prey base, both within and between prey species and allow us to understand potential substitutions.

The objective of diet simulations is to evaluate the robustness of the model in determining a given diet. In simulations, the prey base is randomly split into 2 subsets; a simulation and a modeling subset. The simulation set is sampled in the proportions specified by the simulated diet, with additional random prey added in to create noise (10%), to construct a 'pseudo-seal' signature. Subsequently the 'pseudo seal' is modeled against the modeling set to evaluate how much of a specified diet is returned from the

model. Detailed procedures for simulations are provided in Iverson *et al.* (2004). I constructed and specified 4 diets for simulations. These were based on observed patterns in the literature as well as the initial modeling results and were constructed to represent the diet of free-ranging harp seals. In addition, I sought to evaluate how well prey species that were more similar to one another than to all other species in the fatty acid database. I used hierarchical cluster analysis to determine the relative similarity of prey species' signatures (Fig.5).

Simulation diets contained four to seven prey species (Table A.2). These diets represented difficult or, in some sense, "worst case" estimation scenarios as some prey were more similar to one another than to all other species in the fatty acid database. Diet 1 and 4 were essentially pelagic- and benthic-species based respectively, while diets 2 and 3 were mixes of pelagic and benthic species. Noise was meant to represent the proportion of the diet made up of incidental consumption of prey species that were not included in the assumed diet. As the noise was set at 10% for these simulations, accurate estimation would give a total of 10% other prey. Patterns of values across these simulations provide insight into how the model performed within each diet (Fig 6). The model estimated the true diet rather well (Fig. 6), with the major species in the diet distinguished from others in the prey database with between 71% and 83% of the specified diet returned. Nevertheless, there was some misidentification (7-19%) of the diet composition to other prey types above the added noise. Misclassifications were to closely related species, as outlined in the cluster analysis (Figure A.5). For example, in Diet 1, 10% of the arctic cod signature was proportioned to polar cod and redfish. Atlantic cod was typically substituted by the alternate size split of Atlantic cod, plaice

and shrimp. Diet 2 was the most complex diet and performed the least well. In summary, especially for diets that were specifically chosen to have species with similar signatures, in the worst cases it may be difficult always to separate these species, with an increasingly large percentage being attributed to other prey. However, as would be expected, fits are better and more consistent when diet items are more easily distinguished.
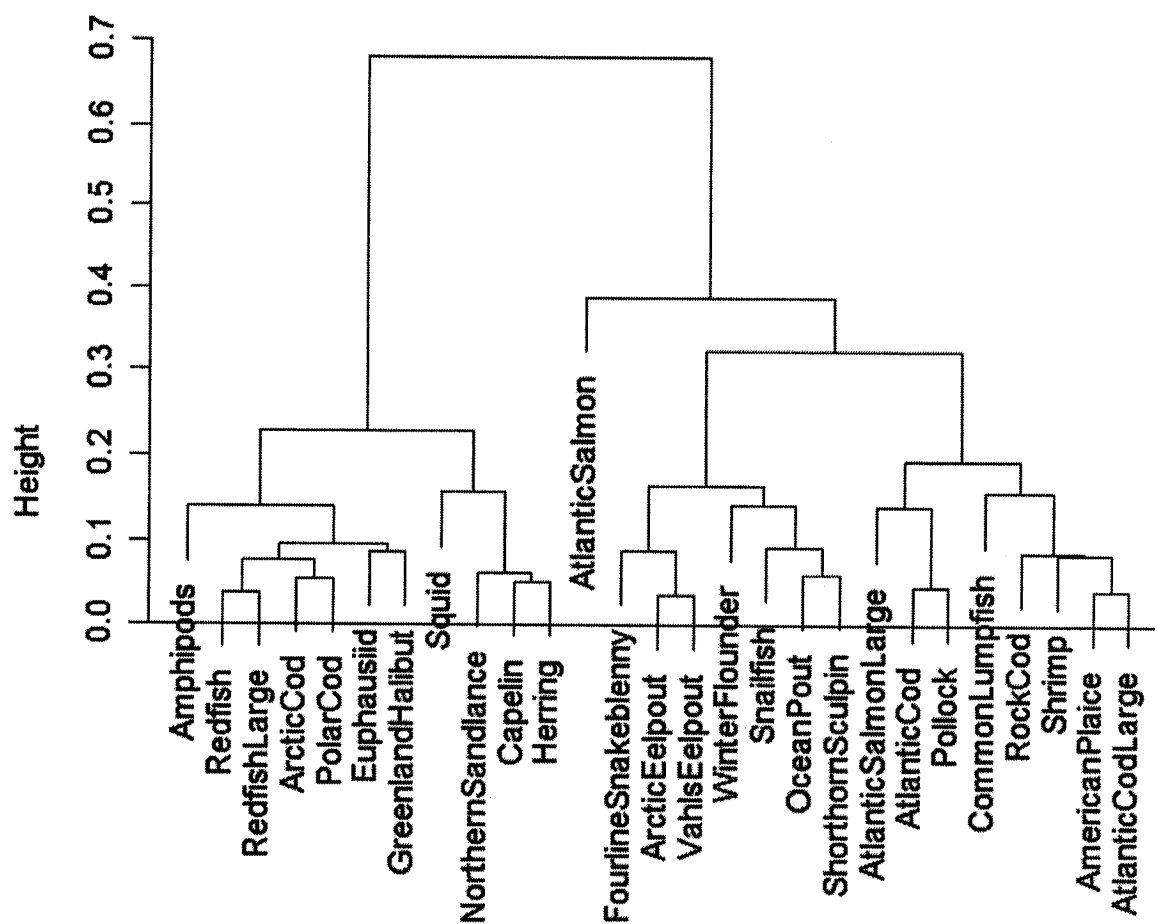
Figure A.5: Hierarchical cluster analysis on the mean fatty acid signatures (extended dietary subset) of 27 prey categories (*n*=2039) for harp seal prey library. The Kulback-Liebler (KL) distance measure was used to determine how similar any two taxa were with respect to their fatty acid signatures. The average linkage method was used.

Table A.2: Mean estimated diets of pseudo-seals over the 1000 simulation runs for each of the four diets with noise set at 10%.

diet	species	Specified diet	Estimate	1 SD
1	Amphipods	0.09	0.08	0.04
	Arctic Cod	0.225	0.18	0.06
	Capelin	0.225	0.22	0.096
	Euphausiids	0.09	0.09	0.063
	Herring	0.18	0.15	0.071
	Northern Sand lance	0.09	0.11	0.069
2	Amphipods	0.135	0.11	0.041
	Arctic Cod	0.27	0.23	0.071
	Atlantic Cod	0.09	0.06	0.073
	Capelin	0.225	0.18	0.072
	Northern Sand lance	0.045	0.06	0.054
	Rock Cod	0.045	0.03	0.027
	Shorthorn Sculpin	0.09	0.04	0.037
3	Atlantic Cod Large	0.045	0.02	0.01
	Capelin	0.09	0.09	0.071
	Herring	0.495	0.47	0.071
	Northern Sand lance	0.045	0.04	0.042
	Redfish Large	0.225	0.19	0.058
4	American Plaice	0.225	0.19	0.081
	Atlantic Cod Large	0.225	0.12	0.078
	Greenland Halibut	0.225	0.20	0.052
	Winter Flounder	0.225	0.22	0.052

Figure A.6: Results of the simulation study for Diets 1-4 as defined in Table 1 with 10% error (noise) added, using the 27 prey catagories (n =2039) and the extended dietary FA subset. In plots, ''a'' denotes the value specified for each of the prey species delineated in the diet. The simulation was run 1000 times, and estimated diet results are represented in box plots, as the median (middle horizontal bar), the 25th percentile (lower bar), and the 75th percentile (top bar) of the data distribution. Dots represent outliers defined as being any value greater or less than 1.5 times the interquartile range (75th percentile–25th percentile) above the 75th (or below the 25th) percentile.

Diet 1
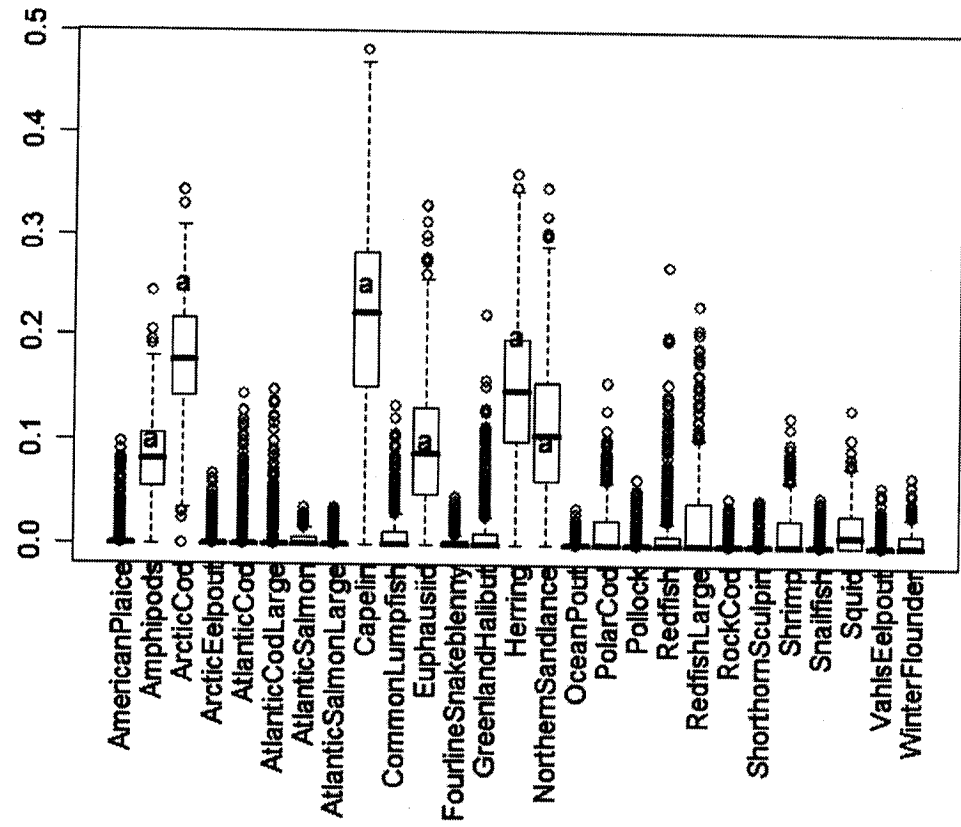
Diet 2
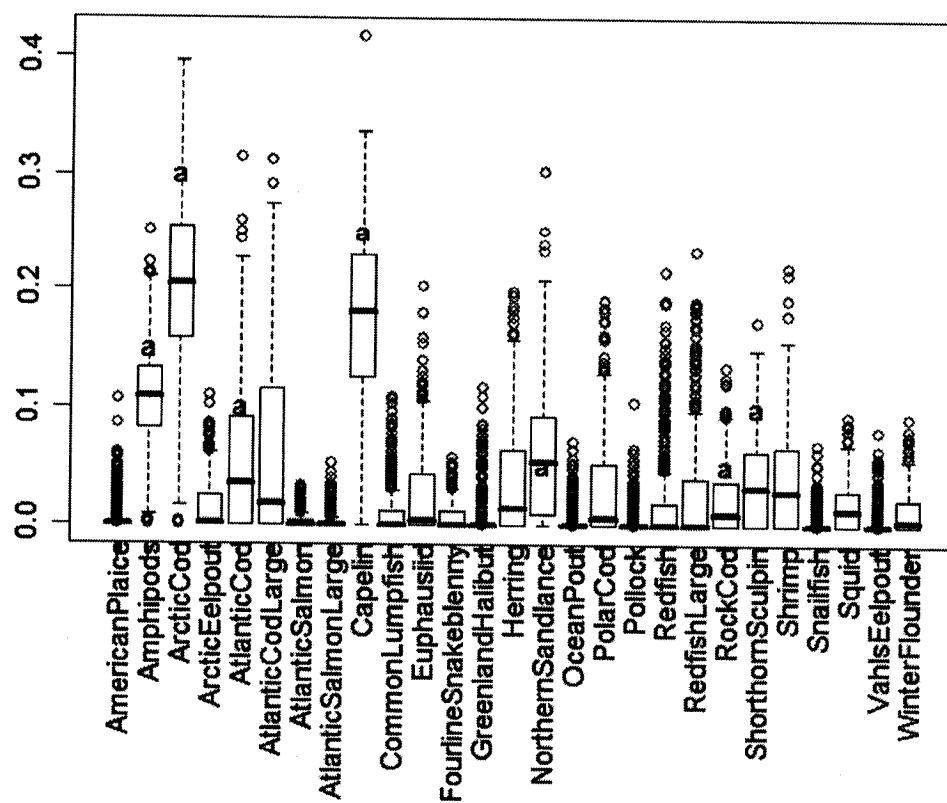
Diet 3
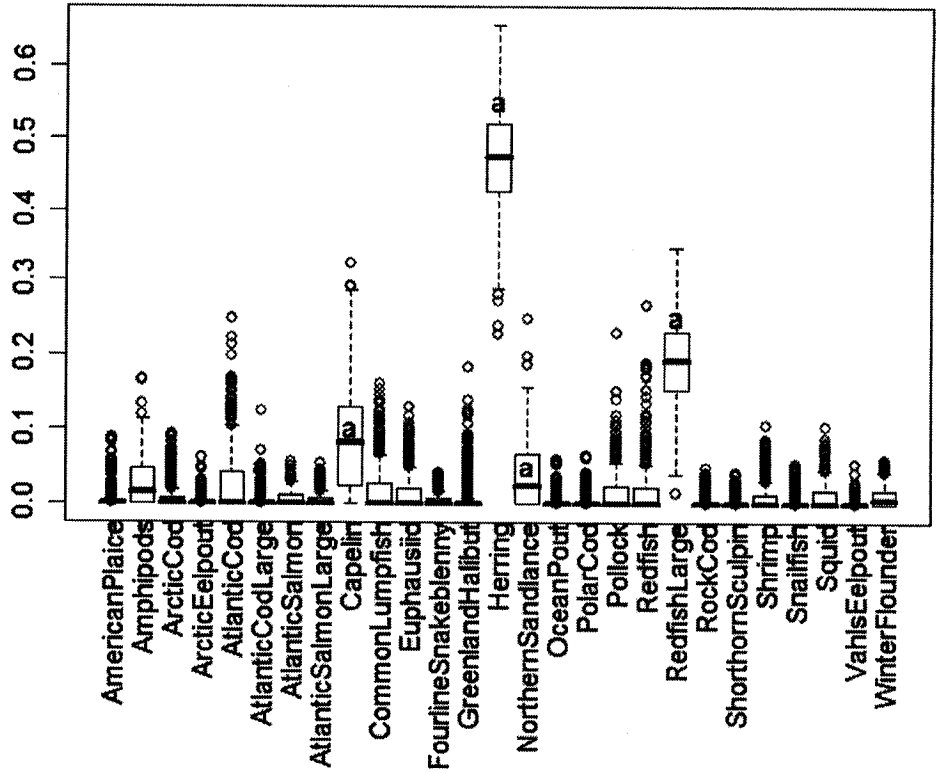
Diet 4
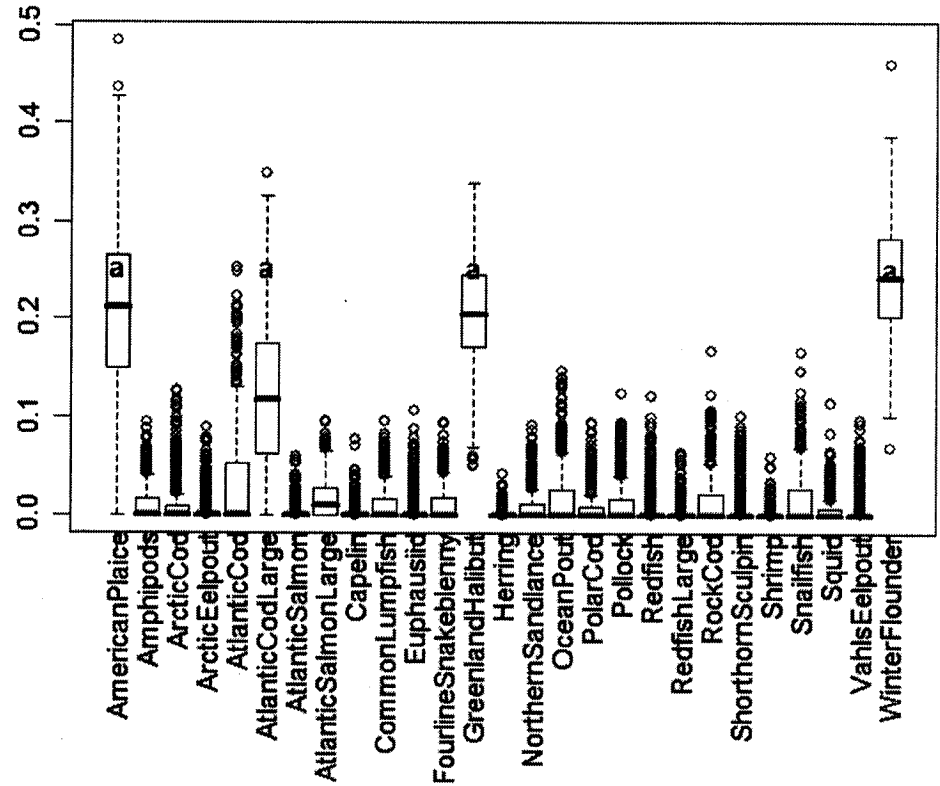
In conjunction with simulations, I preformed prey-on-prey modeling to determine which prey species may be substituted for another. Here, prey species are used as predators in the model. An important caveat here is that these are run without CCs since we do not have this information for fish and invertebrate species, thus there is likely a degree of error associated with the exercise. In prey-on-prey modeling, the prey base is randomly split into 2 subsets for each prey category; a 'predator' subset and a 'prey' subset. Subsequently each 'predator' species is modeled against the whole set of 'prey' species to identify the proportion that QFASA identifies as the original species. I conducted 10 random splits of the prey base and prey-on-prey modeling exercises and averaged results from all 10. For example 90% of the arctic cod signature is identified as arctic cod (Figure A.7). On average, prey species were identified as themselves 82.6% of the time (Figure A.7). This is comparable to results for other prey libraries used in QFASA (Blanchard, personal communication i.e. grey seals, monk seals).
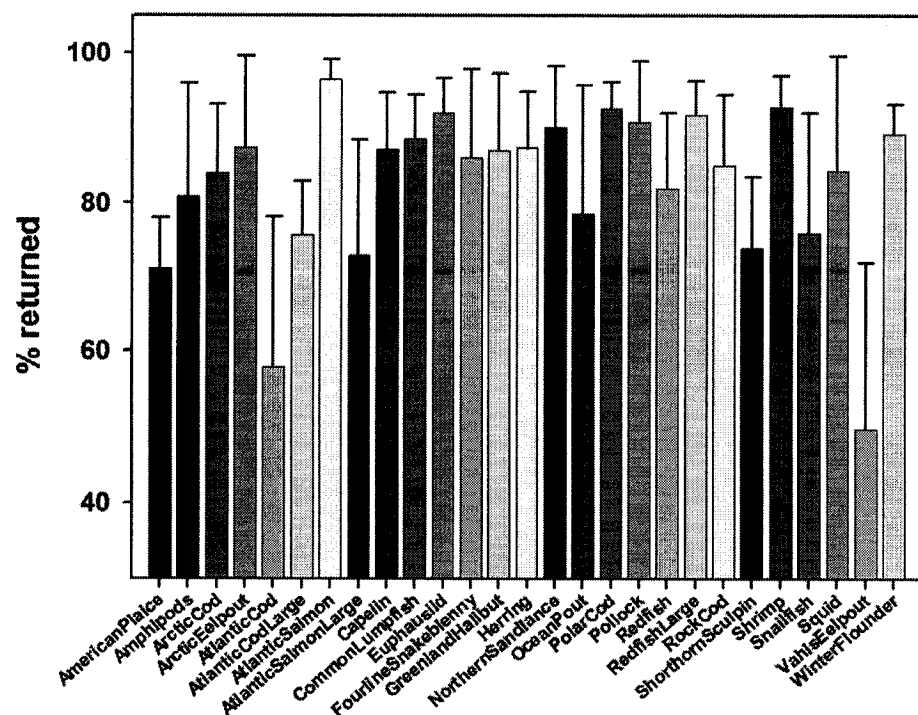
Figure A.7: Proportion of individual prey species identified as the original species in prey-on-prey modeling in harp seal prey library.

HOODED SEAL PREY LIBRARY

### Prey library selection and FA sets

A prey library was similarly compiled for hooded seals. I evaluated the effects of main model parameters (FA subset, CC's, prey library) by estimating diets for all seals (n=153). Given the greater uncertainty in hooded seal diet composition, a far larger secondary prey library (n=50 prey categories) was evaluated. Mean diet estimates are presented in Figure A.8 using the extended dietary FA set and the average of the harp-grey-pup CCs (results were similar for other FA and CC sets). On average, the proportions of main components are very similar (predominantly amphipods, Atlantic argentine, longfin hake, northern sand lance and redfish) between the two prey libraries. Again, the various size splits within species were evaluated by cluster analysis and their ability to be discriminated in QFASA was tested through subsequent modeling procedures. Splits were removed if poorly discriminated or the split resulted in other species being misclassified. In addition closely related species (i.e. shrimps) were evaluated in a similar manner and pooled if poorly discriminated.

Main diet components were similar for the extended dietary and dietary FA sets (Figures A.9 &A.10). However, analogous to harp seals, the extended FA set likely provides a more robust estimate of diet.
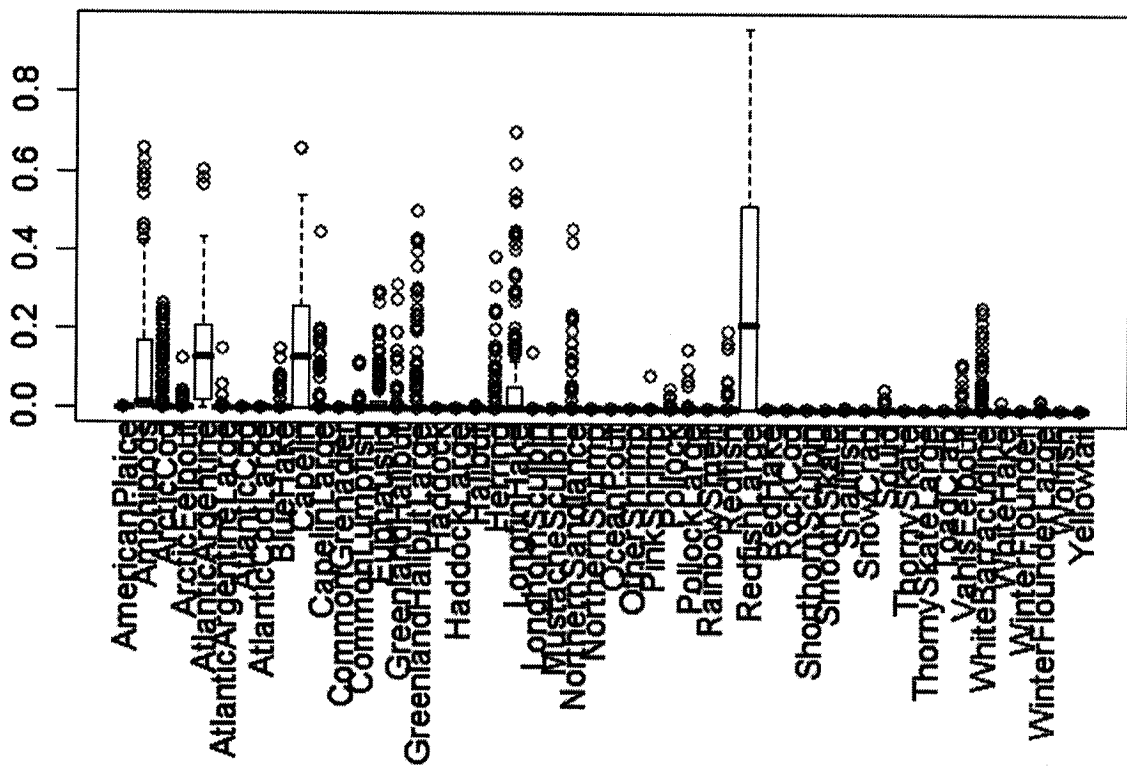
Figure A.8: Average diet estimates (n=526) using grey-harp-pup *CC*s and extended FA set for final prey library and secondary library. Dots represent outliers defined as being any value greater or less than 1.5 times the interquartile range (75th percentile–25th percentile) above the 75th (or below the 25th) percentile.
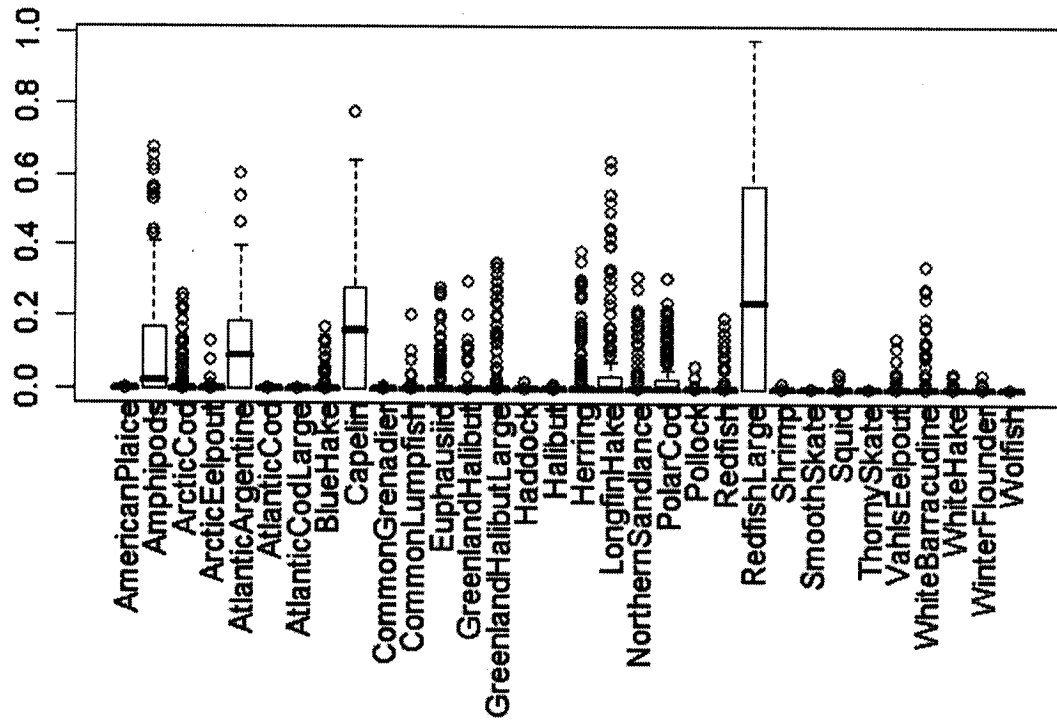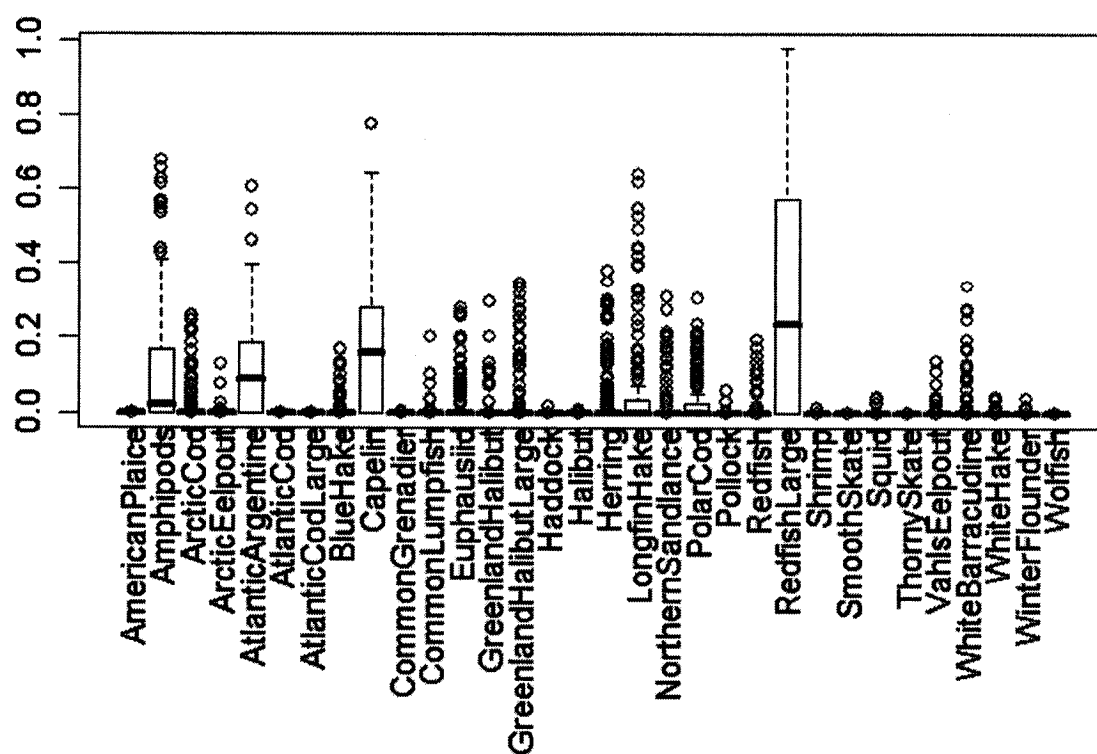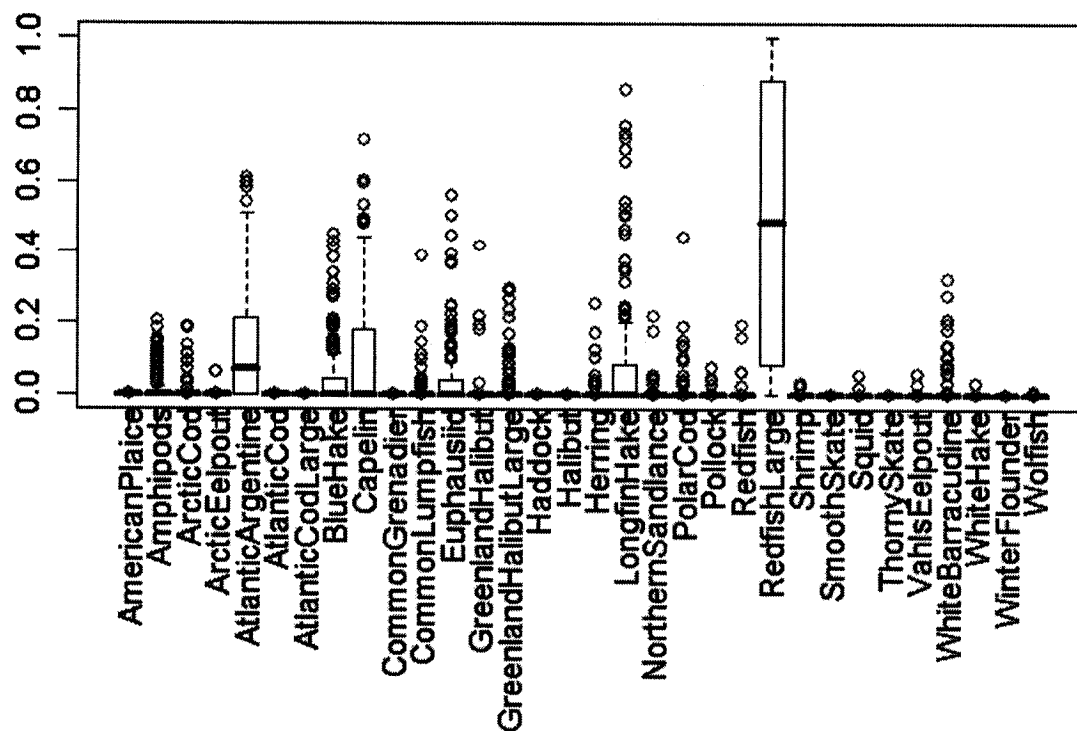
Final prey library

Secondary prey library

Figure A.9: Average diet estimates (n=153) using primary prey library, grey-harp-pup
*CC*s and extended FA set. Dots represent outliers defined as being any value greater or
less than 1.5 times the interquartile range (75th percentile–25th percentile) above the 75th
(or below the 25th) percentile.

Figure A.10: Average diet estimates (n=153) using primary prey library, grey-harp-pup *CC*s and dietary FA subset. Dots represent outliers defined as being any value greater or less than 1.5 times the interquartile range (75th percentile–25th percentile) above the 75th (or below the 25th) percentile.

Calibration Coefficients

Naturally, *CC*s effect the estimation of specific diet components yet there are no species

specific *CC*s for hooded seals. Again, main diet components were similar for the different

*CC*s; however proportions varied (Figure A.11). Therefore, I opted to average diet

estimates made with the grey-harp average CC's and grey-harp-pup average *CC*s.

Diet simulations and prey-on-prey modeling

Again, diets for simulations were constructed to reflect the diet of free-ranging hooded

seals (Table A.3). In addition, I sought to evaluate how well prey species that were more

similar to one another than to all other species in the fatty acid database. Hierarchical

cluster analysis was used to determine the relative similarity of prey species' signatures

(Figure A.12). Given the large proportion of Atlantic Argentine showing up in

preliminary diet estimates, I include them in simulations as well to evaluate how well

they were discriminated within the prey base. Again, the model estimated the true diet

rather well (Fig. 13), with the major species in the diet distinguished from others in the

prey database with between 70% and 82% of the specified diet returned. Nevertheless,

there was some misidentification (8-20%) of the diet composition to other prey types

above the added noise. In prey on prey modeling prey species were identified as

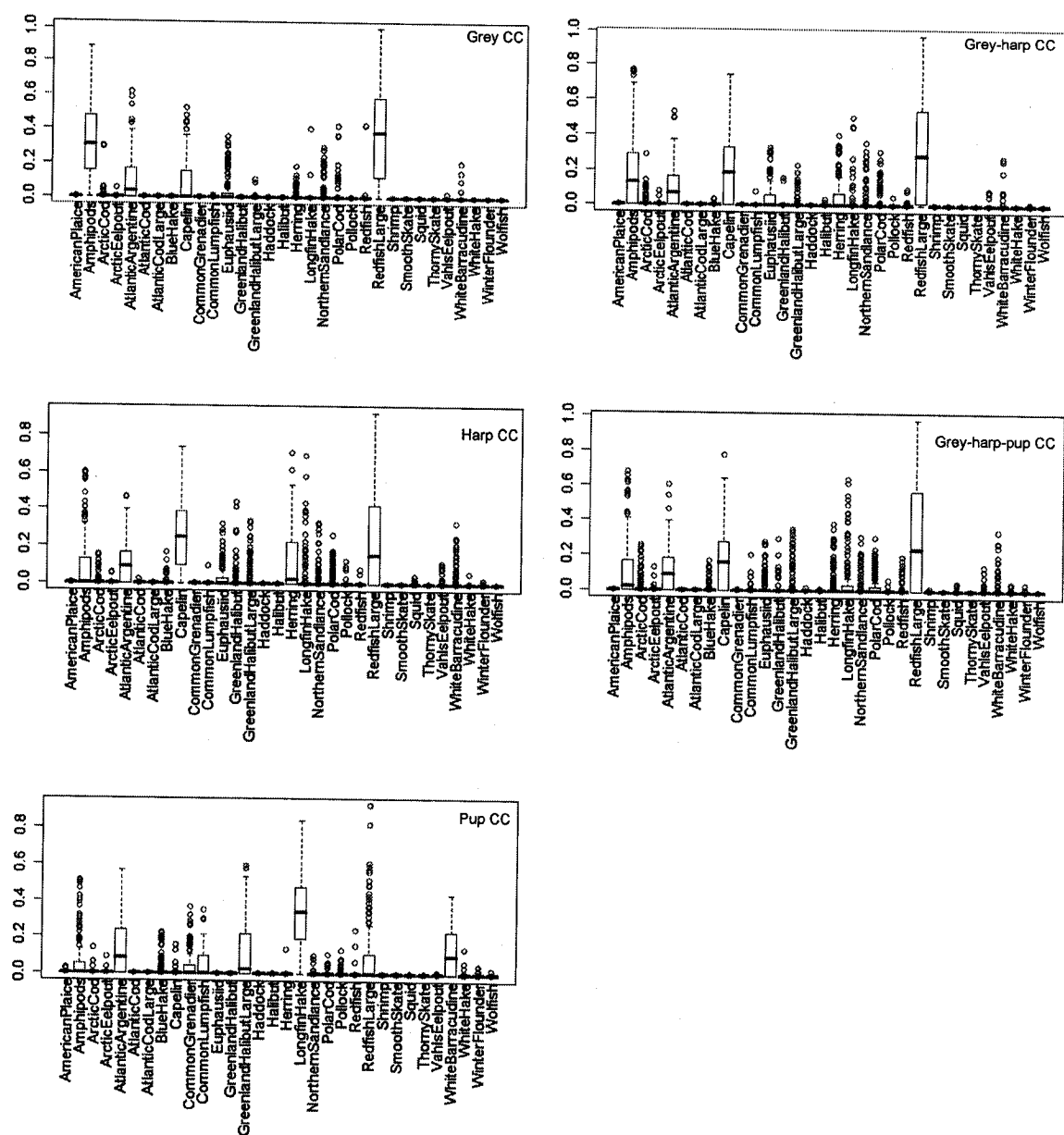themselves 83% of the time (Figure A.14).

Figure A.11: Mean diet estimates (n=153) using grey, harp, pup *CC*s or combinations of those. Dots represent outliers defined as being any value greater or less than 1.5 times the interquartile range (75th percentile–25th percentile) above the 75th (or below the 25th) percentile.
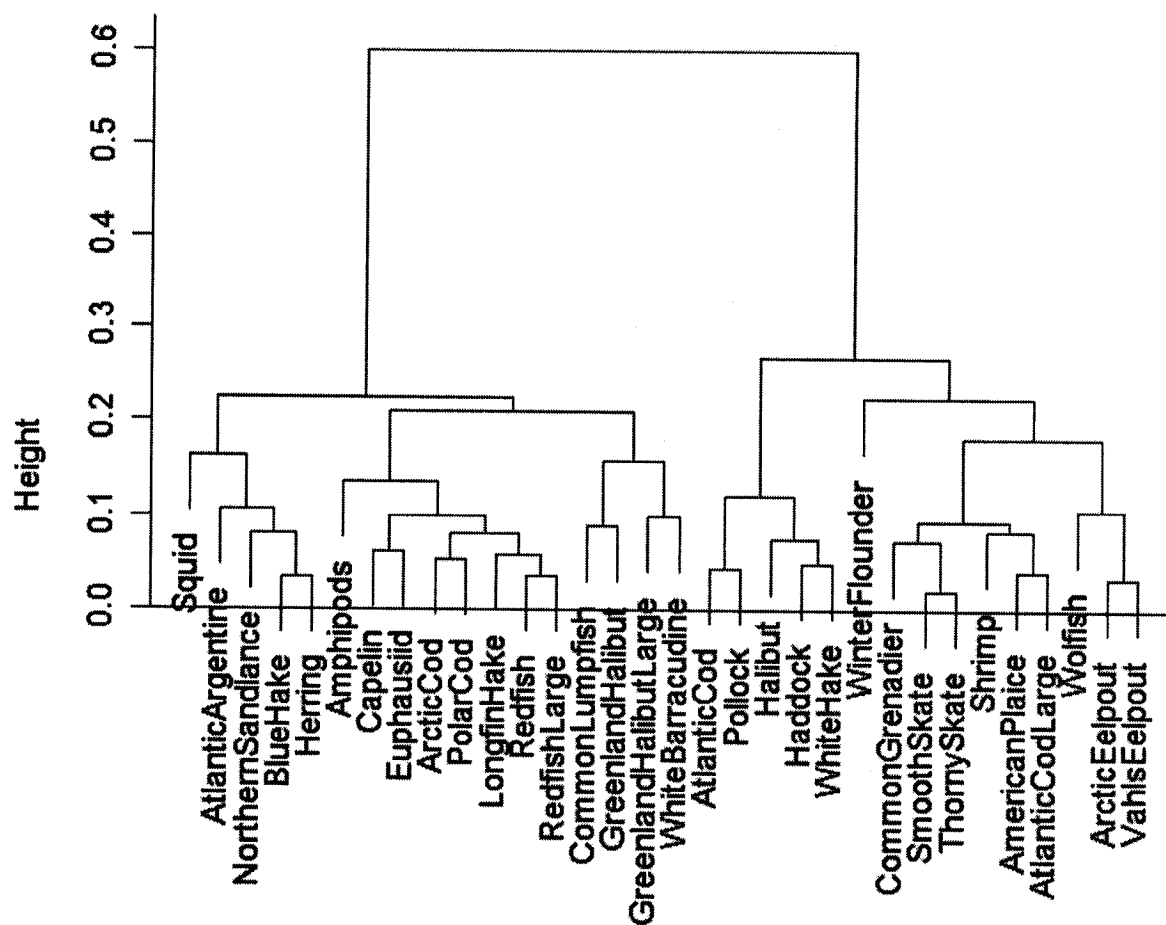
Figure A.12: Hierarchical cluster analysis on the mean fatty acid signatures (extended dietary subset) of 32 prey categories (*n*=2289) for hooded seal prey library. The Kulback-Liebler (KL) distance measure was used to determine how similar any two taxa were with respect to their fatty acid signatures. The average linkage method was used.

Table A.3: Mean estimated diets of pseudo-seals over the 1000 simulation runs for each of the five diets with noise set at 10%.

| diet	species	Specified diet	Estimate	1 SD
1	Amphipods	0.18	0.16	0.047
	Atlantic Argentine	0.18	0.17	0.039
	Capelin	0.18	0.12	0.068
	Longfin Hake	0.09	0.08	0.076
	Redfish Large	0.27	0.28	0.107
2	Arctic Cod	0.225	0.143	0.073
	Atlantic Argentine	0.225	0.218	0.05
	Blue Hake	0.135	0.068	0.051
	Euphausiid	0.135	0.119	0.076
	White Barracudine	0.18	0.145	0.057
3	Atlantic Argentine	0.225	0.226	0.041
	Capelin	0.225	0.191	0.06
	Herring	0.225	0.211	0.062
	Redfish Large	0.225	0.194	0.066
4	Amphipods	0.18	0.167	0.069
	Greenland Halibut Large	0.225	0.143	0.059
	Longfin Hake	0.27	0.249	0.109
	Redfish Large	0.225	0.224	0.105
5	Atlantic Argentine	0.225	0.217	0.042
	Capelin	0.225	0.179	0.072
	Northern Sand lance	0.225	0.22	0.067
	Winter Flounder	0.225	0.208	0.041

Figure A.13: Results of the simulation study for Diets 1-4 as defined in Table 1 with 10% error (noise) added, using the 32 prey categories (n =2289), the extended dietary FA subset. In plots, "a" denotes the value specified for each of the prey species delineated in the diet. The simulation was run 1000 times, and estimated diet results are represented in box plots, as the median (middle horizontal bar), the 25th percentile (lower bar), and the 75th percentile (top bar) of the data distribution. Dots represent outliers defined as being any value greater or less than 1.5 times the interquartile range (75th percentile–25th percentile) above the 75th (or below the 25th) percentile.
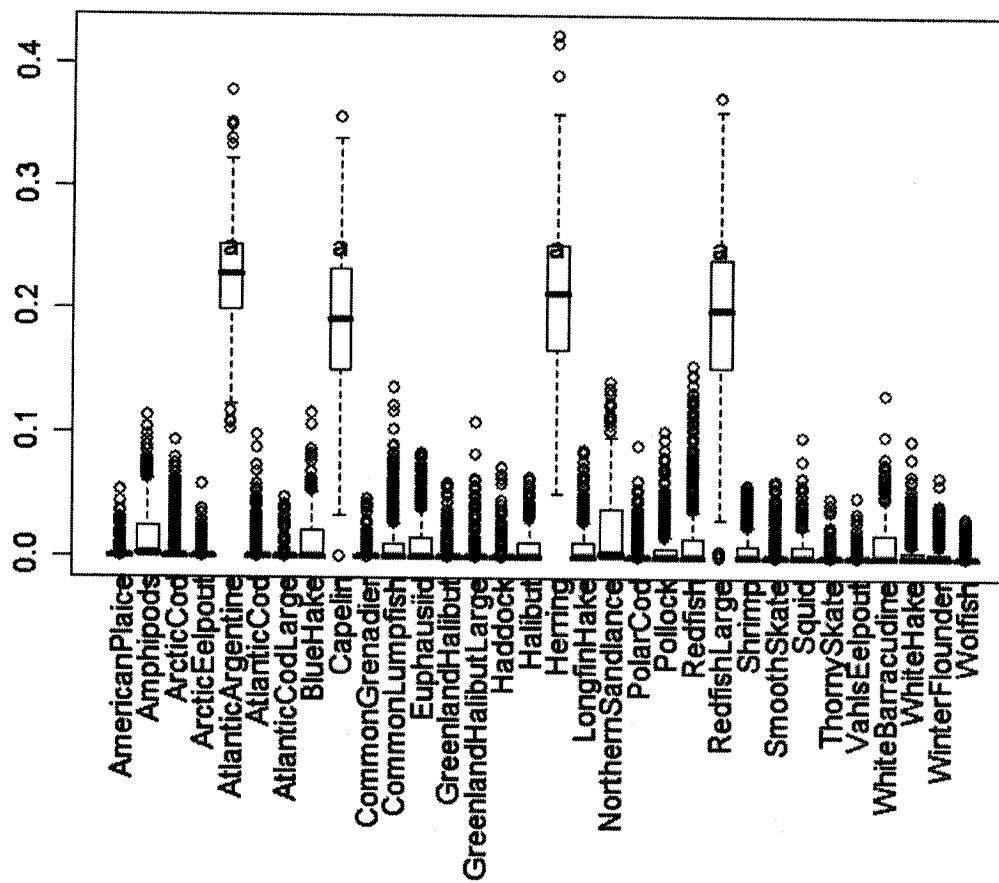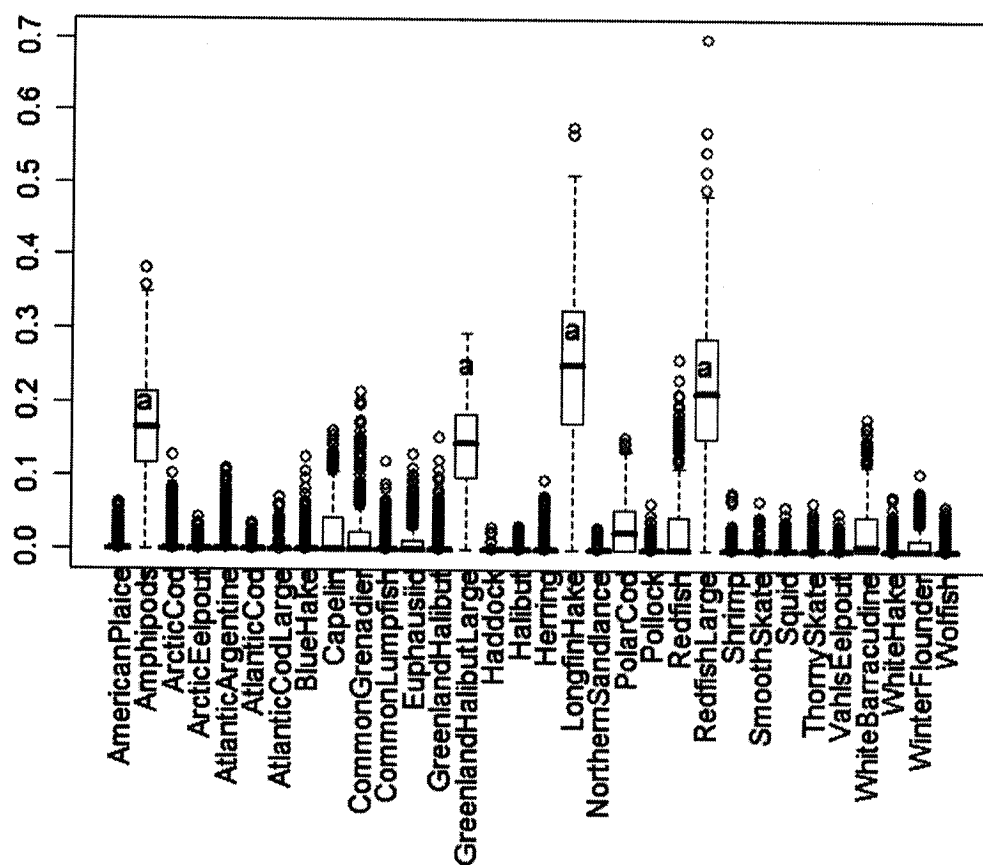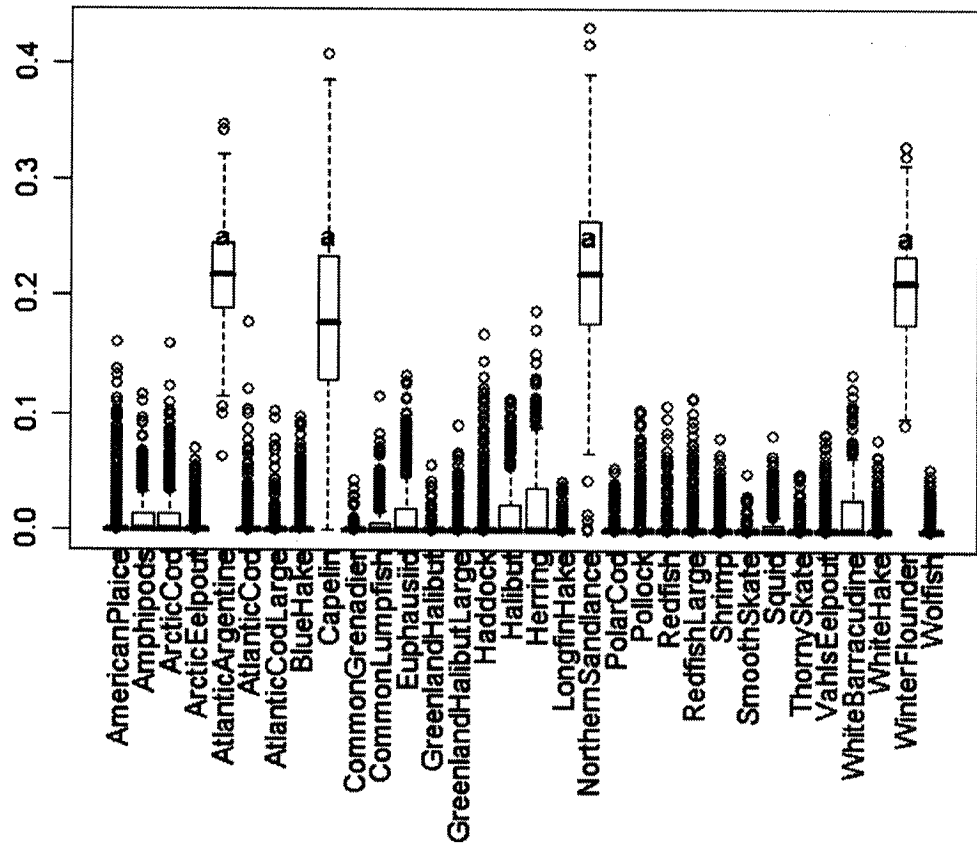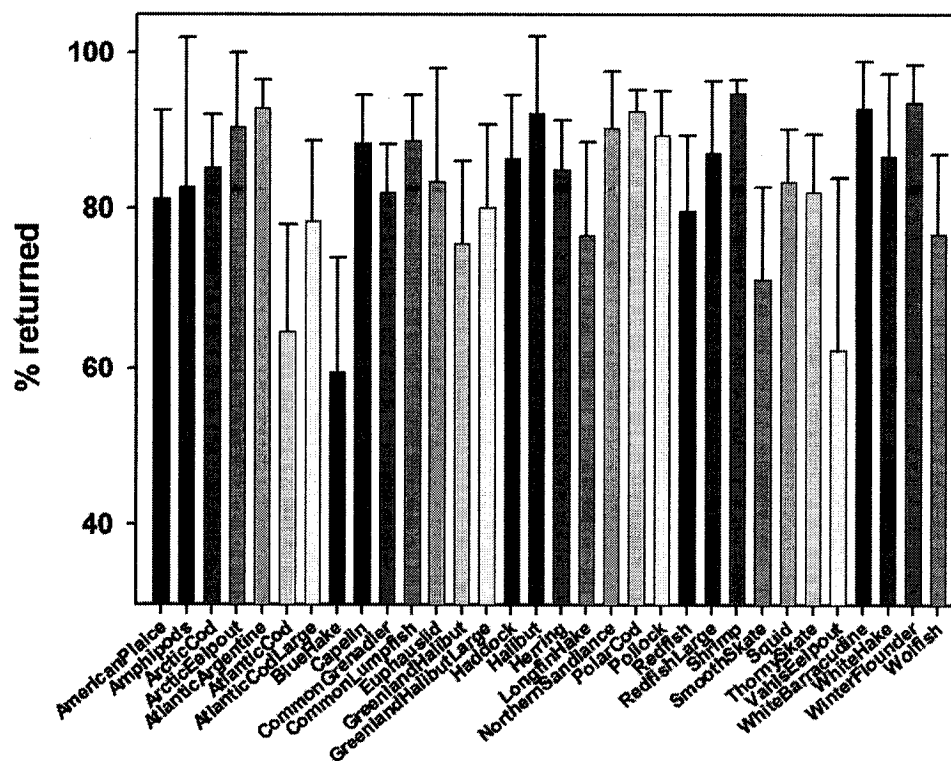
Diet 1
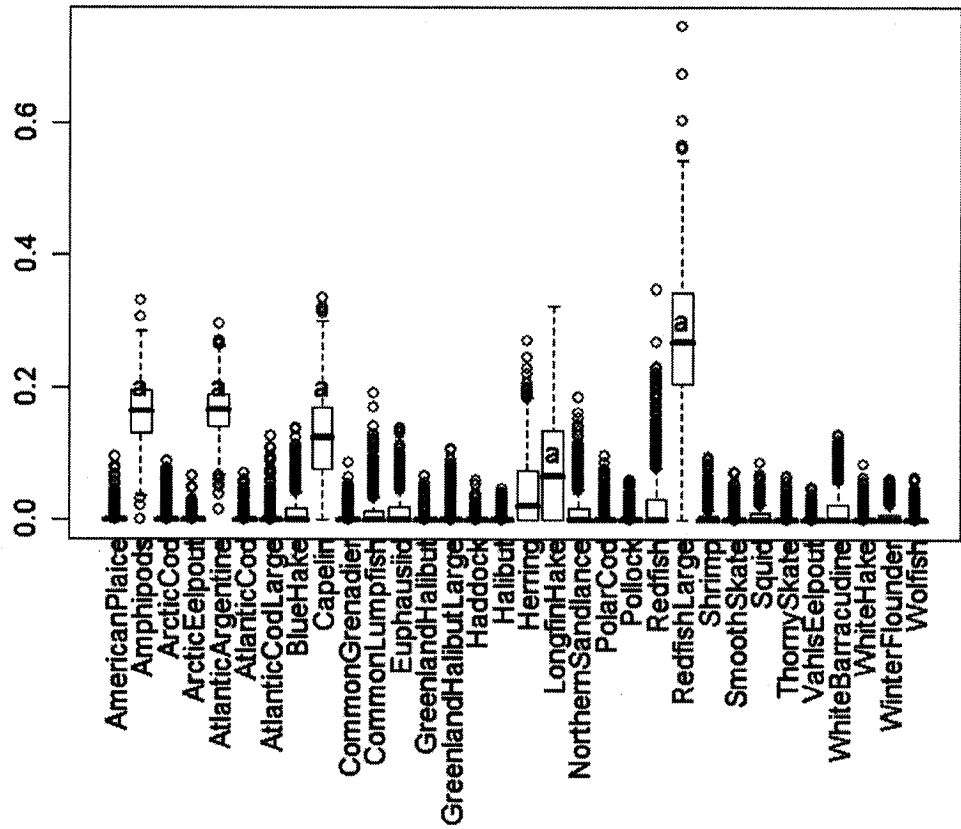
Diet 2
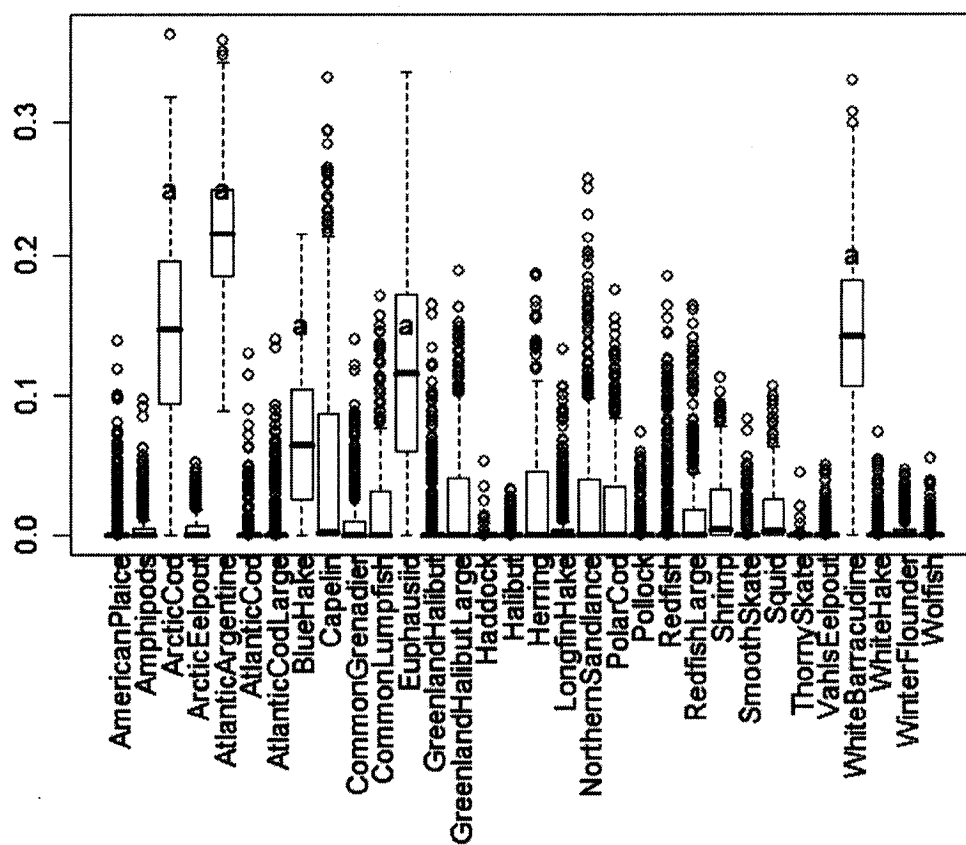
Diet 3

Diet 4

Diet 5

Figure A.14: Proportion of individual prey species identified as the original species in prey-on-prey modeling in hooded seal prey library.

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