THE DIET AND FORAGING ECOLOGY OF GRAY SEALS (*HALICHOERUS GRYPUS*) IN UNITED STATES WATERS

by

KRISTEN AMPELA

A dissertation submitted to the Graduate Faculty in Biology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York

2009

This manuscript has been read and accepted for the
Graduate Faculty in Biology in satisfaction of the
dissertation requirement for the degree of Doctor of Philosophy.

Dr. Richard R. Veit

Date

Chair of Examining Committee

Dr. Laurel A. Eckhardt

Date

Executive Officer

Dr. Gordon T. Waring

Dr. Joseph W. Rachlin

Dr. William G. Wallace

Dr. Gregory P. Cheplick

Supervisory Committee

THE CITY UNIVERSITY OF NEW YORK

Abstract

THE DIET AND FORAGING ECOLOGY OF GRAY SEALS (*HALICHOERUS GRYPUS*) IN UNITED STATES WATERS

by

Kristen Ampela

Advisor: Dr. Richard R. Veit

Once extinct in U.S. waters, there are now more than 7,000 gray seals (*Halichoerus grypus*) that breed and forage in the waters of Maine and Massachusetts. This is the first long-term study of the diet and foraging behavior of this species in its U.S. range. I used hard parts in 305 seal scats and 49 stomachs, and fatty acid profiles in 45 seal blubber cores, to 1) reconstruct the diet of gray seals in U.S. waters, and 2) investigate regional, temporal, and intraspecific variation in the diet. I compared species in the diet with those most abundant in the seals' range, as measured by bottom trawl surveys. I analyzed the tracks of 6 satellite-tagged seals, and asked which prey species were most abundant in areas where foraging activity occurred. I recovered a total of 3,798 otoliths, and 7,005 prey individuals from 34 prey taxa. Sand lance (*Ammodytes spp*.) dominated the diet by weight (53.3% of total) and number (66.3% of total). Sand lance, winter flounder (*Pseudopleuronectes americanus*), red/white hake (*Urophycis spp*.) and Atlantic cod (*Gadus morhua*) together made up 82% of the diet by weight. Cod comprised 6.4% of the diet by weight, although this varied seasonally. Fatty acid profiles were best able

to classify seals by age (young-of-the-year pups vs. yearlings, Wilks-Lambda = 0.27, $F_{25,19}$ = 2.07, p <0.054), suggesting that diet differences were most pronounced between these two groups. Consistent 2:1 ratios of 22:6n3 and 20:5n3 fatty acids occurred in seal blubber (10.12/5.00 = 2.02). These ratios are similar to those in smooth skate (*Malacoraja senta*, 20.87/10.02 = 2.08) and alewife (*Alosa pseudoharengus*, 15.04/7.48 = 2.01), indicating that these species were important in the diet. Seals consumed abundant species, and tracked interannual trends in sand lance abundance, but the diet could not be predicted from prey availability alone. Satellite telemetry of seals revealed area restricted search behavior and central place foraging activity in areas with high abundance of sand lance and winter flounder, and these taxa comprised over 72% of the diet estimated from scats.

ACKNOWLEDGMENTS

For suggesting this project, for his constructive criticism and hearty encouragement, and for driving the boat, my heartfelt thanks go to my advisor, Richard R. Veit.
This project would not have been possible without the guidance of Gordon T. Waring; any and all data contained here, I had access to because of him. Dr. Veit and Dr. Waring, along with Joseph W. Rachlin, William G. Wallace and Gregory P. Cheplick, provided invaluable feedback on this project. For helping this manuscript take shape, and always reminding me of what's possible, I thank Jarrod Santora.

For teaching me all about fish bones and how to take apart a seal stomach, I thank Pam Polloni, and the late James E. Craddock. He was a truly generous spirit and he will be missed. Brett Hayward, William Kramer, Jeremy King, Greg Early, Mike Williamson, Gina Shields and Betty Lentell provided access to critical data. Alex Pyron and Yuri Ivanov helped me with multivariate statistical analysis.

I am grateful to Paul Parker, Melissa Sanderson and everyone at the Cape Cod Commercial Hook Fishermen's Association for providing me with a precious connection to Chatham fishing community, as well as providing logistical support for my project. For giving me a fishermen's perspective, I thank Chip Foster, Renee Gagnee, Mike Russo and Ernie Eldridge.

Chris Van Der Wolk and Fred Bennett provided transportation to seal colonies, and tolerated smelly samples in their boat. Mike Brady, Chad Roderick and Monica Williams did the same, and provided dorm housing with a million-dollar view.

For help in picking through hundreds of seal scats, even if it was in exchange for credit, my thanks go to Charles Johndro, Despina Tsarouhis and Maged Ghoprial. Kinnea Keating and E. Thomas Brown made much of my lab work possible.

The CUNY Dissertation Fellowship Program and the PSC/CUNY Grant Program provided funding for this work. Samples were collected under NMFS Marine Mammal Research Permit # 775-1600-03.

Dr. W. Don Bowen, Dr. Sue Budge and Dr. Dom Tollit kindly shared their expertise on this project. My thanks also go to Andrea Bogomolni, Amy Ferland, Owen Nichols, Lisa Sette, Dana Belden, Dr. Bob Kennedy, Dr. Stephanie Wood, and my wonderful labmates.

For his loving support, thoughtful feedback on this manuscript, and flying 3,000 miles to be at my doctoral defense, my love and gratitude go to Anthony M. Cossio. Thanks to my father James P. Ampela for his warm support. This dissertation is dedicated to my mother, Dr. Jean E. Prendergast, who taught me that it's just as important to be a good person as it is to be a smart person, and who is a wonderful role model for both.

TABLE OF CONTENTS

List of Tables:

List of Figures

Background

Gray seals (*Halichoerus grypus*) were extirpated from U.S. waters in the 19th and early 20th centuries because of unregulated hunting and state-sponsored bounty programs (Andrews and Mott 1967, Lelli *et al.* 2009). Considered locally extinct in the U.S. prior to 1958, gray seals have been steadily recolonizing the New England coast, and today there are more than 7,000 gray seals in the waters of Maine and Massachusetts (Waring *et al.* 2007). This is the first long-term study of the diet and foraging habits of this species in their U.S. range, and the only such study since Rough (1995) described the occurrence of prey recovered in a small number of scat samples collected in Nantucket Sound.

Gray seals have been hunted for centuries, both for subsistence purposes (Bonner 1994), and because of threats to human fishing activities (Lavigne 2006). For the latter reason, a U.S. government-sponsored bounty for seals was in place in Maine and Massachusetts until the 1960's. Changing social attitudes led to the cessation of this practice, and the Marine Mammal Protection Act, which prohibits the killing or harassment of marine mammals in the U.S. was passed in 1972. Populations of gray seals (*Halichoerus grypus*) and harbor seals (*Phoca vitulina*) in New England have recovered steadily since.

Worldwide, three distinct populations of *H. grypus* exist: the northwest Atlantic, the northeast Atlantic, and the Baltic Sea populations (NAMMCO 2007). The northwest Atlantic population extends from northern Labrador to southern New England, and is centered at Sable Island, the largest gray seal colony in the world (Bowen *et al.* 2003). In 1993, 143,000 gray seals were counted at Sable Island and the Gulf of St. Lawrence (Waring *et al.* 2006). Fifty-seven per cent of the northwest Atlantic population is from Sable Island stock (Waring *et al.* 2006). Adult gray seals branded as pups on Sable Island have been seen at breeding sites in Nantucket Sound (Wood et al. 2005, pers. obs.), suggesting a dispersal of these individuals from Canadian waters to establish breeding colonies, and exploit new foraging grounds. Seals instrumented with satellite-tracked tags cross the U.S./Canadian maritime boundary in the Gulf of Maine (Breed et al. 2006). Tissue samples taken from first year pups at breeding sites in the Gulf of St. Lawrence and Nantucket Sound demonstrate the existence of gene flow between gray seals in the U.S. and Canada (Wood *et al.* 2005). Therefore, there is no unique "U.S. population" of gray seals.

Marine mammals can have a variety of effects on their environment, including 1) influencing prey populations via predation and co-evolution with prey species, 2) participation in nutrient cycling within the water column, 3) structuring marine communities, including invertebrates and vegetation, via trophic cascades, and 4) physically altering benthic habitat while foraging (Bowen 1997, Estes and Palmisano 1974). Despite the increasing numbers of gray seals in New England and elsewhere along the continental shelf of the northwest Atlantic, little or nothing is known about their diet composition, feeding habits, or foraging grounds in their U.S. range.

Growing seal numbers often cause concerns, particularly in coastal communities, about competition between seals and commercial and recreational fisheries (Baraff and

Loughlin 2000, Lavigne 2006, Read 2008). Coastal New England is no exception, and in 2007 residents in Chatham, Massachusetts lobbied elected officials to request congressional action on the issue (R. Bergstrom, Selectman, Chatham MA, pers. comm.). The concerns cited include: 1) catch damage by seals, both in commercial groundfish fisheries and in recreational fisheries, particularly for striped bass; 2) reduced catch due to suspected seal predation of economically important fish stocks; 3) introduction by seals of fish parasites and human pathogens into coastal waters, and 4) attraction of sharks to coastal waters that would not otherwise be present, endangering bathers and surfers (P. Bremser, Chatham, MA, pers. comm.).

The issue of seal-fishery interactions is complex, involving human socioeconomic issues, fisheries and marine mammal science, wildlife policy, and animal welfare issues. As a result the debate is often unfocused, and seen differently by stakeholders (Read 2008). Human perception also plays a role in the debate: seals are conspicuous predators that must come out on land to molt, rest and breed, and are therefore visible to humans. This is not true of predatory fish that target the same fish stocks, and which may exert equal or greater predation pressure on these stocks (Trites *et al.* 1997).

Seals and fisheries may interact *directly*, when seals damage gear, catch, and disrupt aquaculture; or when seals are injured or killed by fishing operations (Lavigne 1996). These are referred to as *operational* interactions. Operational interactions occur in both fixed and mobile gear commercial fisheries throughout New England (Belden *et* *al.* 2006, Read 2008), as well as in recreational fisheries (Capt. Michael Eichenseer, Chatham, MA., pers. comm.).

Seals and fisheries may also interact *indirectly*, when seals predate on economically important fish stocks, or when fisheries deplete fish seals rely on for food (DeMaster *et al.* 2001, Read 2008). These are known as *ecological* interactions. Ecological interactions between gray seals and fisheries are difficult to quantify (Yodzis 2001). It is a common perception among fishers that seal predation reduces the number of fish available for them to catch, although this conclusion is based on indirect evidence, including gear interactions, reduced catch, and increasing numbers of seals at local haul out sites. The quantification of ecological interactions requires knowledge of 1) the marine food web involving seals, 2) seal population size, and 3) the age structure of the seal population, in order to infer seals' energy requirements (Lavigne 1996, Navarrete *et al.* 2000, Yodzis 2001). Presently, none of this information is known for gray seals in U.S. waters (Waring *et al.* 2007).

The goals of this work are to 1) estimate the diet of gray seals in their U.S. range, and 2) relate gray seal diet, foraging behavior and habitat use to the distribution and abundance of their prey. Estimation of gray seal diet does not provide quantitative information about the impacts of seal predation on fish stocks. But knowing what, where, when and how gray seals eat is the first step towards understanding their role in marine food webs (Bowen 1997). This information is critical for understanding seal-fishery interactions, and the foraging ecology of this increasingly important marine predator.

Chapter 1. Gray seal diet in United States waters, estimated from hard prey remains in scat and stomach samples

Introduction

Prey remains that resist digestion, such as fish otoliths, bones, and cephalopod beaks, are found in the digestive tracts and scats (feces) of marine mammals (Lance *et al.* 2001a). Sagittal otoliths (ear stones) and cranial bones of fish, as well as cephalopod beaks, often allow identification of these prey to genus and species (Arim and Naya 2003). Otolith size is proportional to the length and weight of a fish, and the rostrum length of a squid beak is proportional to mantle length and mass (Clarke 1986, Staudinger *et al.* 2009). Hard remains recovered in scats and stomach contents of seals therefore provide critical information about the size, weight and type of prey consumed, and the relative proportion of different prey types in the diet.

Scat and stomach content analysis each have advantages and disadvantages, and provide complementary information about seal diets. Scat analysis does not require seals to be sacrificed, is relatively cheap, and allows for large sample sizes, since large numbers of scats may be collected at seal haul out (resting) sites. Material in scats, however, is subject to considerable erosion by gastric juices, and scat analysis using traditional methods does not provide information about the sex or age of the animal. The examination of seal stomach and intestinal contents typically does require the animal to be sacrificed (Labansen *et al.* 2007). In the United States, where marine mammals are protected by law, stomachs are obtained from specimens that have been incidentally killed during fishing operations (Williams 1999). Northeast Fisheries

Observer Program (NEOP) trained observers are deployed on randomly selected fishing vessels to collect fishery data and monitor bycatch of protected species (Bisack 2003). These observers retain the stomachs of bycaught pinnipeds and cetaceans for future analysis, and in some cases retain the entire animal (Bisack 2003). Prey remains recovered in stomachs are subject to somewhat less erosion than those in scats, since they have not yet passed through the intestinal tract. Stomach contents do provide information on sex and age of the seal, since marine mammal carcasses are sexed when biological samples are taken (G. Shield, NOAA Observer Program, NMFS/NEFSC, Woods Hole, MA, pers. comm.).

An advantage of scat and stomach analysis is that gastro-intestinal parasites can be recovered, counted, and identified. Gray seals, along with several species of groundfish, are intermediate hosts in the life cycle of *Pseudoterranova decipiens*, an endoparasitic roundworm. The presence of its larvae in a fish, such as cod, destroys its market value (McClelland *et al.* 2000). The Anisakidae family of roundworms includes the species *Pseudoterranova decipiens*, alternatively called codworm, or sealworm (McClelland 2002, McClelland *et al.* 2000).

The aims of this study are to 1) identify prey taxa of gray seals and their relative importance in the diet; 2) identify spatial and temporal patterns in prey consumption; 3) investigate sex and age differences in prey consumption; 4) compare diet diversity among years, seasons, locations and individuals of different sexes and ages; 5) distinguish between primary and secondary seal prey; 6) identify fish and invertebrate taxa targeted by both seals and fisheries; 7) estimate prey length for economically important fish, and the extent of size overlap between seal prey and fish targeted by humans, and 8) quantify and investigate patterns in gray seal parasite load.

Methods

Study Area

The study region encompassed continental shelf waters from New England to the mid-Atlantic Bight, and two major gray seal haul-out sites in Nantucket Sound (Fig. 1). The former corresponds to the spatial distribution of stomach samples collected by NEOP observers. I collected all scat samples at Muskeget and Momomoy Islands, in Nantucket Sound, where gray seals have a year-round presence. Muskeget, located between Nantucket Island and Martha's Vineyard and is the largest gray seal breeding colony in the U.S. (Bisack 2003, Wood *et al.* 2005). Monomoy Island is 30 km northeast of Muskeget, and adjacent to Chatham, Massachusetts (Fig. 1), and is considered a minor breeding colony. Both islands are surrounded by areas of shallow, sandy bottom and swift currents, and have continually changing shorelines (Rough 1995).

I chose these sites because 1) they have large year-round aggregations of gray seals, and 2) seal species composition at these sites is 90-100% *Halichoerus grypus*, making it likely that scats collected were from this species (Pierce *et al.* 1991). I avoided sites with a mixture of *H. grypus* and *P. vitulina,* such as Jeremy Point on the eastern shores of Cape Cod Bay.

Field Methods

Seal scats and stomachs contain prey consumed within the last ~48 hours (Grellier and Hammond 2006, Tollit *et al.* 2003), and therefore provide a “snapshot” of recently eaten prey. Therefore, I collected as many samples as possible across seasons and years in order to investigate temporal variation in diet, and identify prey species that seals consistently target. I collected scat samples from gray seal haul out sites at least once per season, from 2004-2008. A scat sample was defined as one cluster of fecal material, separated spatially from other such clusters. I conducted sampling trips on an opportunistic basis, dependent on weather conditions and tidal cycles. I collected scats from sandy intertidal areas using a plastic kitty-litter scooper, and immediately placed in sealed one-gallon Ziploc™ freezer bags. I collected only those from the intertidal zone because they were deposited within the last 12 hours, and therefore provided prey information from a known time period. I stored samples at -20° C until processing.

Seal stomach samples came from seals bycaught in gillnet and otter trawl fishing gear operating in the Gulf of Maine, southern New England, and mid-Atlantic Bight waters, within the U.S. EEZ Figure 1.1). NEOP observers are deployed on fishing vessels collected stomachs from seals taken in gear. In some cases observers retained the entire animal, in which case stomachs were removed during subsequent necropsy procedures in Woods Hole, MA. I inferred the age of seals from the recorded straight length of the animal, measured from nose to tail (Table 1.1) (Murie and Lavigne 1992). Stomachs were tied off at the esophageal and pyloric sphincters to secure the contents, placed in sealed plastic bags, and stored at –20^{o} C at the National Maine Fisheries Service Laboratory in Woods Hole, MA, until processing. In two cases portions of the large intestine were also retained, and were included in the analysis. All scats and stomachs were frozen for a minimum of 2 weeks before analysis in order to kill pathogens and parasitic nematodes.

Laboratory Methods

I washed scat and stomach contents with hot water and soap in graduated sieves of 2.0 mm, 1.0 mm and 0.5 mm mesh size, respectively, and examined for fish sagittal otoliths, eye lenses, vertebrae, cranial and jaw bones, crustacean carapaces, denticles from cartilaginous fish, cephalopod pens and beaks. I stored cephalopod remains, crustaceans and parasites in 70% ethyl alcohol to prevent desiccation, and dried and stored all other elements in airtight containers. I identified prey remains to the lowest practicable taxon. I estimated body length and biomass of teleost fish from measurement of recovered sagittal otoliths, and squid biomass and mantle length from measurement of the lower beak rostrum (Clarke 1986, Murie and Lavigne 1992, Staudinger *et al.* 2009). I measured otoliths and cephalopod beaks to the nearest 0.1 mm using a stage micrometer and/or digital calipers.

In order to identify recovered prey structures, I consulted published photographic atlases and keys (Brodeur 1979, Campana 2004, Härkönen 1986, Watt *et al.* 1997), as well as a reference collection of teleost fish and cephalopod remains in the laboratory of Dr. James Craddock, at the Woods Hole Oceanographic Institution. I also created a small personal reference collection of key prey taxa by purchasing representative individuals at local fish markets, and extracting skeletal elements from these undigested specimens. I placed specimens in a microwave oven, heated them at high temperatures, and rinsed off loosened tissue with pressurized water. In some cases, when structures did not permit identification of prey below genus, I was able to infer species according to known distribution in the study area.

Scat analysis is a common technique for reconstructing pinniped diets (Grellier and Hammond 2006) but is subject to a variety of biases (Arim and Naya 2003, Bowen 2000, Jobling and Breiby 1986, Staniland 2002, Tollit *et al.* 2003). Fish otoliths, jaw bones, and squid beaks are subject to erosion as they pass through the digestive tract, and many are eroded to the point that they are misidentified or unrecognizable (Arim and Naya 2003). Some may in fact be digested completely, leaving no material to be analyzed (Bowen 2000). Certain species, and larger individuals within species, have higher probabilities of otolith recovery (Browne *et al.* 2002). For example, species with more robust otoliths, such as gadids (e.g. cod, hake and haddock) tend to be overestimated. Species with smaller, more fragile otoliths, such as clupeids and salmonids, have lower recovery rates and are often underestimated (Browne *et al.* 2002).

To minimize these biases, I applied correction factors to recovered hard parts, which accounted for differential recovery of prey types and for otolith erosion. I identified prey using multiple recovered structures (Table 1.2), which improves estimates of diet composition over otolith use alone (Browne *et al.* 2002). I applied digestion coefficients (DCs) to eroded otoliths in order to infer the original length of a pristine otolith (Table 1.3). Length and mass of the fish was then inferred from this new measurement. Digestion coefficients are derived in captive feeding experiments by feeding prey of known size to seals, and measuring the amount of erosion in recovered otoliths (Grellier and Hammond, 2005). Bowen (2000) found that hard parts from certain prey are often completely digested, causing overestimates of some prey taxa and underestimates of others. To account for differential erosion of prey remains, I applied taxon-specific numerical correction factors (NCFs) to all prey taxa for which they were available (Table 1.3). NCFs, like digestion coefficients, are derived empirically by feeding captive seals a known diet, and subsequently examining scat contents. For example, if on average three Atlantic herring (*Clupea harengus*) are fed, and one is recovered, NCF = 3 (Bowen 2000, Grellier and Hammond 2005, Lundstrom *et al.* 2007). I applied NCFs to the total number of prey individuals recovered for each taxon. For example, if 20 herring individuals total were recovered, and the NCF for herring = 3, the corrected number of herring individuals recovered in the study was 60. Biomass of individuals not recovered, but inferred by NCF calculations, was based on average length and weight of individuals from that prey taxon recovered in specific seasons and years. If an average was not available for a particular season, an average for that season in another year was used (Bowen and Harrison 1996). I applied NCFs to remains in scats, but not stomachs, since these factors are generated empirically from scat studies only (Bowen 2000). I did apply digestion coefficients to remains in both scats and stomachs, since both showed some amount of erosion (Labansen *et al.* 2007, Tollit *et al.* 2004).

In order in infer the number of prey individuals consumed, I counted and paired bilaterally symmetrical (one right and one left) elements, such as otoliths and jaw bones. These were considered in combination with other numerically informative elements to infer the minimum number of individuals (MNI) consumed for each taxon. For example, if 5 left and 3 right cod otoliths are present in a sample, cod MNI=5. Likewise, if 7 squid eye lenses, 3 upper beaks and two lower beaks are recovered, squid MNI=4. Eye lenses of teleost fish and cephalopods are easily distinguishable, and each individual has two lenses. If left and right otoliths could not be distinguished, I pooled them and divided by 2 to infer the number of individuals. For certain samples, I inferred prey MNI entirely from hard parts other than otoliths; for example, preopercular bones or atlas vertebrae in sand lance (*Ammodytes spp*.). I did not apply numerical correction factors to these samples. I only applied these to MNI calculations inferred from otoliths found in scats, since these correction factors are based solely on otolith recovery rates in scats (Bowen 2000, Grellier and Hammond 2006, Tollit *et al.* 2004).

I applied morphometric regression equations to corrected otolith and beak length measurement to estimate prey biomass (Table 1.4). Whenever possible, I used equations that were generated for prey from New England and/or New York Bight waters, since body length-weight relationships vary regionally (Wigley *et al.* 2003). When these were not available, I used equations generated in the Northwest Atlantic. If neither of these were available, I used equations for fish in the Northeast Atlantic or

Pacific. Length-weight relationships also vary seasonally; therefore, I applied season-specific equation whenever possible (Wigley *et al.* 2003). When otolith digestion coefficients were not available for a given prey taxon, I used equations for prey with a similar otolith size and topology (W.D. Bowen, Bedford Institute of Oceanography, NS, Canada, pers. comm.). Likewise, if length-weight regression equations were not available for a certain prey taxon, I used equations for closely related taxa. I coded otoliths from 0 through 4 for degree of erosion (Table 1.5). I only used otoliths coded 0-2 to estimate prey biomass (Bowen and Harrison 1996). I included otoliths with a code of 3 to count prey individuals, but biomass for these individuals was estimated using an average weight for that prey taxon within that season and year (Bowen and Harrison 1996). If an average was not available for a particular season, I used an average for that season in another year (Bowen and Harrison 1996).

Since skates do not have identifiable otoliths, I could not infer length and weight inferred from hard parts. All skates were assumed to be 20.34 cm long, which was the average length of all flatfish individuals recovered. Skates have a body shape closer to that of flatfish than roundfish. Skate body mass was calculated using length-weight relationships for thorny skate *(Amblyraja radiata)*, since many skin denticles recovered in this study roughly resembled those of thorny skate (Gravendeel *et al.* 2002), and this species is one of the most abundant skates found in the study area (Bigelow and Schroeder 2002).

Statistical Methods and Data Analysis

I calculated three diet indices for recovered prey: frequency of occurrence (FO), relative abundance of prey individuals (RA), and biomass of ingested prey (Lance *et al.* 2001a). Each index was then expressed as a percentage of the total, in order to compare taxa across multiple indices. Frequency of occurrence (FO) (Lance *et al.* 2001a) was calculated as:

$$FO_i = \frac{\sum_{k=1}^{s} \emptyset_{ik}}{s}$$

Where: $\emptyset_i$ = 0 if taxon *i* is absent in sample *k;* 1 if taxon *i* is present in sample *k*
s = total number of samples that contained prey

Percent FO (Lance *et al.* 2001b) was calculated as:

$$\%FO_i = \frac{100\ FO_i}{\sum_{i=1}^{n} FO_i}$$

Where: *n* = total number of prey taxa recovered in all samples

FO indicates the presence or absence of prey in a sample, but does not provide information about prey number or size. FO does provide information about species that can only be diagnosed by elements that are not informative of prey number, such as dermal denticles (thorns) from skates.

Minimum number of individuals (MNI) for each prey taxon was estimated using the methods outlined above. The total number of prey individuals recovered from a given taxon, in relation to the number of individuals from another taxon, is referred to as the relative abundance (RA) of that taxon (Lance *et al.* 2001a). This index was calculated as:

$$RA_i = \frac{\sum_{k=1}^{s} n_{ik}}{\sum_{k=1}^{s} n_k}$$

Where: n_{ik} = (minimum) number of individuals of taxon *i* in sample *k*
n_k = (minimum) number of individuals of all taxa in sample *k*
s = total number of samples that contained prey

Percent RA (Lance *et al.* 2001b) was calculated as:

$$\%RA_i = \frac{100\ RA_i}{\sum_{i=1}^{n} RA_i}$$

Where: *n* = total number of prey taxa recovered in all samples

Ingested biomass was calculated for individual prey items, for all prey items ingested per sample, and for each prey taxon across all samples. Reconstructed biomass proportion (π) (Lance *et al.* 2001a) was calculated as follows:

$$\pi_i = \frac{\sum_{k=1}^{s} b_{ik}}{\sum_{k=1}^{s} b_k}$$

Where: b_{ik} = biomass of prey taxon *i* in sample *k*
b_k = biomass of all prey taxa in sample *k*
s = total number of samples that contained prey

Percent biomass (Lance *et al.* 2001b) was calculated as:

$$\%\pi_i = \frac{100\ \pi_i}{\sum_{i=1}^{n} \pi_i}$$

Where: n = total number of prey taxa recovered in all samples

A prey taxon was considered "important" if it comprised ≥ 5.0 % of the diet by any of the above indices. Biomass was estimated for prey individuals if the taxon to which they belonged comprised ≥ 1.0% of the diet by frequency and/or relative abundance. I calculated all diet indices using the total number of samples that contained prey, and excluded samples that were empty (Casaux *et al.* 2003).

Prey diversity in the diet was estimated using a modified Shannon-Weiner index (Beck *et al.* 2007a):

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

Where:
H'= standardized measure of diversity
p_j = proportion of prey species j in the diet
S = total number of prey taxa consumed by all individuals

Spatial variation in diet was investigated between two scat collection sites, as well as among stomachs from seals caught in different areas of the study region. The latter was analyzed within the framework of fishery statistical areas defined by the Northwest Atlantic Fisheries organization (NAFO, Figure 1.1, Table 1.6). Statistical fishing areas in the NW Atlantic were first developed in the 1930's, in order to provide organized sampling units for the collection of fishery data (Halliday and Pinhorn 1990). These units were based on stock distribution areas of commercially important species, and were "designed to correspond with the natural divisions of fish populations and barriers to migrations" (Halliday and Pinhorn 1990). NAFO areas therefore provide a spatial structure relevant to 1) the distribution and abundance of various gray seal prey taxa, and 2) the commercial fishing effort, catch and landings associated with these taxa, and 3) distribution of gray seals at sea, which can travel 0.9 m s^{-1}, or 78 km day^{-1} (McConnell *et al.* 1992).

Stomach samples were collected from 1998-2008, and scats were collected from 2004-2008 (Tables 1.7 and 1.8), allowing investigation of seasonal and annual variation in diet. I defined seasons as follows: *winter* = December 21-March 20; *spring* = March 21-June 20; *summer* = June 21-September 20; *fall* = September 21-December 20.

I performed all statistical analyses on prey abundance (number of individuals), because this index estimates diet better than frequency of occurrence (Reid *et al.* 2006, Tollit *et al.* 2007). I used General Linear Model analysis of variance (ANOVAs and MANOVAs) to investigate temporal, spatial, and intraspecific variation in diet composition, diet diversity, and parasite load. I employed Bonferroni pairwise comparisons post-hoc, at a significance level of 0.05, to determine which groups were different. Data were normalized using log +1 transformation (Lea *et al.* 2002). I used nonparametric ANOVAs to test for differences in diet diversity, since H' indices were not normally distributed. Each scat was assumed to represent an individual seal, and samples were considered independent of one another.

Secondary prey

For the most part, I distinguished secondary prey (items consumed by the primary prey of the seal and therefore recovered in scats) from primary prey by size. I considered fragments of bivalve shells and crustacean carapaces measuring < 1.0 cm to be secondary prey, since I assumed that gray seals would not profit energetically by targeting such small prey items. Except for very large fish, gray seals swallow prey whole (Bonner 1994), so I considered it unlikely that bivalve fragmentation occurred during the digestion process. I considered all copepods and amphipods to be secondary prey.

Sand lance are small (< 30 cm) fish that are common prey of gray seals in other parts of the world (Geddes and Frank 1996, Hammond *et al.* 1994). Sand lance are preyed upon by fish that also appear in seal diets: cod, silver hake (*Merluccius bilinearis*), white hake (*Urophycis tenuis*), sculpin (*Myoxocephalus octodecemspinosus*) and yellowtail flounder (*Limanda ferruginea*) (Auster and Stewart 1986). I investigated the possibility that sand lance individuals recovered in scats are not consumed directly by the seal, but are present in the stomachs of larger fish, and are therefore secondary, rather than primary prey. If sand lance remains were present in scats not because they are primary prey, but because they are already in the stomachs of primary prey, I expected 1) a strong correlation between the presence of sand lance and their fish predators in seal scats; 2) a higher degree of erosion of sand lance remains than of other prey taxa, since they are subject to erosion in the stomach of the fish as well as the seal, and 3) to find sand lance remains in the stomachs of whole fish that are in turn recovered in seal stomachs. Therefore, a partial correlation matrix was constructed to investigate significant co-occurrence of prey in samples. Whenever whole fish were encountered in seal stomachs, I examined the stomachs of these fish for the presence of secondary prey. I counted and weighed all parasitic nematodes recovered in scat and stomachs, identified them to the lowest practicable taxon, and stored them in 70.0% EtOH.

Results

A total of 3,798 otoliths, and 7,005 prey individuals from 34 prey taxa, were recovered in this study. The average length of all prey items was 22.5 cm, although this varied with prey species (Figures 1.2A-H)

Diet composition

Four prey taxa could only be identified to genus. Red and white hake (*Urophycis chuss* and *Urophycis tenuis*) have otoliths that are difficult to distinguish, and were therefore pooled in this study, as were species of sand lance, sculpin and wolffish (*Anarhichas spp.*). Skates and cusk-eels were only identifiable to family (Rajidae and Ophidiidae, respectively). Reference specimens were not available for cusk eel otoliths, and skates lack identifiable otoliths. Skates that occur in the study area, and therefore those most likely to be preyed upon by gray seals, are: winter skate (*Leucoraja ocellata),* barndoor skate (*Dipturus laevis),* thorny skate, smooth skate (*Malacoraja* *senta)*, little skate (*Leucoraja erinacea),* clearnose skate (*Raja eglanteria),* and rosette skate (*Leucoraja garmani)*(Bigelow and Schroeder 2002).

Scat and stomach sampling presented a widely divergent picture of diet, and I therefore treated these two datasets separately. Gadids made up 65.8% of the prey biomass in stomachs, and only 10.3% of the biomass in scats (Figures 1.3A and B). While sand lance and skates were important prey in scats, they made up 1.1 % of the prey biomass in stomachs combined (Tables 1.9 and 1.10). American eel (*Anguilla rostrata*), silversides (*Menidia menidia*) and redfish (*Sebastes marinus*) were only recovered in stomachs; wolfish, blue mussel (*Mytilus edulis*), and lumpfish (*Cyclopterus lumpus)* were only found in scats.

Scats

I recovered 29 prey taxa in scats (Table 1.9). Nine of these were "important', comprising at least 5% of the diet by frequency, number, and/or weight: sand lance, red/white hake (*Urophycis spp.*), skates, winter flounder (*Pseudopleuronectes americanus*), windowpane flounder (*Scophthalmus aquosus*), Atlantic cod (*Gadus morhua*), cusk eel (Ophidiidae), sculpin, and longfin inshore squid (*Loligo pealeii*) (Figure 1.4). Sand lance was most abundant in the diet (4198 individuals) and contributed the most biomass (53.3% of total, Table 1.9). Red and white hake were the second most abundant taxon (530 individuals). Winter flounder was the second-most important taxon in terms of biomass (19.0% of total). Skate was the most frequently recovered taxon, in 24.5% of samples. The majority of biomass (75.0%) was contributed by three taxa: sand lance, winter flounder, and Atlantic cod. Ninety-six percent of the biomass was contributed by 8 prey taxa: sand lance, winter flounder, cod, *Urophycis*, skates, herring, squid, and windowpane flounder. The remaining 21 taxa contributed the remaining 4% of biomass (Table 1.9).

Eighty-three percent (252 of 305) of scat samples contained prey. Empty scats were no more likely to be collected in any particular month or year. Prey in scats varied significantly by year (MANOVA $F_{60, 912} = 1.54$, $p < 0.001$), season (MANOVA $F_{45, 696} = 4.15$, $p < 0.001$) and location (MANOVA $F_{15, 232} = 5.14$, $p < 0.001$). Bonferroni post-hoc tests, at a significance level of 0.05, indicated that more *Urophycis* was recovered in winter and spring than in other seasons (Figure 1.6), and more prey individuals were recovered at Muskeget than Monomoy. When location was kept constant, and only Muskeget seals were included in the analysis, this seasonal effect persisted ($F_{3, 179} = 5.63$, $p = .001$), but did not persist in Monomoy scats ($F_{3, 60} = 0.83$, $p = 0.480$).

Overall, more sand lance was recovered in scats in 2006 and 2007 than in 2004 (Figure 1.7), and more was recovered in scats at collected at Monomoy than Muskeget (Figure 1.8). When Monomoy and Muskeget scats were tested separately, an annual effect persisted at Muskeget (more in 2006 than in 2004, $F_{4, 178} = 2.62$, $p = 0.036$) but not at Monomoy ($F_{4, 59} = 1.82$, $p = 0.137$). Prey diversity was significantly higher in scats collected at Muskeget (H'=0.57 ± 0.067) than Monomoy (H'=0.30 ± 0.151) (K-W H = 5.33, $p = 0.021$).

More winter flounder was recovered in spring and summer than in fall and winter ($F_{3, 248} = 5.70$, $p < 0.001$). Winter flounder reach sexual maturity in New England and mid-Atlantic waters at 25-29 cm (Pereira *et al.* 1999), and seals consumed this size class significantly more in winter and spring ($F_{3, 97} = 21.15$, $p < 0.001$, Figure 1.9). More cusk eel was recovered in fall than in other months ($F_{3, 248} = 7.24$, $p < 0.001$), and no cusk eel individuals were recovered in summer. More skates were recovered in fall and winter than in other seasons (Figure 1.10).

Although not statistically significant ($F_{3, 248} = 2.50$, $p = 0.060$), Figure 1.11 shows a strong seasonal trend in cod consumption. Cod made up 47% of the winter diet by biomass, but only 17%, 25% and < 0.01% of the spring, fall, and summer diet respectively (Figure 1.11). Seals appeared to switch to cod from other prey taxa, such as sand lance and flatfish, in winter months.

Stomachs

Forty six of 49 stomach samples contained prey. Ninety-three percent of the prey biomass in stomachs was contributed by 7 prey taxa: *Urophycis*, silver hake, winter flounder, pollock (*Pollachus viriens*), fourspot flounder (*Paralichthys oblongus*), gulfstream flounder (*Citharichthys arctifrons*) and redfish. Sixty-five percent of the biomass was contributed by gadids: particularly red/white and silver hake. Of 25 taxa recovered in stomachs, 6 were classified as important: *Urophycis*, silver hake, winter flounder, gulfstream flounder, fourspot flounder and sand shrimp (*Crangon septemspinosa*) (Figure 1.5). Only one stomach contained *C. septemspinosa,* but contained >300 individuals. Therefore, this species was important by number, but not frequency or biomass. Juvenile seals prey on shrimp to a greater extent than adults (Bowen and Harrison 1996), and the stomach containing shrimp was from a pup <1 year old.

Red and white hake varied significantly by statistical area of capture (MANOVA $F_{56, 124} = 2.01$, $p = 0.001$). More *Urophycis* was recovered in stomachs from statistical areas 537 (southern New England) and 616 (New York Bight) ($F_{8, 28} = 6.83$, $p < 0.001$). I did not detect significant differences in stomachs samples from the Gulf of Maine vs. Southern New England. More silver hake was found in stomachs from male seals than from female seals ($F_{1, 35} = 6.33$, $p = .017$).

Ninety percent of seal stomach specimens examined in this study were from animals taken in anchored gillnets, and the remaining 10% were taken in otter-trawl gear. Of the 46 stomachs containing prey, 100% contained species that belong to the groundfish complex targeted by these fisheries. The mean prey length in stomach contents was 22.10 ± 10.43 (approximately 8 in), and the gillnet mesh diameter in the large-mesh/groundfish fishery, which yielded 90% of bycatch specimens, is between 6.5 and 10 inches, depending on the type of fish targeted.

Unsurprisingly, otoliths in scats showed a higher degree of erosion than those in stomachs (Figure 1.12). However, even after accounting for erosion, reconstructed prey length was longer in stomachs than in scats ($F_{1, 2394} = 44.28$, $p <0.001$). Stomachs contained a higher number of prey taxa per sample than did scats ($F_{1,352} = 8.86$, p =

0.003), and although mean diet diversity was higher in stomach samples than in scats, this difference was not significant. Most (47 of 49 stomachs) in this study were from juveniles < 6 years old (Table 1.1), whereas scats were from a mixture of adults and juveniles. Therefore, stomach samples largely reflected the diet of young seals, whereas scats reflected the diet of all age classes.

Secondary prey

Sand lance was correlated with the presence of silver hake in scats ($r = 0.57$, $p < 0.05$), as well as sculpin ($r = 0.45$, $p < 0.05$) and windowpane flounder ($r = 0.52$, $p < 0.05$) (Table 1.11). However, recovered sand lance otoliths (N = 873) were actually *less* eroded than those of their larger, potential fish predators (N = 1073) ($F_{1, 1944} = 12.99$, p <0.001). In addition, the stomachs of whole fish recovered in stomach samples (N = 31) did not contain sand lance.

All crustaceans identified as primary prey were either sand shrimp or Jonah crab (*Cancer borealis*), and were pooled as "Crustacea". No American lobster (*Homarus americanus*) was recovered in this study. The only bivalves classified as primary prey were blue mussels (4 individuals recovered, Table 1.9). Stomach contents of whole fish (N = 31) recovered in seal stomachs did not yield identifiable prey.

Parasites

I recovered several types of parasitic nematodes in samples. The two most common were acanthocephalans, a balloon-shaped worm that attaches to the intestinal wall using a spiny proboscis, and anasakid nematodes, worms that burrow into the walls of the stomach. Although I could not identify parasites to species, I made a distinction between anasakids and acanthocephalans, and preserved all parasites for later identification. Acanthocephalans were recovered in 15.1% of scats, and 0.02% of stomachs (Table 1.12). This is consistent with other findings that acanthocephalans infest the intestinal tract of gray seals, rather than the stomach lining (O'Neill and Whelan 2002). Anisakid nematodes were found in 100% of stomach samples (Table 1.12). The mean number of anisakid worms per stomach was 181.26 ±197.08. Parasite load was higher in fall months, and peaked in 2007 (Table 1.13). Parasite load in stomachs varied significantly by region ($F_{9,36} = 2.62$, $p < 0.05$), and scats collected at Monomoy Island contained more parasites than those collected at Muskeget Island (Table 1.13). Anisakid worms in stomach samples were not positively correlated with any particular prey taxon. In fact, heavy parasite load was negatively correlated with the number of *Urophycis* individuals in stomach contents ($r = -.22$, $p < 0.05$).

Discussion

Sources of error

I inferred prey length-weight relationships using morphometric regression equations. In some cases, equations were not available for prey species in the study area, and I used equations developed for these species in other areas, or for related species with similar otolith topology. Length-weight relationships vary between species, and within species based on location (Anderson and Neumann 1996). Therefore, prey mass may have been under-or overestimated, particularly for gulf stream flounder, for which I used equations for windowpane flounder, and cusk eel, for which I used a Pacific species (spotted cusk eel, *Chilara taylori).* Since skate individuals could not be enumerated based on recovered hard parts, each occurrence was registered as one individual. This likely underestimated the actual number of skates ingested, and therefore the total biomass that skates contributed to the diet.

In certain cases, I estimated length and weight for prey individuals that were not actually recovered. In order to infer the relative weight of each prey taxon to the total weight of all prey, I used two pieces of information: 1) the estimated weight of individual prey items, and 2) the number of all prey items recovered. Since certain prey types are more likely to be completely digested, I used numerical correction factors to obtain a more accurate estimate of prey number (Table 1.3). That is, I estimated the number of prey items that were recovered, and also those that were not recovered, but *should* have been recovered. Failure to do this would result in skewed proportions of prey taxa in the diet, with some overestimated, and some underestimated (Bowen 2000). I used average length for prey that *were* recovered, specific to season, and year, when possible, to estimate the dimensions of prey not recovered. This method has been used to estimate prey length and biomass from otoliths that are too eroded to provide reliable morphometric information (Bowen and Harrison 1996). Even though this method introduced a source of error, I felt this was outweighed by the bias that would have occurred had differential erosion of prey not been accounted for. As a result of NCF application, the prey taxa that changed the most, in terms of both number and weight, were: sand lance, *Urophycis*, winter flounder, squid, windowpane flounder, and herring (Table 1.14).

Gray seals have been observed selectively removing the viscera, and avoiding the heads, of certain fish, including cod (M. Russo, Chatham, MA, pers. comm.), summer flounder (*Paralichthys dentatus*) sea bass (*Centropristis striata*), sea robin (Prionotus *carolinus*) and menhaden (*Brevoortia tyrranus*) (E. Eldridge, C. Foster, Chatham, MA, pers. comm.). If the seals sampled in this study consumed fish without consuming any hard parts, I would not have detected the presence of these prey individuals. If seals consumed everything but the heads of fish, it is possible that I would have recovered at least some vertebrae from partially consumed fish. Even so, it is difficult to identify vertebrae below the level of family (Watt *et al.* 1997) and it is not possible to infer the number of individuals ingested from vertebrae alone. Therefore, partially consumed prey would have been underrepresented in samples, if they were detected at all.

I detected sex differences in diet from prey recovered in seal stomachs. These stomachs came from seals taken in fisheries, and in some cases the animals were sexed at sea by fishery observers, and in some cases during necropsy procedures. If both methods of sexing seals were equal, there should be no difference in the observed sex ratio of seals inspected by observers, and those inspected by biologists performing necropsies. A non-parametric ANOVA revealed significant differences in the sex ratio inferred by these methods (K-W H (1, N= 210) = 17.74, $p < 0.001$, Figure 1.13).

Therefore, it is possible that some seals were classified to sex incorrectly, and caution should be used in interpreting results pertaining to sex differences in diet.

Diet composition and variation

Although gray seals tend to target demersal prey such as sand lance, gadids and flatfish (Bowen and Harrison 1994, Hammond *et al.* 1994, Ridoux *et al.* 2007), the particular species consumed varies with temporal availability of prey (Bowen *et al.* 1993, McConnell *et al.* 1999). Seal diets also vary with location because of differences in prey assemblages (Garrison and Link 2000). I detected significant patterns in diet composition by year, season and region, shown in figures 1.5-1.10 and 1.14. These figures show statistically significant differences among groups, though some confidence intervals overlap (these may overlap by as much as 25% of their length and still show significant differences between group means (Zar 1998)).

There was an increasing trend in sand lance consumption between 2004 and 2007 (Figure 1.7). This trend corresponded with increasing abundance of *Ammotytes americanus* in the Gulf of Maine and southern New England during this time ($F_{3, 397}$ = 2.81, p <0.05, Figure 1.14). This suggests that seals tracked the interannual abundance of this prey species. Gray seal diet in relation to prey distribution and abundance is discussed in further detail in Chapter 3.

More sand lance was recovered in scats from Monomoy than from Muskeget. Monomoy is a barrier island located at the eastern extreme of Nantucket Sound, and is exposed to the open Atlantic on its eastern shore (Figure 1.15). The adjacent sediment is subjected to higher wave energy than sediments surrounding Muskeget Island, which is located 30 km to the southwest, and is protected from the open ocean by Cape Cod to the north, Martha's Vineyard to the west, and Nantucket Island to the south and east (Rough 1995). Sand lance feed diurnally, schooling in daylight hours, and taking refuge in sandy sediments at night (Auster and Stewart 1986). Sand lance therefore require highly oxygenated sediment habitat (Holland *et al.* 2005). The highly aerated sediments around Monomoy may therefore be preferred habitat for sand lance, and would explain the higher prevalence of sand lance in the diet of seals foraging in this area. Conversely, diet diversity was significantly higher at Muskeget than Monomoy, possibly because preferred prey items, such as sand lance, are less abundant around Muskeget, and must seals supplement their diet with a wider variety of taxa.

More *Urophycis* was recovered in scats collected at Muskeget than at Monomoy, and more was recovered in Muskeget scats in spring and winter months. Red and white hake migrate to inshore bays and estuaries in spring and summer, and in winter move to offshore waters near the continental shelf, south of Georges Bank (Steimle *et al.* 1999). The fact that hake consumption peaked in spring and winter indicates that seals hauled out at Muskeget targeted these species in both inshore and offshore waters. Hake may be taken offshore in winter because other prey types are less available inshore at this time of year.

Differences in diet persisted between haul out sites, even when year and season were held constant. However, the two sites are close enough to one another for a gray seal to travel between them in a matter of hours. If seals are distributing their foraging effort over a large area, we would expect the diet at these two sites to be relatively homogenous. The diet differences detected at the two sites suggests that seals are, to a large extent, foraging inshore, close to haul out sites. This strategy maximizes energy gained from prey and reduces effort spent in foraging, and is consistent with the predictions of optimal foraging theory (Bowen *et al.* 2002, MacArthur and Pianka 1966). Prey taken in offshore waters, far from haul out sites (such as *Urophycis*) was targeted in winter, when other prey items (such as sand lance and flatfish) are typically less available inshore (Bigelow and Schroeder 2002).

Although most seals forage close to haul out sites, this varies with sex and time of year. For example, male and female adult gray seals at Sable Island (180 km southeast of Nova Scotia) use different foraging grounds in the months before and after the breeding season: males distribute their foraging effort along the Scotian Shelf, whereas females forage on banks closer to the island (Breed *et al.* 2006). This difference is attributed to intraspecific niche divergence, which allows males and females to reduce competition for resources, and also to the different energetic requirements of pre-breeding and post-breeding males and females.

Seasonal variation in gray seal diet may reflect seasonal movements of prey (Bowen *et al.* 1993). However, most significant seasonal patterns in prey consumption did not correspond to seasonal migrations or movements of prey species. Skates move inshore in winter and spring, and offshore in summer and fall, in response to changing water temperature (NEFCS Status of Fishery Resources: Skates http://www.nefsc.noaa.gov/sos/spsyn/op/skates/). More skates were recovered in fall and winter months than in spring or summer. Seasonal peaks in skate consumption, therefore, did not correspond to the presence of skates inshore or offshore. Another prey species that varied in the diet by season, windowpane flounder, does not undertake migrations or seasonal movements, and is largely stationary (Dawson 1990). Distinct seasonal patterns were observed in cusk eel consumption. The behavior of cusk eel in the study area is not well known, and it is not clear if these species undertake seasonal movements (Bigelow and Schroeder 2002). It is known that fishes in this family are primarily nocturnal (Retzer 1991), and gray seals do forage at night (Anderson 1978). Therefore, gray seals may target these fish during nocturnal foraging bouts.

Seals appeared to switch to cod from other prey taxa, such as sand lance and flatfish, in winter months. This may also be due to reduced availability of sand lance and flatfish at this time of year. Even though cod in the study area have a winter spawning season, it is unlikely that the seals sampled in this study were targeting spawning cod. In the northwest Atlantic, cod females reach maturity at between 40 and 45 cm (O'Brien 1999). The majority of cod individuals recovered in this study were smaller than this (mean 31.96 cm ± 16.23, N = 30, Figure 1.2A). Winter flounder spawning occurs in spring, and gray seals consumed more sexually mature winter flounder individuals in spring than at other times of year. Therefore, gray seals may positively select spawning flounder, because of increased energy content and biomass (Hammond *et al.* 1994).

Scat analysis did not allow investigation of sex differences in diet, since both males and females were present at haul out sites, and I was unable to assign scats to a particular sex. However, sex differences in diet were apparent in stomach samples. This result is noteworthy because sex differences in gray seal diets have normally been attributed to size dimorphism in sexually mature animals, owing to divergence in nutritional requirements both before and after the breeding season (Beck *et al.* 2003, Beck *et al.* 2007a). However, I detected sex effects among sexually immature seals < 6 years old. One possible explanation is that sex differences in prey preference are innate, and do not begin with the onset of breeding effort. Alternative explanations are that the sex differences observed in this study are an artifact of small sample size, or are due to individual differences in prey preferences based on foraging experience, and are unrelated to sex.

Stomachs contained a higher number of prey taxa per sample than did scats, and mean diet diversity was higher in stomach samples than in scats. This effect could be due to the lack of developed prey preferences in young seals. Most (47 of 49 stomachs) in this study were from juveniles < 6 years old, whereas scats were from a mixture of adults and juveniles. Therefore, stomach samples largely reflected the diet of young seals, whereas scats reflected the diet of all age classes. Young seals lack foraging experience, since they are completely weaned at 3-4 weeks, have no parental care when they enter the sea, and must learn to hunt on their own. As a result it may take time for these animals to learn to reliably exploit profitable foraging grounds (Austen *et al.* 2004, Beck *et al.* 2007a).

Comparison of scats and stomachs as measures of diet

Prey composition in scats differed substantially from that in stomach contents (Figure 1.3A-B). It is unlikely that this effect is due to differential erosion of hard parts in the two sample types. More fragile elements are less likely to survive intact in scats than in stomachs, because of a higher degree of erosion in the gastrointestinal tract (Bowen 2000). For example, gadid otoliths, such as cod and hake, are more robust than those of flatfish, herring and mackerel, and have higher recovery rates in scats than these other prey (Bowen 2000). Therefore one might expect to find different prey composition in the two sample types. However, if the difference in prey composition in scats and stomachs is due to more extensive digestion in scats, we would expect gadids to comprise a higher percentage of the diet in scats than they do in stomachs; in fact, the opposite was true (Figure 1.12).

Stomach contents examined in this study came from seals caught in commercial fisheries, which target a complex of groundfish species such as cod, hake and flatfish. These fisheries do not target sand lance, cusk eel, or other important gray seal prey (Wang and Rosenberg 1997). It is therefore possible that diet inferred from stomachs is based on a small subset of seals that are following fishing vessels, and is not representative of the seal population as a whole. Although seals consumed fish of a different size class than caught by the gillnet fishery, they did consume the same species complex targeted by both the otter trawl and gillnet fisheries. Most fish consumed by seals in this study were small enough to escape from the fishing gear in which seals themselves became entangled. This suggests that seals are not, for the most part, consuming prey scavenged from fishing gear; it is more likely that seals and fishing vessels are targeting the same prey assemblages, and seals consume fish that are able to move through gillnets. Seals are known to follow fishing vessels, and exploit prey that have been slowed, confused or dispersed by fishing activities (B.I.M. 1997, Read 2008). Prey composition in stomachs was likely influenced by fishing activities, either though ship following or consumption of discarded fish. However, no diet measure is representative of an entire gray seal population, since there is considerable intraspecific variation in diet (Austen *et al.* 2004). Only by piecing together examples of diet in different regions and times, and from individuals of different age, sex, and foraging experience, can we hope to get a picture of population-wide patterns in prey consumption. The diet of seals associated with fishing vessels represents one part of this picture, but is not representative of all seals.

Another explanation for different diet picture in scats and stomachs is that each may contain prey captured in different geographical regions. Prey contained in scats was likely caught within 80 km from shore (Bowen and Harrison 1994), and seal bycatch specimens were obtained between 10 km and 300 km from shore (Figure 1.1). The maximum daily foraging range of gray seals is approximately 80 km (Bowen and Harrison 1994), although most travel between 10 and 40 km day^{-1} (Austen *et al.* 2004, McConnell *et al.* 1999). Most scats collected in the wild contain prey consumed in the last 24-48 hours (Prime and Hammond 1990, Tollit *et al.* 2003). Therefore, scats in this study likely contained prey consumed within 80km from shore. Prey in stomachs was likely consumed within the last 6 hours, based on average digestion rates for phocid seals (Grellier and Hammond 2006, Murie and Lavigne 1985). Therefore, prey recovered in stomachs was likely caught in the immediate vicinity of where fishing vessels deployed gear.

Despite some spatial overlap in the two sample types, 75% of stomach samples came from outside of the foraging area represented in scats. Therefore, the majority of stomach samples represent a separate geographical foraging range than do scats. Since seal diets vary with location because of differences in prey habitat, and therefore species composition (Bowen and Harrison 1996), the differences in diet observed in the two sampling methods are, at least in part, due to the fact that seals were exploiting inshore (scats) and offshore (stomachs) prey assemblages.

Secondary prey

It is unlikely that sand lance recovered in this study were a result of secondary predation. Although the presence of sand lance in samples was correlated prey that are their predators, sand lance otoliths were less eroded than those of these fish, the opposite of what would be expected if these otoliths were subjected to erosion in both the stomach of a fish and a seal. This finding, as well as the lack of sand lance in any of the whole fish stomachs recovered in seal stomachs, suggests that seals are foraging in demersal prey assemblages including sand lance and their predators, but consume these prey types separately.

Fishery conflicts

Quantifying the impact of seal predation on fish stocks is beyond the scope of this work. However, it was possible to assess the degree of prey size overlap with certain commercial fisheries, since hard part analysis allowed estimation of prey length from otoliths and cephalopod beaks (Bowen *et al.* 1993) (Figures 1.2A-H). Of the prey taxa with minimum legal size limits, gray seals consumed, on average, fish that were smaller than the minimum legal catch size (Table 1.15). Thirteen percent of cod individuals were of legal catch size for commercial and recreational fisheries, and 0% of windowpane flounder were of legal size (Table 1.15). This is consistent with other findings that seals tend to target smaller prey than do fisheries (Bowen *et al.* 1993, Williams 1999). However, 42% of winter flounder prey individuals recovered were of legal catch size (Table 1.15). This finding, along with the fact that winter flounder was heavily represented in the diet (19.0% by weight) indicates that potential conflict exists between seals and the winter flounder fishery, although the extent of this conflict is not quantified here.

Gray seals prey on a complex of demersal species, including sand lance, gadids, and flatfish. Small “forage” or “bait” fish such as sand lance and cusk eel dominate the diet estimated from scat analysis (54.0% by weight, 69.0% by number). Sand lance is not considered an economically important resource in the United States (Auster and Stewart 1986). Other species important (i.e. that comprised ≥5%) in the diet, however, are fished commercially and recreationally on a large scale in the U.S.: winter flounder, windowpane flounder, Atlantic cod, squid, skates, *Urophycis*, and silver hake (also known as whiting). Of the 15 types of groundfish regulated under the Northeast Multispecies Fishery Management Plan, 5 are important in the diet of gray seals: *Urophycis*, silver hake, cod, winter flounder, and windowpane flounder (Wang and Rosenberg 1997). Other species of economic and recreational importance, such as Atlantic herring and striped bass, appeared in the seal diet, but together comprised less than 4% of the diet by weight, and were not considered important prey. Only 2 striped bass individuals were recovered in this study, and no lobster was recovered.

Parasites

Of the several types of endoparasites recovered in this study, the one that attracts the most general interest is *Psuedoterranova decipiens*, or sealworm. Since gray seals are the primary marine mammal host for this parasite (McClelland 2002, McClelland *et al.* 1983), the possibility of increased parasite transmission is one of the main concerns surrounding the growing gray seal population in the U.S. and Canada (Marcogliese 1997). The temporal patterns detected in parasite load could be attributable to changing ocean temperatures and salinity in the Northwest Atlantic (Rahmstorf *et al.* 2007). *P. decipiens* eggs are shed in seal feces that settle to the ocean floor, and their survival is dependent on sea bottom temperature and salinity (McClelland *et al.* 1983). Anisakid parasite infestation varied with location in both scats and stomachs, which is consistent with other findings that length, and therefore fecundity, of *P. decipiens* varies geographically.

Gray seals are generalist feeders: a total of 34 prey taxa were recovered in this study. The most important were sand lance, gadids (dominated by *Urophycis*), skates, squid, and a complex of flatfish species, including winter flounder, windowpane flounder, gulfstream flounder, and fourspot flounder. Broad prey taxa (Gadidae, Pleuronectiformes) were similar to those found in gray seal diets in other parts of the world (Beck *et al.* 2007a, Hammond *et al.* 1994, Lundstrom *et al.* 2007, Ridoux *et al.* 2007). However, the complex of flatfish species recovered (particularly windowpane, gulfstream, and fourspot flounder) appears to be unique to U.S. waters. Cusk eel is important in the diet of U.S. seals, and has not been recovered in other studies. Prey distribution in time and space clearly influences which species are included in the diet.

Chapter 1: Tables

Age	Age class	Length (cm)
0-1 yrs	Young-of-the-year pup (YOY)	≥105
1-2 yrs	Yearling	106-115
2-5 yrs	Subadult	116-160
≥ 6 yrs	Adult	> 160

Table 1.1: Seal age as inferred from length at necropsy

COMMON NAME	SCIENTIFIC NAME	STRUCTURES USED FOR IDENTIFICATION
Atlantic herring	*Clupea harengus*	Otoliths, vertebrae, pro-otic bullae
Blue mussel	*Mytilus edulis*	Shell fragments > 1cm
Crab	Arthropoda	Carapace fragments > 1cm
Cusk eel	Ophidiidae	Otoliths, vertebrae
American eel	*Anguilla rostrata*	Otoliths, vertebrae
Flounder	Pleuronectiformes	Otoliths, vertebrae, teeth, premaxillae, urohyals,
Gadid	Gadiformes	Otoliths, vertebrae, teeth, premaxillae, maxillae, dentaries, articulars
Hagfish	*Myxine glutinosa*	Buccal funnel teeth
Ocean pout	*Macrozoarces americanus*	Otoliths, teeth
Atlantic mackerel	*Scomber scombrus*	Otoliths, vertebrae
Sand lance	*Ammodytes spp.*	Otoliths, vertebrae, atlas vertebrae, subopercular, premaxillae, maxillae, dentaries, articulars, hyomandibulars
Sculpin	*Myoxocephalus spp.*	Otoliths, spines
Skates	Rajidae	Denticles, vertebrae, teeth, cartilage
Squid	*Loligo pealeii*	Eye lenses, beaks, pens
Tautog	*Tautoga onitis*	Otoliths, teeth, pharyngeal jaws
Wolffish	*Anarhichas spp.*	Otoliths, vomerine and palatine teeth

Table 1.2: Structures used to identify prey

Prey Taxon	Digestion coefficient	Source	Number correction factor	Source
Atlantic cod	1.56	1	1.20	2
Fourspot flounder	1.10 (1) 1.10 (2) 1.32 (3)	1	1.24	1
Gulfstream flounder	1.10 (1) 1.10 (2) 1.32 (3)	1	1.24	1
Atlantic herring	1.04 (1) 1.11 (2) 1.32 (3)	1	3.00	2
Atlantic mackerel	1.22	1	1.39	2
Merluccius spp.	1.73	1	1.40	2
Ocean pout	1.25	1	1.16	2
Pollock	1.40	1	1.30	2
Red/white hake	1.08 (1) 1.08 (2) 1.40 (3)	1	2.10	2
Redfish	1.12(1) 1.42(2)	1	none	*
Sand lance	1.25 (1) 1.25 (2) 1.58 (3)	1	3.60	2
Sculpin	1.12	1	2.1	2
Silver hake	1.73	1	1.40	2
Squid	1.02	1	2.30	2
Unknown flatfish	1.10 (1) 1.10 (2) 1.32 (3)	1	1.24	1
Unknown gadids	1.40	1	1.07	2
Windowpane fl.	1.10 (1) 1.01 (2) 1.32 (3)	1	1.24	1
Winter flounder	1.10 (1) 1.10 (2) 1.32 (3)	1	1.60	2
Yellowtail flounder	1.10 (1) 1.10 (2) 1.32 (3)	1	2.20	2

Table 1.3: Digestion and number correction factors.
Sources: 1. Grellier and Hammond 2006; 2. Bowen 2000.
For digestion coefficients, (1) (2) and (3) refer to degree of otolith erosion

Common name	Scientific name	Prey length (cm)		Prey wet mass (g)	
		Equation	**Source**	**Equation**	**Source**
Sand lance	*Ammodytes spp.*	FL=-4.377+9.024(OL,mm)	1	W=0.1248(FL)^1.75	1
Winter flounder	*Pseudopleuronectes americanus*	FL=8.559+8.389(OL,mm)	1	W=0.0079(FL)^3.12	2
Atlantic cod	*Gadus morhua*	ln(FL)=3.3138+1.6235 ln(OL,cm)	1	Winter: W=(LN(FL)*3.0527)-11.7677 Spring: W=(LN(FL)*3.0606)-11.7803 Fall: W=(LN(FL)*3.1262)-11.9920	7
Pollock	*Pollachus viriens*	ln(FL)=3.2510+1.6251 ln(OL,cm)	2	Winter: W= (LN(FL)*3.0766)-11.8062 Spring: W=(LN(FL)*3.0766)-11.8062 Fall: W=(LN(FL)*3.0888)-11.8111	7
Skate	Rajidae	----		W=(LN(FL)*3.1197)-12.0880	7
Red/white hake	*Urophycis spp.*	FL=1.5250 (OL,mm)^1.1456	1	W=0.003998(FL)^3.1718	2
Herring	*Clupea harengus*	FL=6.341 (OL,mm)-2.057	1	Winter: W=(LN(FL)*2.8559)-11.2575 Spring: W=(LN(FL)*3.0314)-11.7972 Fall: W=(LN(FL)*2.9794)-11.5760	7
Windowpane flounder	*Scopthalmus aquosus*	SL(mm)= (OL,mm)-0.4216)/.02	3	Winter: W=(LN(FL)*3.0418)-11.5177 Spring: W=(LN(FL)*2.9982)-11.3526 Fall: W=(LN(FL)*2.8721)-11.0093	7
Squid	*Loligo pealeii*	DML=(92.29*LRL) - 2.12	4	LN (W)=1.773+2.40 LN®	8
Cusk eel *	*Lepophidium cervinum*	(SL,cm)=2.51(OL,mm)+2.15	5	W=(LN(FL)*3.2359)-13.7333	7
Sculpin **	*Myoxocephalus spp.*	---	---	W=6.289 e^(0.353 OL)	9
Sand shrimp	*Crangon septemspinosa*	---	---	logW (mg) = 3.079 log (L,mm) - 2.191	10
Fourspot flounder***	*Paralichthys oblongus*	FL=8.559+8.389(OL,mm)	1	Winter: W=(LN(FL)*3.2932)-12.8160 Spring: W=(LN(FL)*3.1463)-12.3202 Fall: W=(LN(FL)*3.1463)-12.3202	7
Yellowtail flounder	*Limanda ferruginea*	FL= -6.979+6.709(OL,mm)	1	Winter: W=(LN(FL)*3.2408)-12.4209 Spring: W=(LN(FL)*3.2099)-12.3581 Fall: W=(LN(FL)*3.0559)-11.8381	7
Silver hake	*Merluccius bilinearis*	ln(FL)=3.0111+1.0276 ln(OL,cm)	2	Winter: W=(LN(FL)*3.1056)-12.3367 Spring: W=(LN(FL)*3.1512)-12.4934 Fall: W=(LN(FL)*3.0606)-12.1353	7

Table 1.4: Otolith length-prey length and prey length-prey weight equations

Gulfstream flounder****	*Citharichthys arctifrons*	*SL(mm)= (OL,mm)-0.4216)/.02*	*3*	*Winter: W=(LN(FL)*3.2408)-12.4209* Spring: W=(LN(FL)*3.2099)-12.3581 Fall: W=(LN(FL)*3.0559)-11.8381	*7*
Atlantic mackerel	*Scomber scombrus*	FL = ((OL,mm) + 0.298)/0.152	6	Winter: W=(LN(FL)*3.3128)-12.6661 Spring: W=(LN(FL)*3.3119)-12.6713 Fall: W=(LN(FL)*3.2615)-12.3766	7
Ocean pout	*Macrozoarces americanus*	FL=11.045+6.23(OL,mm)	2	Winter: W=(LN(FL)*3.2995)-13.5168 Spring: W=(LN(FL)*3.3459)-13.6429 Fall: W=(LN(FL)*3.2995)-13.5168	7
Redfish	*Sebastes spp.*	ln(FL)=3.1273+1.1436 ln(OL,cm)	2	W=0.0130(FL)^3.06	2

Table 1.4 (continued): Otolith length-prey length and prey length-prey weight equations. Sources: 1. Bowen and Harrison 1994; 2. Bowen and Harrison 1996; 3. Neuman *et al.* 2000; 4. Staudinger 2009; 5. Harvey *et al.* 2000; 6. Grellier and Hammond 2006; 7. Wigley *et al.* 2003; 8. Clarke 1986; 9. Härkönen 1986; 10. Taylor and Peck 2004. * Used equation for spotted cusk-eel; ** used equation for four-horn sculpin; *** used equation for winter flounder; **** used equation for windowpane flounder

Otolith Code	Degree of Erosion	Appearance of Otolith
0	None	Still contained in fish skull
1	Minor	Lobation and sulcus pronounced
2	Moderate	Lobation and sulcus discernable
3	Severe	Lobation and sulcus not discernable Overall shape of otolith intact Still diagnostic of taxon
4	Severe	Overall shape of otolith distorted Not diagnostic of taxon

Table 1.5: Otolith coding guidelines

Stomach #	Sex	Straight Length (cm)	Age	Fishery	Year	Season	Statistical Area
1	U	110	Yearling	anchored sink gillnet	2004	Spring	537
2	Female	112	Yearling	anchored sink gillnet	2005	Winter	537
3	Female	101	YOY	anchored sink gillnet	2005	Winter	537
4	Female	101	YOY	anchored sink gillnet	2004	Spring	521
5	Female	114	Yearling	anchored sink gillnet	2004	Spring	521
6	Male	115	Yearling	anchored sink gillnet	2004	Spring	537
7	Female	115	Yearling	anchored sink gillnet	2004	Spring	537
8	Male	106	Yearling	anchored sink gillnet	2004	Spring	537
9	Female	109	Yearling	anchored sink gillnet	2004	Spring	521
10	Female	107	Yearling	anchored sink gillnet	2004	Spring	521
11	Female	124	Subadult	anchored sink gillnet	2007	Spring	526
12	Female	118	Subadult	anchored sink gillnet	2004	Winter	521
13	Male	118	Subadult	anchored sink gillnet	2003	Spring	537
14	Male	105	YOY	anchored sink gillnet	2003	Winter	537
15	Male	116	Subadult	anchored sink gillnet	2005	Spring	537
16	Male	103	YOY	anchored sink gillnet	2007	Spring	526
17	Female	87	YOY	bottom otter trawl	2005	Spring	525
18	Female	117	Subadult	anchored sink gillnet	2004	Summer	521
19	Female	163	Adult	anchored sink gillnet	2005	Summer	514
20	Female	131	Subadult	anchored sink gillnet	2004	Fall	537
21	U	U	Unknown	anchored sink gillnet	2004	Spring	539
22	Female	98	YOY	anchored sink gillnet	2004	Spring	521
23	Male	138	Subadult	anchored sink gillnet	2007	Winter	537
24	Female	117	Subadult	anchored sink gillnet	2007	Winter	537
25	Female	108	Yearling	anchored sink gillnet	2004	Winter	539
26	Male	136	Subadult	anchored sink gillnet	2007	Winter	537
27	Male	171	Adult	anchored sink gillnet	1998	Winter	521
28	Male	138	Subadult	anchored sink gillnet	2001	Spring	616
29	Male	101	YOY	anchored sink gillnet	1998	Spring	513
30	Male	114	Yearling	anchored sink gillnet	1999	Summer	513
31	Male	108	Yearling	anchored sink gillnet	1999	Fall	513
32	Male	115	Yearling	anchored sink gillnet	2000	Winter	537
33	Male	104	YOY	anchored sink gillnet	2000	Winter	537
34	Female	98	YOY	anchored sink gillnet	2004	Winter	515
35	Female	120	Subadult	anchored sink gillnet	2006	Fall	513
36	Male	111	Yearling	anchored sink gillnet	2005	Winter	514
37	Male	114	Yearling	anchored sink gillnet	2004	Spring	521
38	Female	111	Yearling	anchored sink gillnet	2000	Spring	537
39	Male	117	Subadult	anchored sink gillnet	2005	Fall	521
40	Female	114	Yearling	anchored sink gillnet	2007	Spring	537
41	Male	108	Yearling	bottom otter trawl	2005	Spring	562
42	Female	108	Yearling	anchored sink gillnet	2005	Spring	537
43	Male	114	Yearling	anchored sink gillnet	2005	Spring	537
44	Female	87	YOY	anchored sink gillnet	2007	Winter	514
45	Male	111	Yearling	anchored sink gillnet	2007	Spring	515
46	U	U	U	Unknown	2007	Spring	U
47	U	U	U	Unknown	2007	Winter	U
48	Male	100	YOY	anchored sink gillnet	2008	Spring	537
49	Male	99	YOY	anchored sink gillnet	2008	Spring	537

Table 1.6: Summary of seal stomach samples

	Winter	Spring	Summer	Fall
2004	1	31	13	28
2005	6	9	10	21
2006	22	45	21	44
2007	13	21	7	7
2008	6	0	0	0
Total: 305 seal scat samples				

Table 1.7: Overview of scat sample collection

	Winter	Spring	Summer	Fall
1998	1	1	0	0
1999	0	0	1	1
2000	1	2	0	0
2001	0	0	1	0
2002	0	0	0	0
2003	0	1	1	0
2004	2	9	1	1
2005	1	7	2	2
2006	0	0	1	0
2007	6	4	1	0
2008	0	2	0	0
Total: 49 seal stomach samples				

Table 1.8: Overview of stomach sample collection

Common name	Scientific name	MNI	% RA	% FO	% Biomass	Biomass (kg)
Sand lance	*Ammodytes spp.*	4198	66.3	14.0	53.3	138.8
Winter flounder	*Pseudopleuronectes americanus*	162	2.6	6.9	19.0	49.6
Atlantic cod	*Gadus morhua*	25	<1.0	2.0	6.4	16.6
Skates	Rajidae	159	2.5	24.5	5.7	14.8
Red/white hake	*Urophycis spp.*	530	13.5	9.4	3.3	8.6
Atlantic herring	*Clupea harengus*	93	1.5	2.3	3.7	9.6
Windowpane flounder	*Scopthalmus aquosus*	118	1.9	7.1	2.2	5.6
Squid	*Loligo pealeii*	219	3.4	6.2	1.4	3.6
Cusk eel	Ophidiidae	159	2.5	5.2	<1.0	0.5
Sculpin	*Myoxocephalus spp.*	132	2.1	2.5	4.0	10.3
Shrimp/crab	Crustacea	32	<1.0	1.7	<1.0	0.1
Fourspot flounder	*Paralichthys oblongus*	22	<1.0	1.9	<1.0	2.1
Yellowtail flounder	*Limanda ferruginea*	20	<1.0	1.9	<1.0	1.1
Silver hake	*Merluccius bilinearis*	22	<1.0	2.0	<1.0	1.5
Gulfstream flounder	*Citharichthys arctifrons*	22	<1.0	2.0	<1.0	0.3
n/a	*Merluccius spp.*	13	<1.0	1.1	<1.0	0.2
Atlantic mackerel	*Scomber scombrus*	13	<1.0	1.1	<1.0	0.2
Unidentified flatfish	*Pleuronectiformes*	21	<1.0	3.0	<1.0	0.1
Unidentified gadids	Gadiformes	14	<1.0	3.0	<1.0	0.1
Ocean pout	*Macrozoarces americanus*	6	<1.0	<1.0	<1.0	<0.1
Lumpfish	*Cyclopterus lumpus*	4	<1.0	<1.0	*	*
Blue mussel	*Mytilus edulis*	4	<1.0	1.0	*	*
Hagfish	*Petromyzon marinus*	3	<1.0	<1.0	*	*
Tautog	*Tautoga onitis*	3	<1.0	<1.0	*	*
Spiny dogfish	*Squalus acanthias*	2	<1.0	<1.0	*	*
Striped bass	*Morone saxatilis*	2	<1.0	<1.0	*	*
Eel	*Anguilla rostrata*	1	<1.0	<1.0	*	*
Scup	*Stenotomus chrysops*	1	<1.0	<1.0	*	*
Wolffish	*Anarhichas spp.*	1	<1.0	<1.0	*	*
Unknown	Unknown	13	<1.0	1.0	*	*
TOTAL		**6013**	**100.0**	**100.0**	**100.0**	**263.6**

Table 1.9: Prey in 252 seal scats
MNI = Minimum number of individuals; RA = Relative abundance; FO = Frequency of occurrence
* Biomass not estimated

Common name	Scientific name	MNI	%RA	%FO	% Biomass	Biomass (kg)
Red/white hake	*Urophycis spp.*	301	30.3	22.1	32.5	29.9
Silver hake	*Merluccius bilinearis.*	69	7.0	10.4	29.7	26.7
Winter flounder	*Psuedopleuronectes americanus*	13	1.3	4.1	15.1	13.9
Pollock	*Pollachus viriens*	12	1.0	1.0	2.3	2.3
Fourspot flounder	*Paralichthys oblongus*	34	3.4	7.6	7.7	7.1
Gulfstream flounder	*Citharichthys arctifrons*	128	12.9	7.6	3.1	2.8
Redfish	*Sebastes sp.*	14	1.4	2.1	2.3	2.1
Atlantic cod	*Gadus morhua*	10	1.0	3.5	1.7	1.5
Squid	*Loligo pealeii*	16	1.6	3.5	1.6	1.5
Shrimp/crab	Crustacea	306	30.8	4.1	1.3	1.2
Yellowtail flounder	*Limanda ferruginea*	17	1.7	3.5	0.9	0.8
Ocean pout	*Zoarces americanus*	8	0.8	3.5	0.6	0.5
Skates	Rajidae	7	0.7	4.8	<0.1	0.5
Sand lance	*Ammodytes spp.*	15	1.5	1.4	<0.1	0.5
Atlantic herring	*Clupea harengus*	4	<0.1	2.8	<0.1	0.4
Windowpane flounder	*Scophthalmus aquosus*	4	<0.1	2.1	<0.1	0.2
Cusk eel	Ophidiidae	8	0.8	2.1	<0.1	0.1
Unidentified gadid	Gadidae	5	0.5	2.1	*	*
n/a	*Merluccius spp.*	4	<0.1	2.1	*	*
Unidentified flatfish	Pleuronectes	2	<0.1	0.7	*	*
Sculpin	*Myoxocephalus spp.*	1	<0.1	0.7	*	*
Tautog	*Tautoga onitis*	5	0.5	2.8	*	*
American eel	*Anguilla rostrata*	4	<0.1	2.8	*	*
Unknown	n/a	3	<0.1	2.1	*	*
Hagfish	*Myxine glutinosa*	1	<0.1	0.7	*	*
Atlantic silverside	*Menidia menidia*	1	<0.1	0.7	*	*
TOTAL		**992**	**100.0**	**100.0**	**100.0**	**102.4**

Table 1.10: Prey in 46 seal stomachs
MNI = Minimum number of individuals; RA = Relative abundance; FO = Frequency of occurrence
* Biomass not estimated

	Phycid hake	Silver hake	Fourspot flounder	Gulfstream flounder	Windowpane flounder	Winter flounder	Cusk eel	Sand lance	Squid	Crustacea
Phycid hake	1.00	0.20	-0.01	-0.10	0.02	0.13	-0.18	-0.11	**0.45**	-0.03
Silver hake	0.20	1.00	-0.01	-0.10	-0.03	0.12	-0.06	***0.57***	0.17	***0.76***
Fourspot flounder	-0.01	-0.01	1.00	-0.08	**0.45**	0.18	-0.19	0.38	**0.51**	-0.09
Gulf stream flounder	-0.10	-0.10	-0.08	1.00	-0.10	-0.01	**0.41**	0.23	-0.05	-0.15
Windowpane flounder	0.02	-0.03	**0.45**	-0.10	1.00	**0.41**	-0.22	***0.52***	-0.09	-0.01
Winter flounder	0.13	0.12	0.18	-0.01	**0.41**	1.00	-0.20	0.24	-0.28	0.13
Cusk eel	-0.18	-0.06	-0.19	**0.41**	-0.22	-0.20	1.00	0.10	-0.05	-0.10
Sand lance	-0.11	***0.57***	0.38	0.23	***0.52***	0.24	0.10	1.00	0.06	**0.42**
Squid	**0.45**	0.17	**0.51**	-0.05	-0.09	-0.28	-0.05	0.06	1.00	-0.05
Crustacea	-0.03	***0.76***	-0.09	-0.15	-0.01	0.13	-0.10	**0.42**	-0.05	1.00

Table 1.11: Partial correlations among important prey taxa
Correlations marked in bold are significant at $p < 0.05$, N = 26; italicized values indicate potential secondary prey
Correlations calculated by prey number

% Scats with parasites	% Scats with Anisakids	% Scats with Acanthocephalans
24.3	16.7	15.1
% Stomachs with parasites	**% Stomachs with Anisakids**	**% Stomachs with Acanthocephalans**
100.0	100.0	0.02

Table 1.12: Prevalence of parasite infestation in scat and stomach samples

Patterns in parasite load: 305 seal scats			
Parasite type	**Seasonal effects**	**Regional effects**	**Annual effects**
Anasakids	none	More at Monomoy than Muskeget (H =10.11, p =0.001)	More anisakids in 2006 and 2007 than in other years: (H =15.21, p <0.01)
Acanthocephalans	More recovered in spring and winter months (H=18.36, p <0.001)	More at Monomoy than Muskeget (H =7.10, p <0.01)	none
Total	Higher total parasite load in spring and winter (H =16.01, p =0.001)	Higher total parasite load in scats collected at Monomoy than Muskeget (H =8.80, p <0.05)	Higher total parasite load in 2007 than other years (H =14.35, p <0.05)
Patterns in parasite load: 49 seal stomachs			
Parasite type	**Seasonal effects**	**Regional effects**	**Annual effects**
Anasakids	More recovered in spring and fall months $F_{3, 42} = 5.52$, $p < 0.05$	More in 513, 525, 562 ($F_{9, 36} = 2.62$, $p < 0.05$)	none

Table 1.13: Spatial and temporal patterns in gray seal parasite load

Taxon	# of prey individuals recovered	NCF*	Corrected # of prey individuals	Difference
Sand lance	1166	3.6	4198	3032
Red/white hake	408	2.1	857	449
Winter flounder	101	1.6	162	61
Squid	95	2.3	219	124
Windowpane flounder	95	1.241	118	23
Herring	31	3	93	62
Atlantic cod	21	1.2	25	4
Fourspot flounder	18	1.241	22	4
Gulfstream flounder	18	1.241	22	4
Silver hake	16	1.4	22	6
Yellowtail flounder	9	2.2	20	11
Mackerel	9	1.391	13	4
Ocean pout	5	1.157	6	1

*Number correction factors; see table 1.3 for sources

Table 1.14: Effect of number correction factors (NCFs) on prey number

Prey taxon	Length consumed by seals	Min. legal size	% prey of legal size
Winter flounder	**27.42 cm** ± 14.62, N = 114	**30.5 cm** (12 in)	**42.1%**
Atlantic cod	**31.96 cm** ± 16.23, N = 30	**55.9-61 cm** (22-24 in)	**13.3%**
Windowpane flounder	**14.77 cm** ± 4.73, N = 98	**30.5 cm** (12 in)	**0.0%**
Squid *(Loligo pealeii)*	20.10 cm ± 6.18, N = 61	none	n/a
Red/white hake	12.03 cm ± 5.48, N = 410	none	n/a
Silver hake	29.72 cm, ± 14.24, N = 94	none	n/a

Table 1.15: Average length of economically important prey consumed by gray seals

Chapter 1: Figures

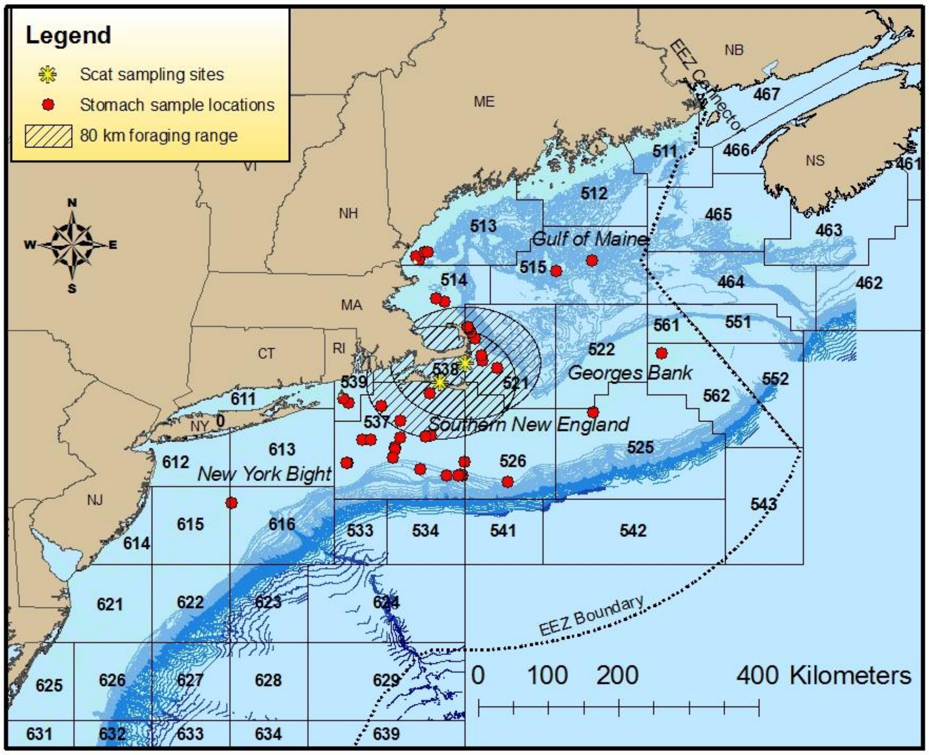

Figure 3.1: Seal scat and stomach sampling locations

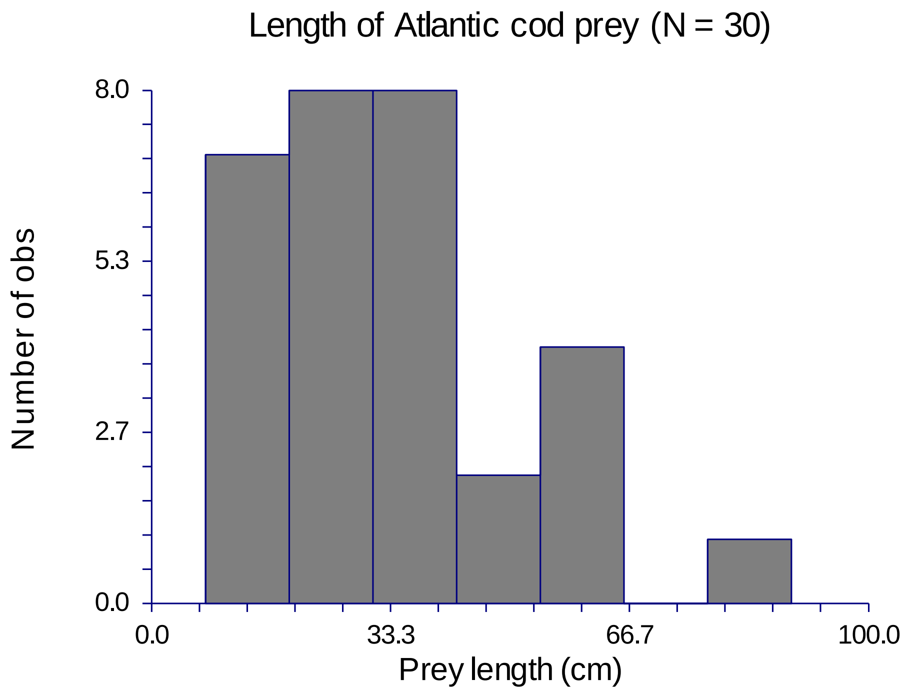

Figure 1.2A: Estimated fork length of ingested Atlantic cod (*Gadus morhua*) prey

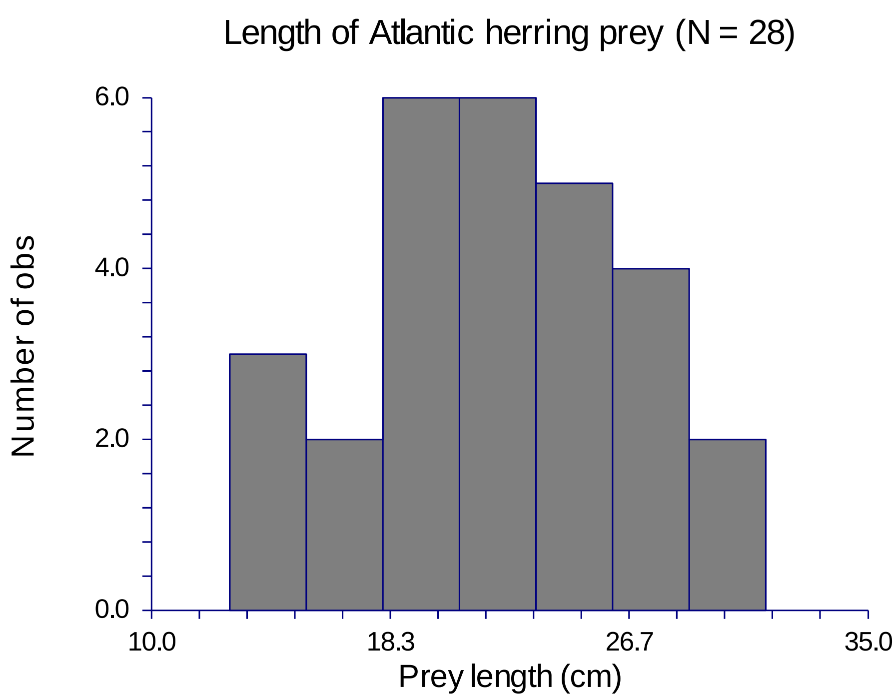

Figure 1.2B: Estimated fork length of ingested Atlantic herring (*Clupea harengus*) prey

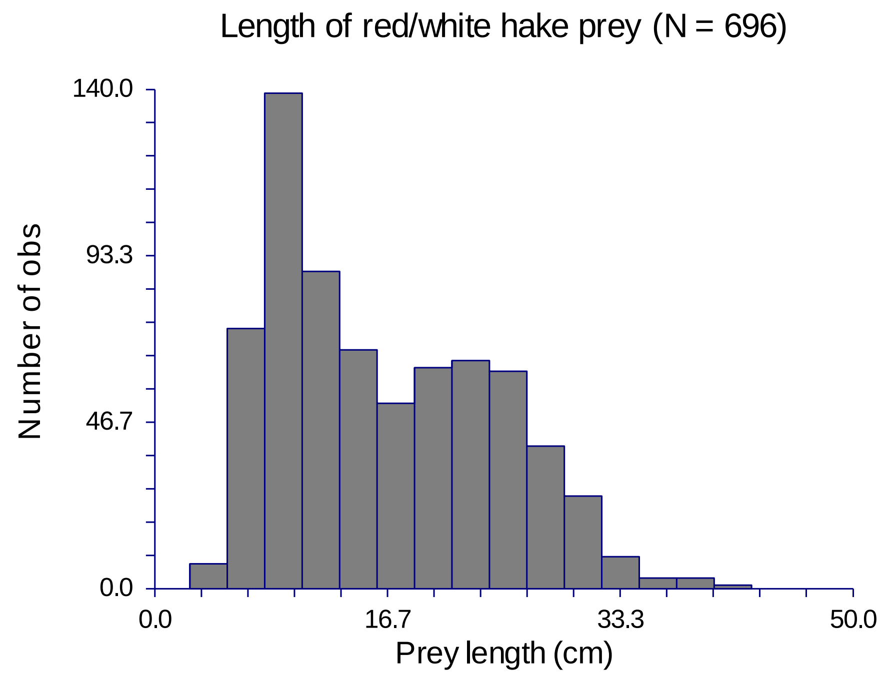

Figure 1.2C: Estimated fork length of ingested red/white hake (*Urophycis spp*.) prey

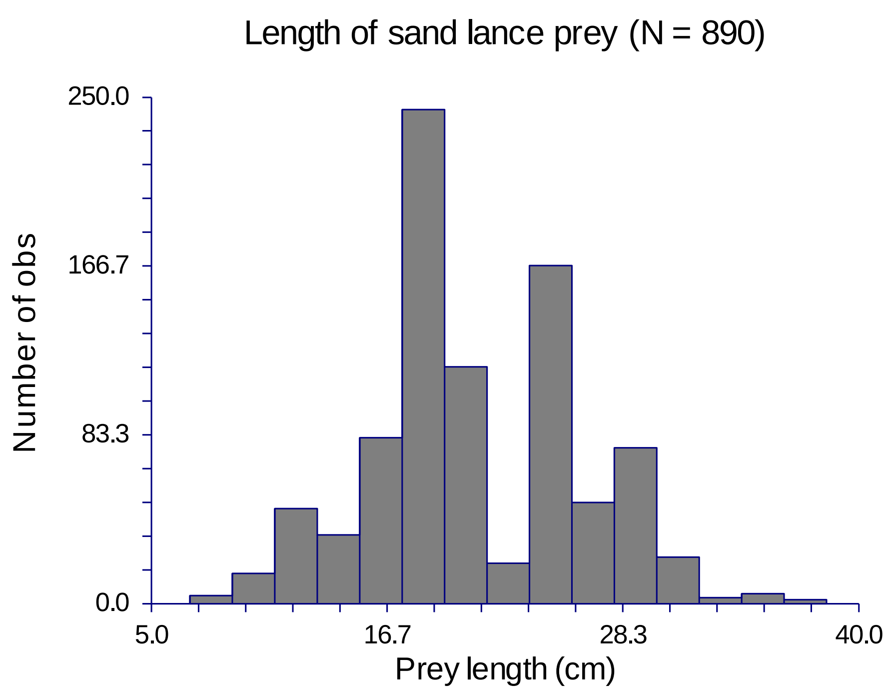

Figure 1.2D: Estimated fork length of ingested sand lance (*Ammodytes spp.*) prey

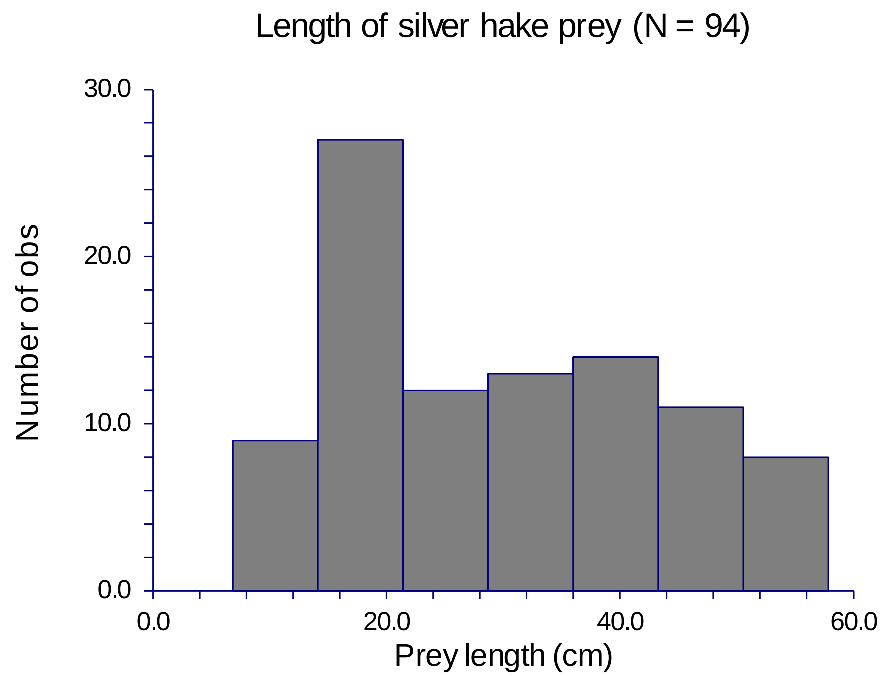

Figure 1.2E: Estimated fork length of ingested silver hake (*Merluccius bilinearis*) prey

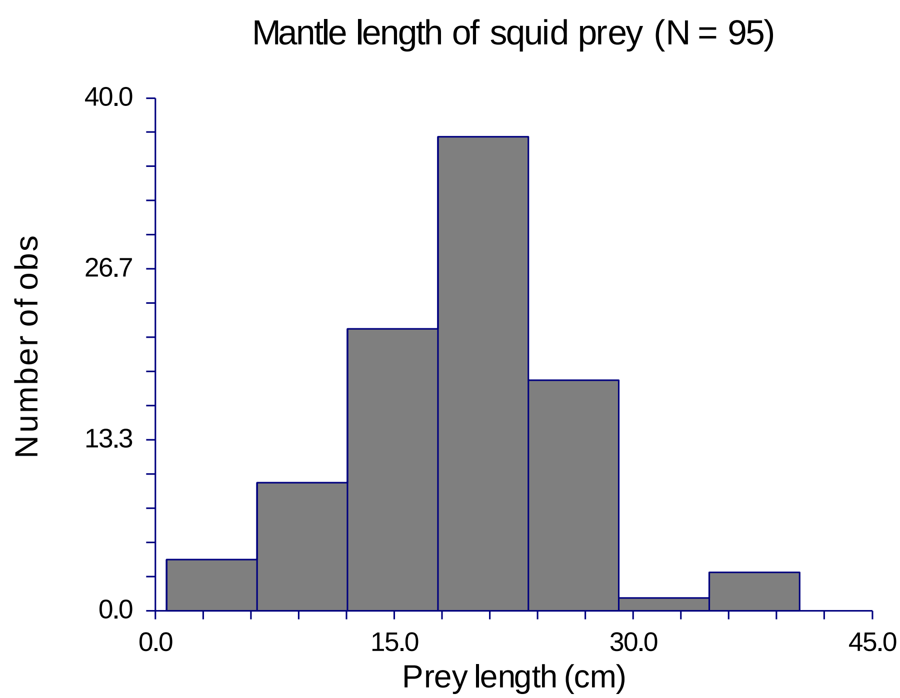

Figure 1.2F: Estimated mantle length of ingested squid (*Loligo pealeii*) prey

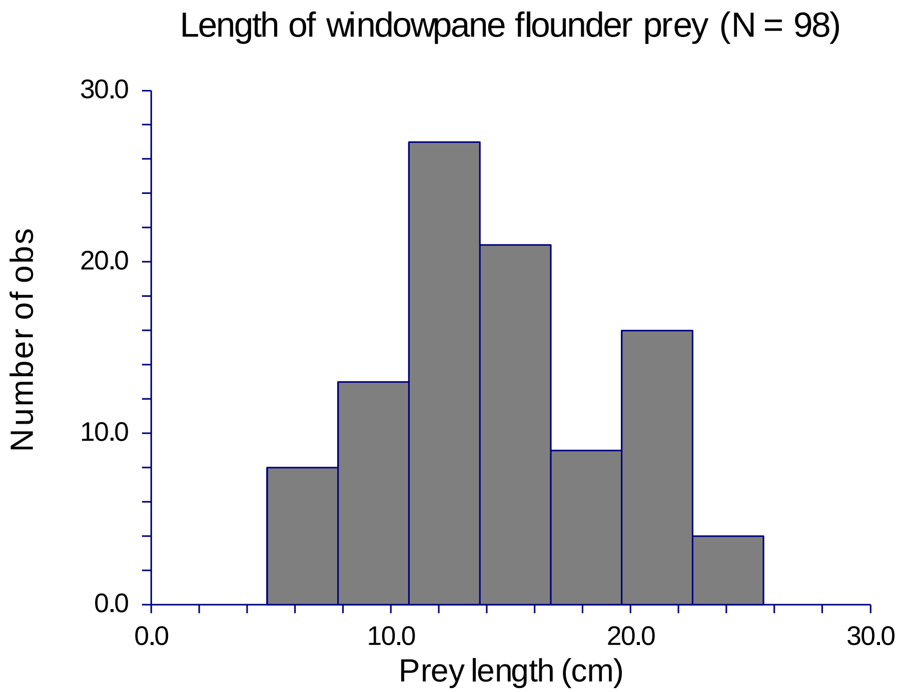

Figure 1.2G: Estimated fork length of ingested windowpane flounder (*Scophthalmus aquosus*) prey

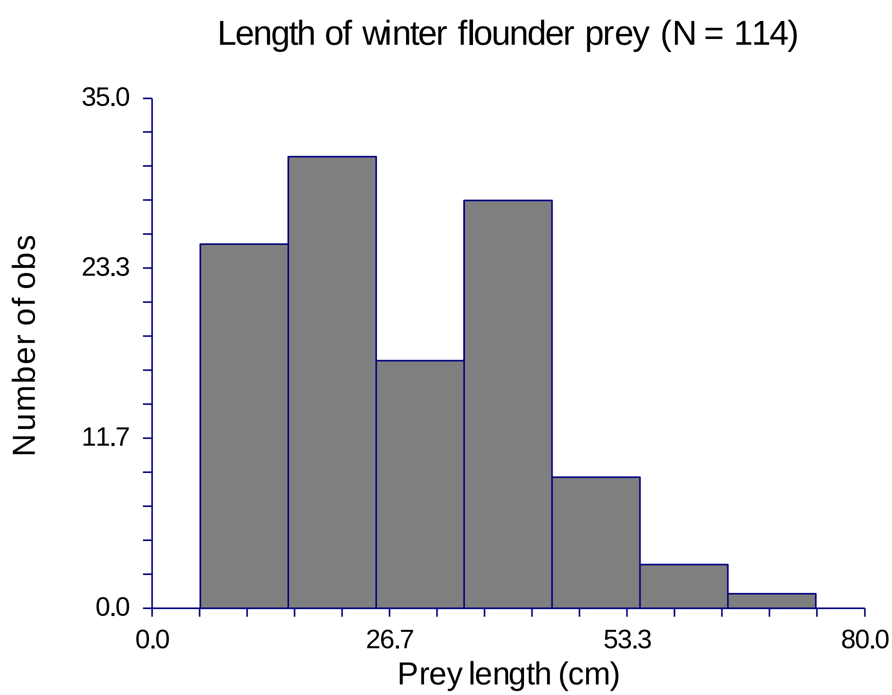

Figure 1.2H: Estimated fork length of ingested winter flounder (*Pseudopleuronectes americanus*)

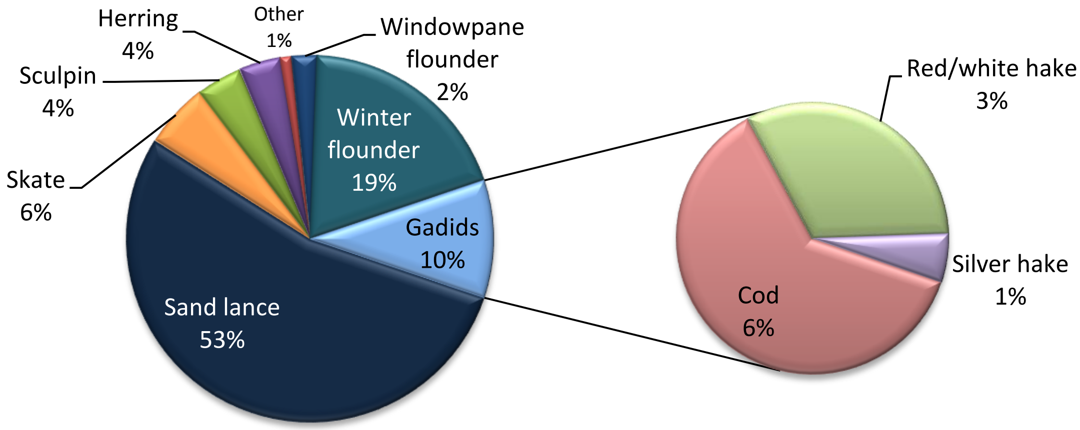

Figure 1.3A: Percent wet weight (biomass) of prey taxa in gray seal scats

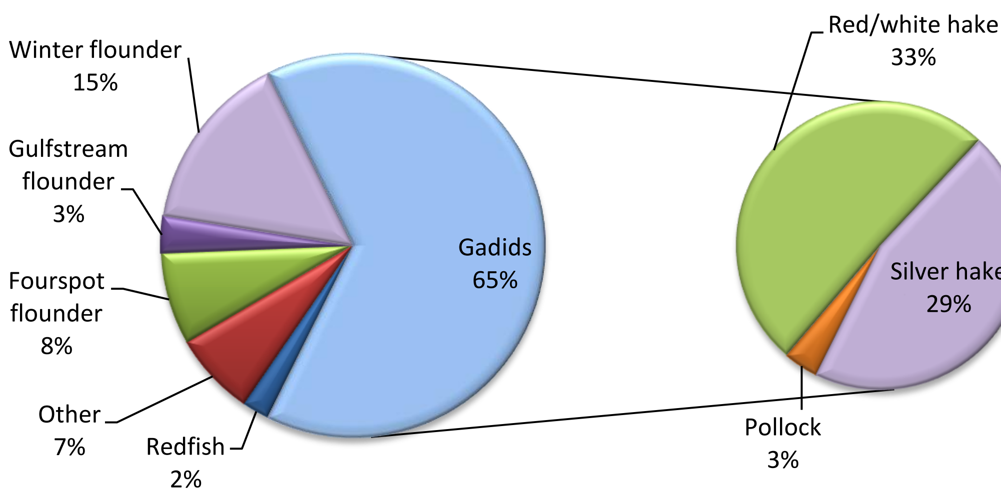

Figure 1.3B: Percent wet weight (biomass) of prey taxa in gray seal stomachs

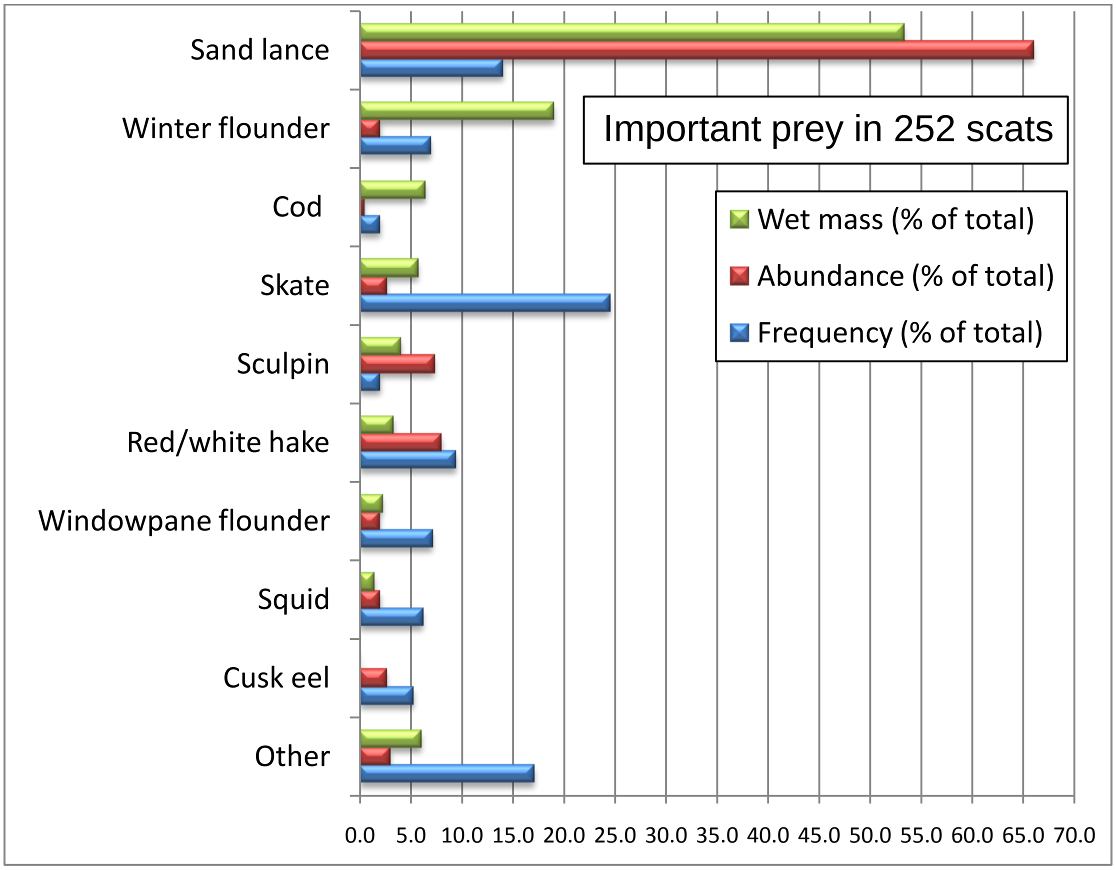

Figure 1.4: "Important" prey, comprising ≥5% of diet by weight, number and/or frequency, in 252 seal scats

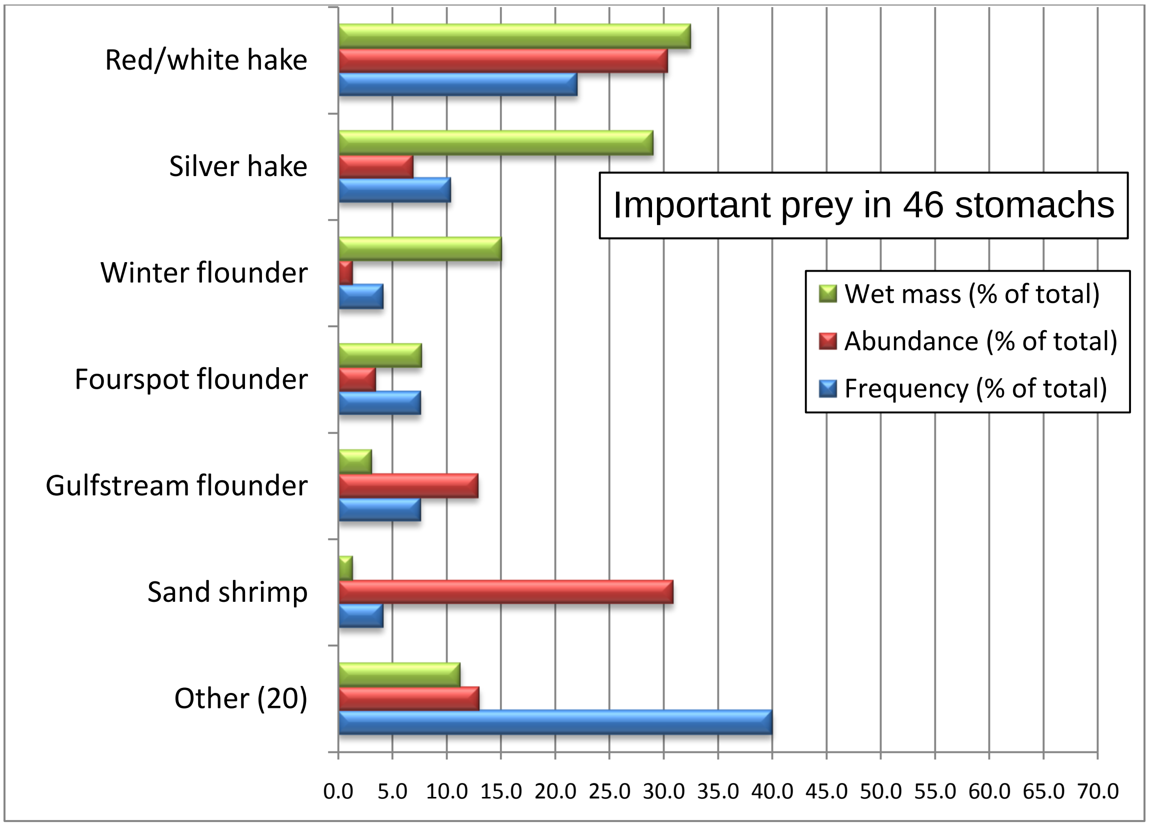

Figure 1.5: "Important" prey, comprising ≥5% of diet by weight, number and/or frequency, in 46 seal stomachs

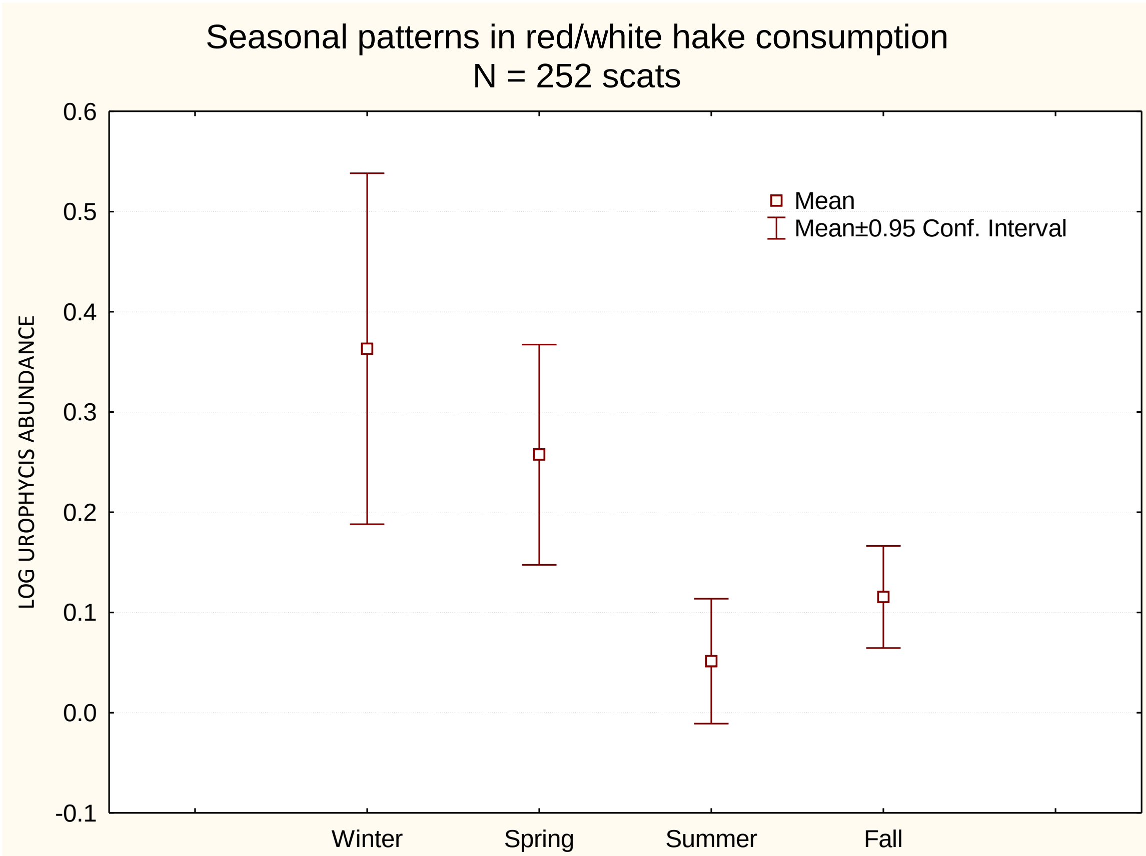

Figure 1.6: Seasonal patterns in red/white hake (*Urophycis spp*.) consumption

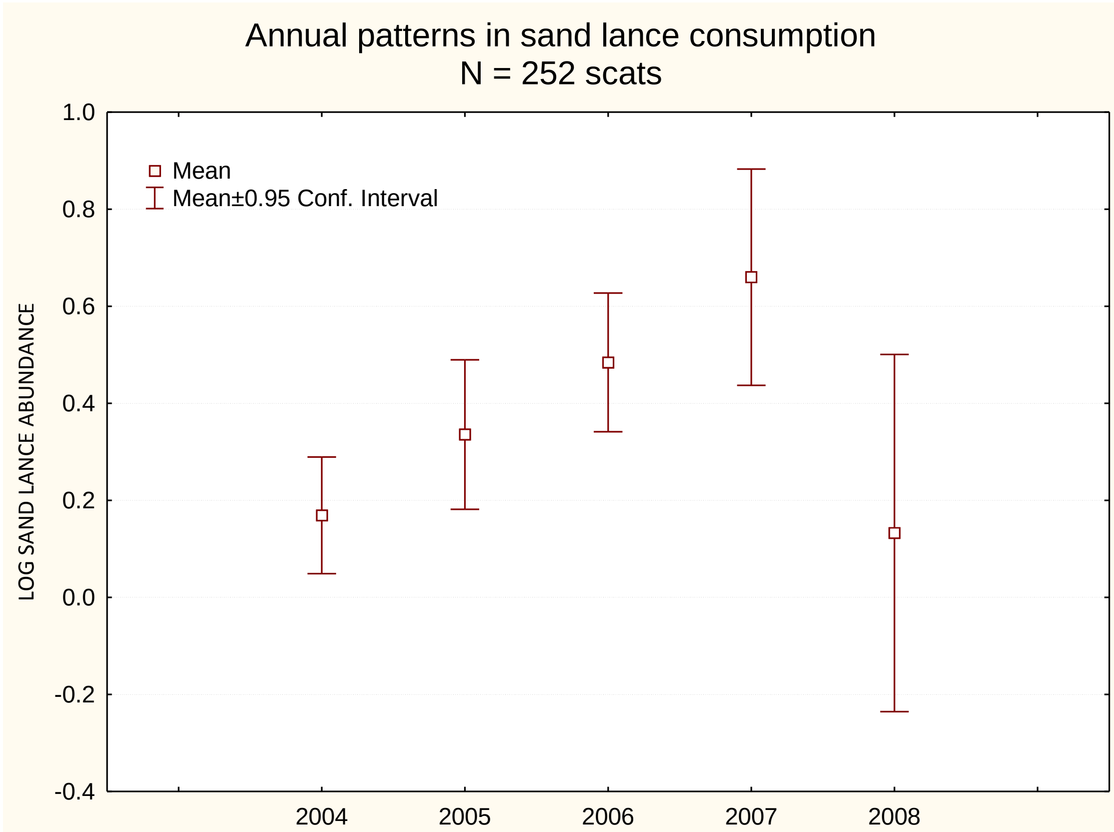

Figure 1.7: Annual patterns in sand lance (*Ammodytes spp*.) consumption

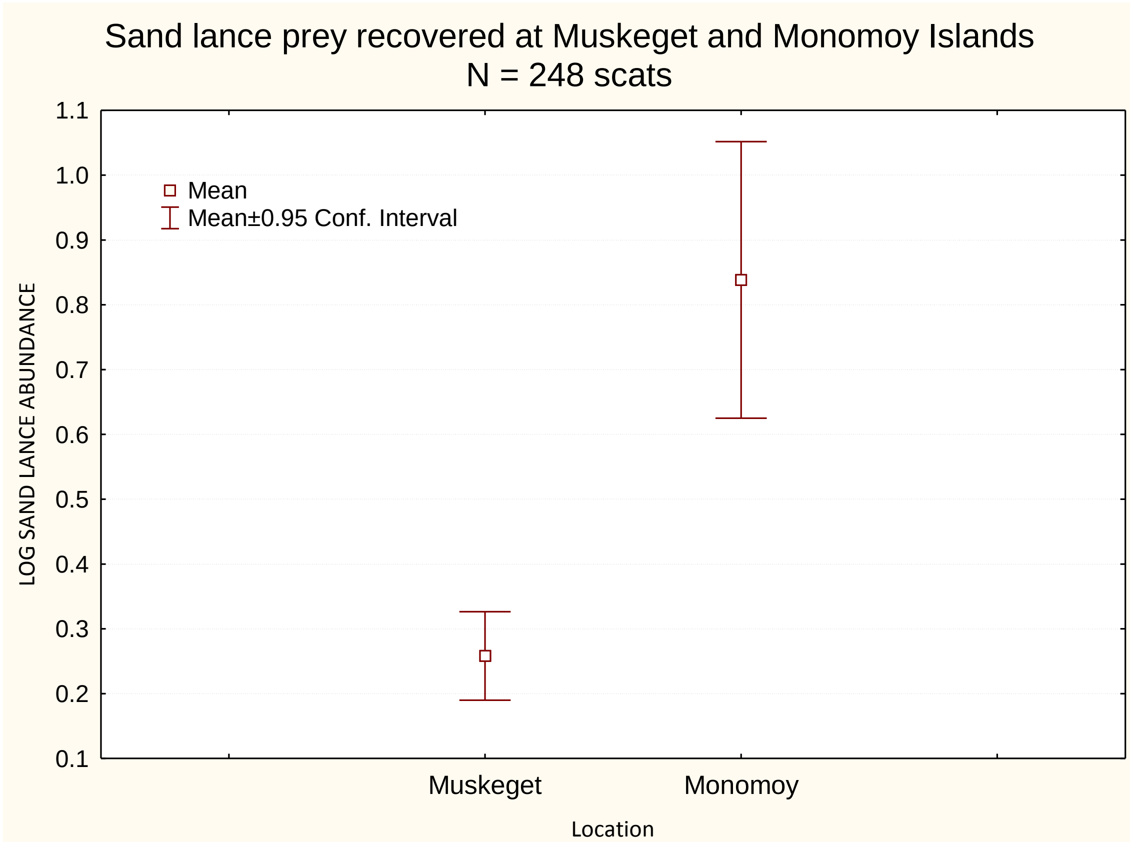

Figure 1.8: Number of sand lance (*Ammodytes spp.*) prey individuals recovered in scats collected at Muskeget and Monomoy Islands, Nantucket Sound, MA

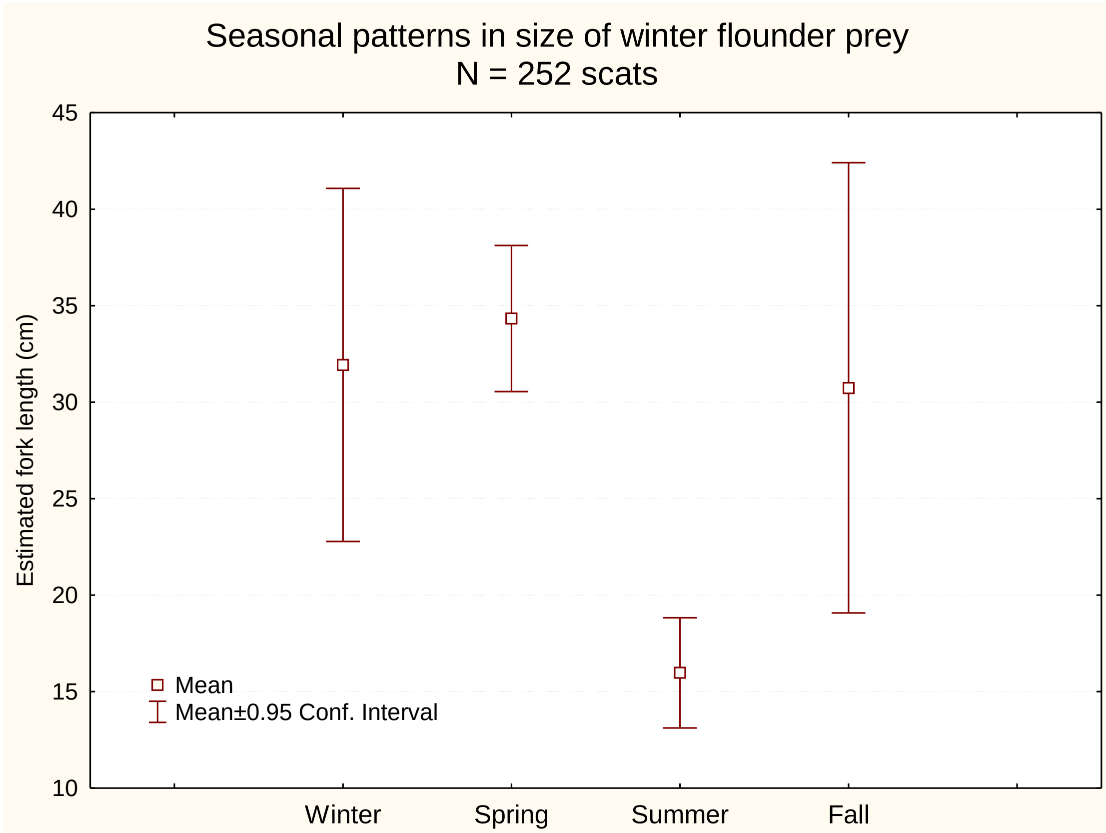

Figure 1.9: Seasonal patterns in reconstructed size of winter flounder (*Pseudopleuronectes americanus*) prey

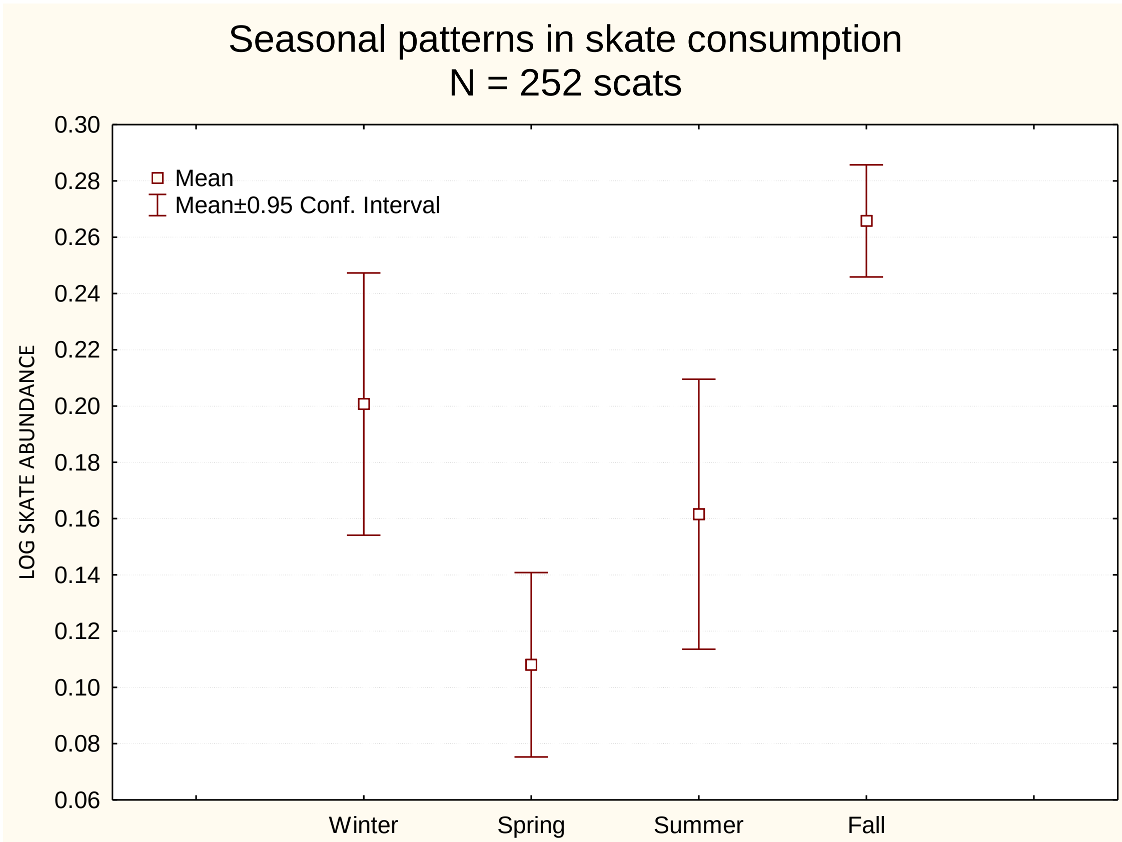

Figure 1.10: Seasonal patterns in consumption of skates (Family Rajidae)

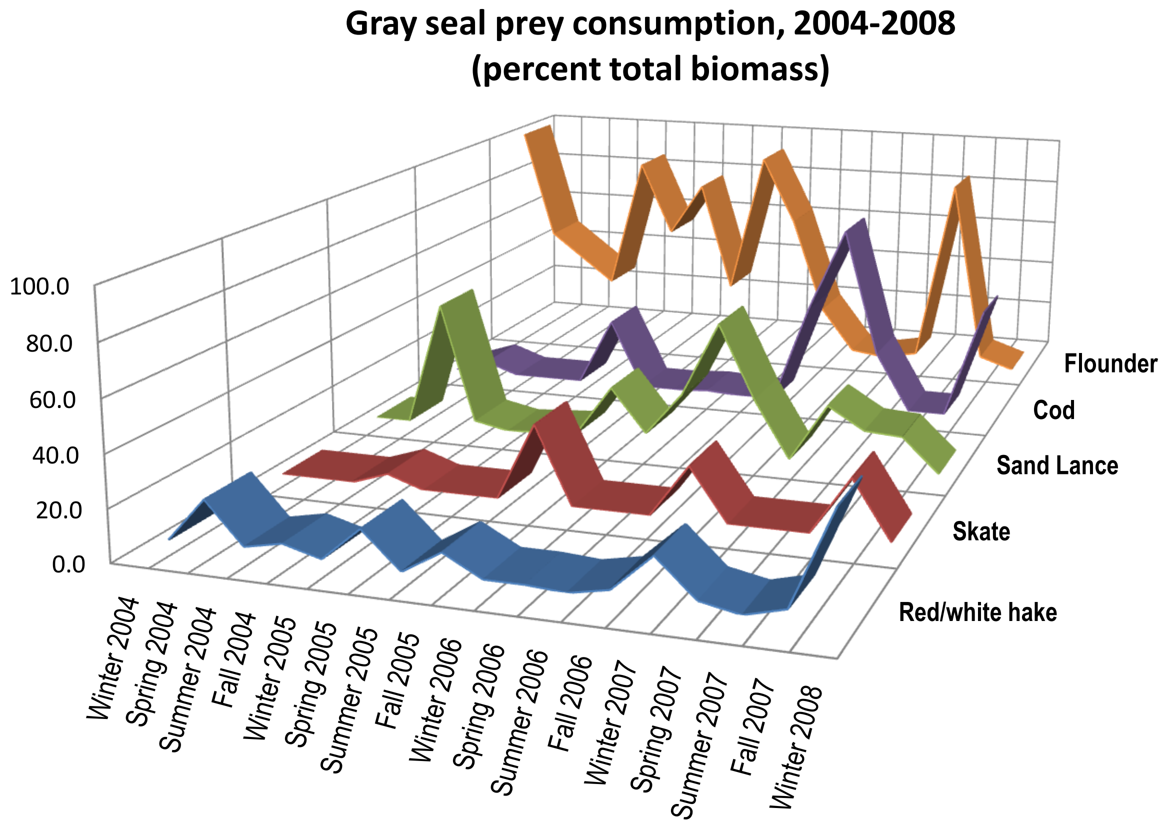

Figure 1.11: Gray seal prey consumption (% of total biomass, based on scat sampling), 2004-2008

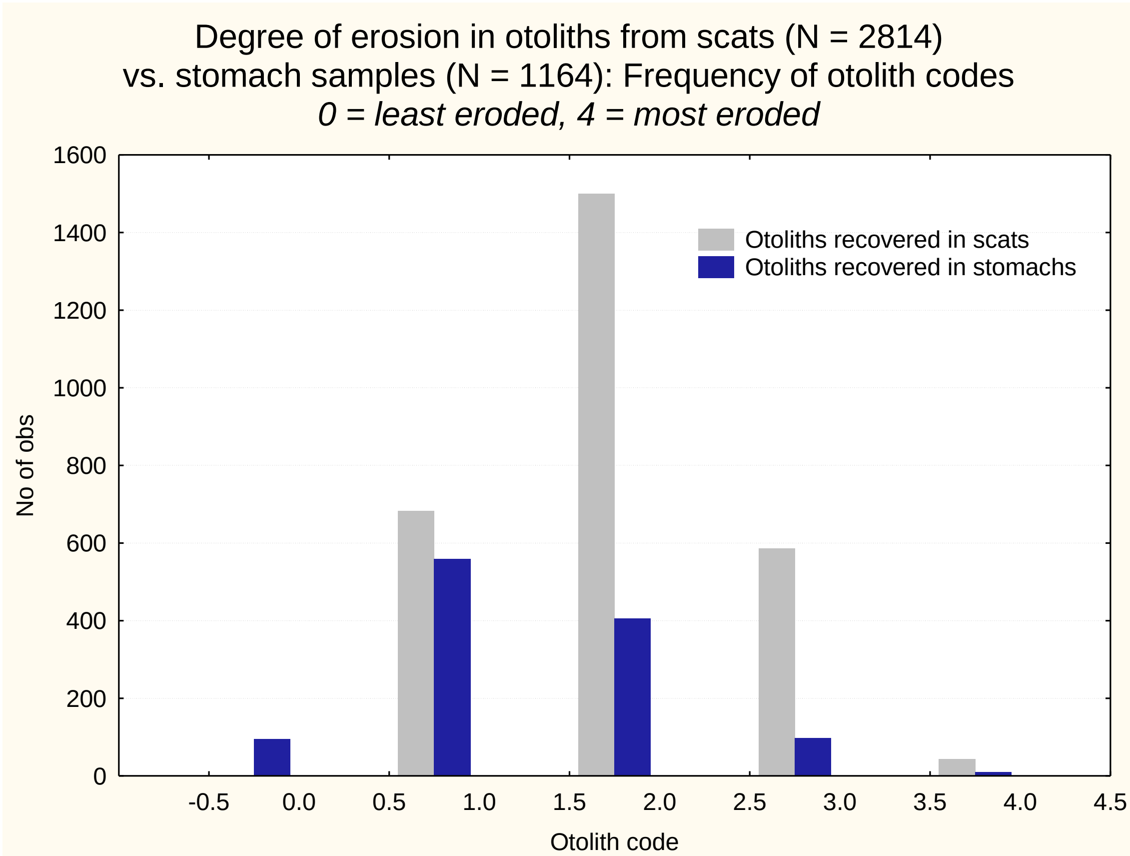

Figure 1.12: Degree of otolith erosion in scats vs. stomachs: frequency of otolith codes

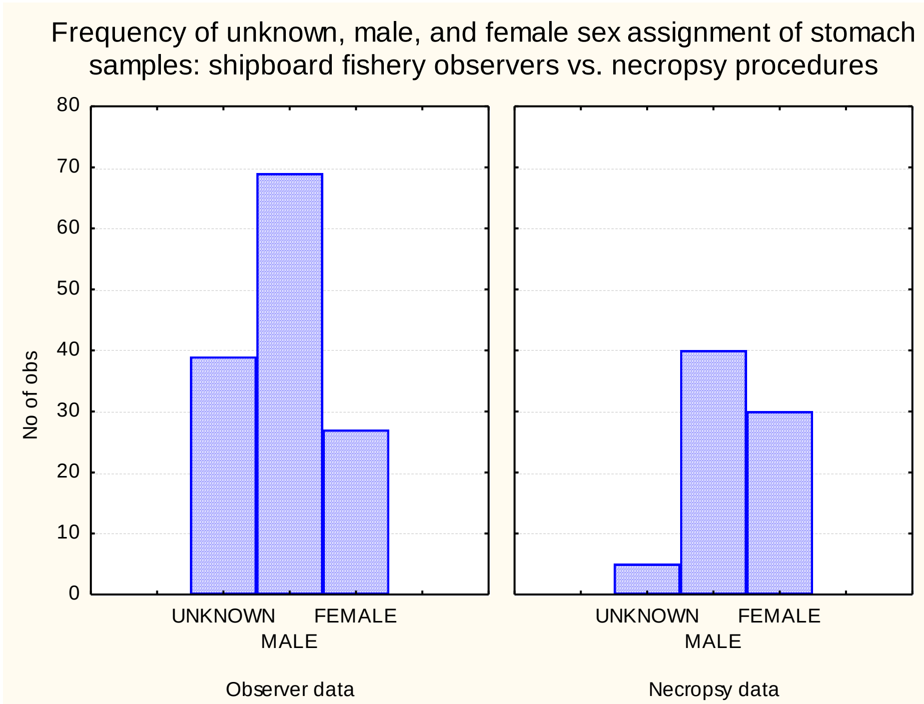

Figure 1.13: Frequency of unknown, male, and female sex assignment of stomach samples: shipboard fishery observers vs. necropsy procedures.

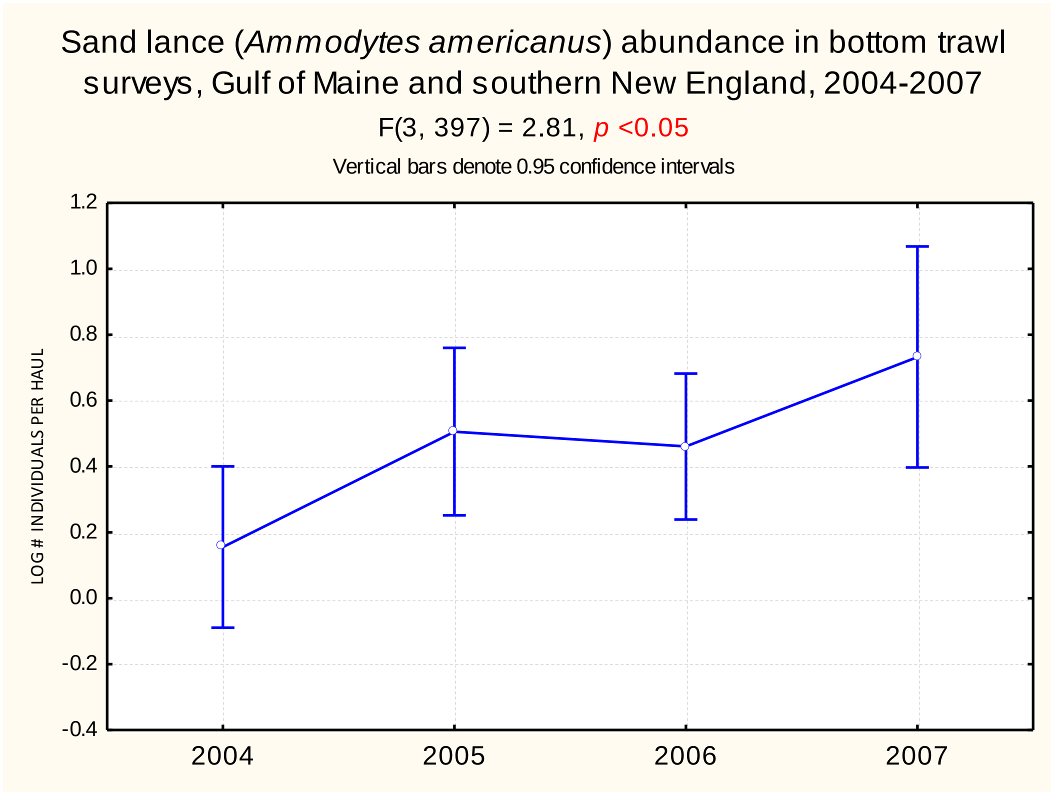

Figure 1.14: Increasing trend in sand lance (*Ammotytes americanus*) abundance, from bottom trawl surveys in the Gulf of Maine and southern New England

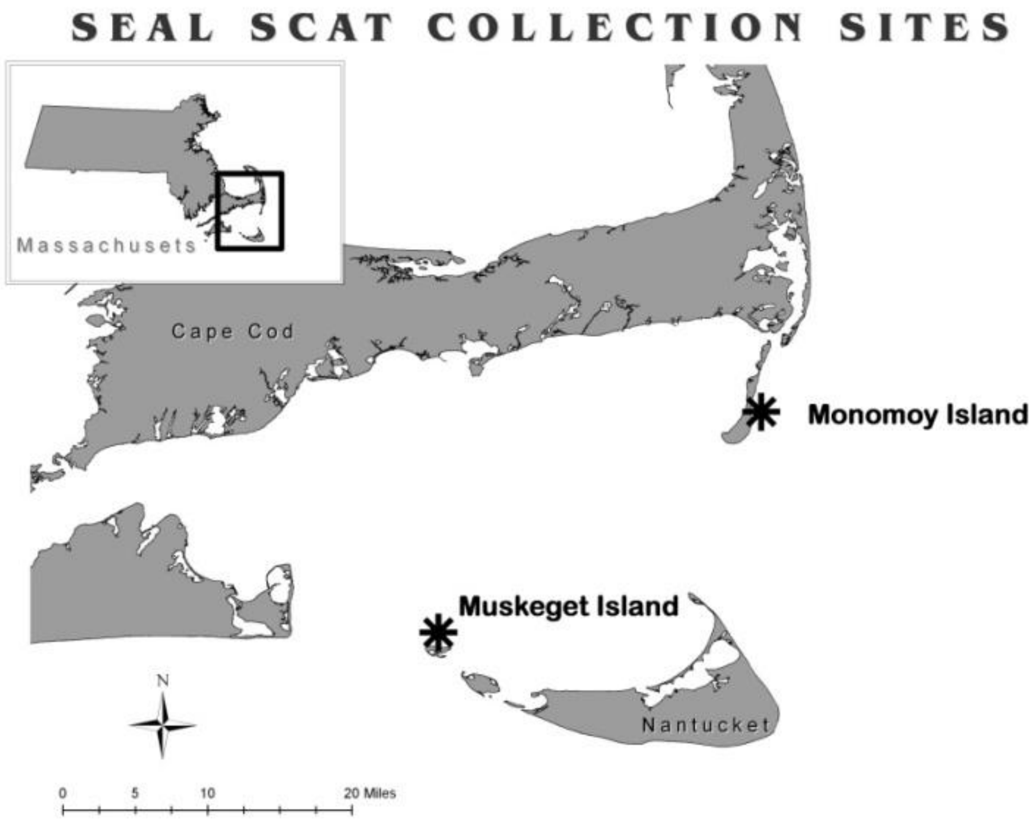

Figure 1.15: Scat sampling sites

Chapter 2. Gray seal diet in United States waters, estimated from fatty acid profiles in seal blubber

Introduction

Most studies of pinniped diet analysis involve inspection of hard prey remains (Bowen 2000). This technique is useful in order to 1) provide baseline knowledge of prey taxa in the diet, particularly in pinniped populations where no previous diet information exists, and 2) reconstruct prey size and mass using measurement of otoliths and cephalopod beaks. However, seals may not consume hard parts of certain prey taxa. For example, gray seals interacting with the coastal fixed-gear weir fishery off Chatham and Harwich, MA have been observed removing only the viscera of Atlantic menhaden, scup, sea robin, alewife and blueback herring (O. Nichols, U. Mass. Dartmouth, North Dartmouth, MA, unpubl. data; E. Eldridge, Chatham, MA, pers. comm.). Gillnet and demersal longline fishermen report widespread damage of Atlantic cod catch due to “belly biting” from seals (Read 2008), and commercial lobstermen contend that gray seals are a major predator of molting lobsters (called “softies”), although evidence of lobster is not recovered in diet studies (Bowen and Harrison 1994, Rough 1995, see chapter1). It is not known if these prey items are an important food source for gray seals foraging and breeding in the U.S., or if these incidents involve a small subset of animals that have learned to exploit fish that have been slowed or immobilized by human fishing activities, thus reducing their own energy expenditure in pursuing prey (Bowen *et al.* 2002). In part to address these questions, an alternative technique, called fatty acid analysis, has been developed to investigate the diet of various marine and terrestrial predators, including pinnipeds (Beck *et al.* 2007a, Ridoux *et al.* 2007), cetaceans (Thiemann *et al.* 2009), seabirds (Raclot *et al.* 1998) and bears (Iverson *et al.* 2001).

Fatty acids (FAs) comprise the bulk of all lipid, or fat, molecules (Budge *et al.* 2006), and a predator's fat deposits contain FAs that are contributed by their prey (Iverson *et al.* 2004). The proportion of various FAs in an individual's fat tissue, be it a predator or potential prey, is referred to as its fatty acid *signature,* or *profile*. During the digestion process, FA chains are removed from their glycerol backbones and then reattached to others, but are relatively unchanged (Iverson *et al.* 2004). The FAs present in a seal's blubber, therefore, provide information about the diet of these predators, and in a way that is complementary to hard part analysis. Hard parts provide a snapshot of diet, since scats contain prey consumed in recent days, and stomachs contain prey consumed in recent hours (Grellier and Hammond 2006, Tollit *et al.* 2003). FA profiles in blubber reflect an animals' diet over weeks and months (Beck *et al.* 2007b). Fatty acid profiles are not subject to the biases arising from differential erosion of hard parts in the digestive tract, and may reveal the presence of prey items that have no hard parts. Since blubber cores are removed from dead animals whose biological information has been recorded, FA profiles may be analyzed within the context of the sex and age of the seal, which scats cannot.

Fatty acids are distinguished by the number of carbon atoms they contain, and the number and position of their double-bonds (Budge *et al.* 2006). For example, the fatty acid **16:4n3** has 16 carbons and four double bonds, the first of which occurs 3 carbons away from the terminal methyl group, which forms the tail end of the fatty acid molecule (Budge *et al.* 2006). Since the 16: 4n3 FA has more than one double bond, it is termed a *polyunsaturated* fatty acid (PUFA). An FA with one double bond is a *monounsaturated* fatty acid (MUFA). An FA molecule with no double bonds is *saturated*. Two types of fatty acid molecules exist in seal blubber: those that are contributed by prey, and those that are synthesized by the predator's own metabolism (Iverson *et al.* 2004). The former are *dietary* fatty acids, and the latter are *endogenous* fatty acids. Only dietary FAs contain information about the animal's diet history. Dietary FAs can be distinguished, in most cases, by the number of carbon double-bonds present in the molecule. Since mammals have very little ability to synthesize unsaturated fatty acids, polyunsaturated FAs (those with two or more double bonds) are contributed by diet (Budge *et al.* 2006). However, certain monounsaturated FAs are also dietary (Iverson *et al.* 2004).

Knowledge of spatial, temporal and intra-specific diet variation is essential in understanding the seal's role in marine food webs (Bowen 1997). Age and sex differences in diet provide information about species niche breadth (Beck *et al.* 2007a). Diet differences between individual seals, as well as variation across regions, seasons, and years, allows the construction of more accurate consumption estimates, sometimes used to quantify seals' impact on fish stocks (Hammill and Stenson 2000). One method of inferring diet from FAs involves the qualitative comparison of FA signatures in individual predators to investigate diet variation over time, and among different demographic groups, such as age, sex, and region (Budge *et al.* 2006). Adult gray seals are able to dive deeper and longer than young seals, allowing them to exploit demersal prey, while young seals exploit pelagic species to a greater extent (Bowen and Harrison 1994). Young seals include more prey types in their diet, since they are less selective about prey than adults due to lack of foraging experience, and have not yet learned to reliably exploit profitable foraging grounds (Austen *et al.* 2004, Sjöberg and Ball 2000). Adult male and female gray seals use different foraging grounds, and target different prey, according to proximity to the breeding season (Beck *et al.* 2003, Breed *et al.* 2006). Seal diets vary regionally, since fish prey assemblages vary by location (Bowen and Harrison 1994, Gabriel 1992).

Seal diets can also be estimated quantitatively using Quantitative Fatty Acid Signature Analysis, or QFASA (Iverson *et al.* 2004). This technique uses a statistical model to infer the prey species most likely consumed, and their relative proportions, by comparing the FA signatures of potential prey and the FA signature of the predator (Budge *et al.* 2006). A complex of ~80 fatty acids in the marine environment is present in the tissues of both fish and in seals, in varying frequencies. Since there exists no "unique molecule" to identify particular prey taxa consumed by a seal (Budge *et al.* 2006), biologists have relied upon distinctive groupings to identify these taxa. QFASA requires the identification of all potential prey species, and their respective FA signatures (a fatty acid "library"), in order to statistically infer those species most likely represented in the FA signature of a seal (Iverson *et al.* 2004). Adequate within-species sampling of prey groups is necessary when constructing a prey library, since FA signatures vary within prey species, due to regional differences in diet and age-related diet shifts (Budge *et al.*

2002). Since a complete prey library is not available for U.S. waters, I was unable to carry out this method of diet estimation. However, I identified the FA signatures of 45 gray seals, and these may be used to perform QFASA at a future time, when a comprehensive prey library becomes available.

Although the relative proportions of prey in the diet can only be inferred using QFASA, it is possible to identify general trends in prey consumption by comparing the ratio of dominant FAs in those of seals and potential prey (Budge *et al.* 2006). For example, there may be a 3:1 ratio of two FA molecules in seal blubber. If a certain potential prey item also has this ratio of FA molecules, it suggests that prey item is important in the diet of the seals sampled.

The aims of this study are to 1) identify any existing regional, temporal, sex, and age differences in gray seal diet inferred from blubber fatty acids, 2) identify the particular fatty acids that contribute the most to within-group variation, 3) compare relative amounts of FAs in seal blubber and in prey, and infer species that may be important in the diet, and 4) compare findings from blubber and stomach analysis, and see if these methods give similar results.

Methods

I used a qualitative approach to compare the fatty acid profiles of individual seals (Beck *et al.* 2007b, Ridoux *et al.* 2007), and investigated regional, temporal, sex and age differences in diet. I used the following nomenclature for fatty acid molecules (Budge *et al.* 2006):

A:BnX

Where:
A = the number of carbon atoms in the molecule
B = the number of double bonds in the molecule
X = the position of the first double bond relative to the terminal methyl group

I included only dietary FAs in the analysis. I selected a subset of 31 monounsaturated and polyunsaturated FAs known to be of dietary origin in gray seals (Iverson *et al.* 2004) (Figure 2.1).

I obtained seal blubber samples from animals taken in commercial fisheries operating in the Gulf of Maine, southern New England, and mid-Atlantic Bight waters (Figure 2.2, Table 2.1). Northeast Fisheries Observer Program (NEOP) observers deployed on commercial fishing vessels extracted and preserved blubber samples from marine mammals for future analysis (Bisack 2003). In some cases observers retained the whole animal, in which case blubber samples were removed during subsequent necropsy procedures in Woods Hole, MA (G. Shields, NEOP, Woods Hole, MA, pers. comm.). In both cases a 10 cm^2 section of blubber, which extended to the intersection of the muscle layer, was removed from the ventral area, approximately 6 inches anterior to the navel (G. Shield, NOAA Observer Program, NMFS/NEFSC, Woods Hole, MA, pers. comm.). I inferred the age of seals from the recorded straight length of the animal, measured from nose to tail (Table 2.2) (Hall and McConnell 2007). The entire blubber layer was used for lipid analysis in order to get the maximum amount of diet information possible. The inner blubber layer, closer to the muscle, reflects a more recent diet, (on the order of days), whereas blubber near the skin layer reflects prey integrated over weeks and months (Thiemann *et al.* 2009).

Samples were placed in sealed plastic bags, and stored at –20^{o} C at the NMFS facility in Woods Hole, Massachusetts. Cores used in this study were stored for a period of between 1 and 14 years, depending on date of collection. Taken from animals dead <48 hrs. Some samples oxidized during long storage. Twenty-nine of 45 (64%) of blubber and stomach samples were taken from the same animal. I inspected the stomach contents of 29 seals that provided blubber samples, and asked if similar patterns emerged from fatty acids and stomach contents. I investigated temporal, regional and intraspecific diet differences in these two diet measures, and compared results.

I investigated regional variation in FA profiles in the context of fishery statistical areas defined by the Northwest Atlantic Fisheries Organization (NAFO) (Figure 2.2). I chose these spatial units because 1) they are outlined based on stock distribution areas of commercially important species, and were "designed to correspond with the natural divisions of fish populations and barriers to migrations" (Halliday and Pinhorn 1990); 2) all marine mammal bycatch is reported in terms of statistical area of capture; 3) NAFO areas provide a spatial structure relevant to commercial fishing effort, catch and landings, of interest when relating seal foraging behavior to commercial fisheries, and 4) the exact coordinates of vessels reporting marine mammal bycatch is confidential, whereas the statistical area of bycatch locations is not (A. Van Atten, NOAA Observer Program, NMFS/NEFSC, Woods Hole, MA., pers. comm.).

Forty-nine gray seal blubber cores collected by NMFS fishery observers were sent to the Food Science Program laboratory at Dalhousie University for analysis. Of these, three were duplicate samples taken from the same animal, and one sample was extremely oxidized and could not be separated from the plastic bag. Therefore, a total of 45 samples were analyzed for fatty acid content. Fatty acid molecules were extracted from homogenized fat tissue and converted to fatty acid methyl esters (FAMEs) using gas chromatography, according to methods described by Budge *et al.* (2006). Seventy-eight FAMEs were identified and reported as percent weight of total fatty acids (Table 2.3).

I compared ratios of individual FAs within seal blubber samples, to ratios within fish and crustacean species sampled by Budge et al (2002). I calculated as the quotient of FA_1/FA_2, where the values of each were the percent weight contributed to the total weight of all fatty acids in a sample (Table 2.3). A complete catalog of fatty acid profiles was not available for the fish, squids and crustaceans important in gray seal diets in their U.S. range. FA profiles were available for a subset of these species, identified from specimens collected in Scotian Shelf waters (Iverson *et al.* 2004, Tables 2.4 A-E). FA profiles in fish show significant regional variation (Budge *et al.* 2002), and prey should be sampled in the region where seals are foraging in order to infer meaningful relationships in FA patterns between prey and predator (Beck *et al.* 2007a). However, gray seals instrumented with satellite-tracked tags move across the maritime border, and forage in both U.S. and Canadian waters (Breed *et al.* 2006). The gray seals sampled in this study, although taken in U.S. waters, had the potential to forage in Scotian Shelf waters, and I felt confident inferring broad trends in prey consumption based on available published FA profiles.

Data analysis

I analyzed data on a subset of 31 of the original 78 FAMEs identified by gas chromatography (Figure 2.1, Table 2.3). I chose these 31 FAs because their length and number of carbon atoms indicated that they were contributed by the seal's diet, and not endogenously produced (Iverson *et al.* 2004). I used two multivariate methods to investigate grouping of individuals based on their FA profiles. First, I explored the raw data using hierarchical tree clustering (Statistica 7, StatSoft), which forms natural clusters of groups based on their similarity or dissimilarity. Similarity among individuals was defined by the Euclidean distance between FA datapoints. Linkage distance was scaled using Dlink/Dmax*100, resulting in distances between 1 and 100, with 1 representing the closest possible relationship between individuals, and 100 the furthest. This technique does not require the data to be normalized, and allows visualization of the data even when within-group sample sizes are small (Smith *et al.* 1997). Tree cluster analysis does not report statistical significance of grouping patterns, however; it only allows identification of relatively homogenous groups of individuals based on their FA composition (Budge *et al.* 2006), resulting in a hierarchical tree diagram, known as a dendrogram.

I also tested the ability of fatty acid profiles to predict a seal's membership in a particular group using discriminant function analysis (Statistica 7, StatSoft), which predicts a given categorical independent variable (in this case sex, age, season, year and region) using a set of continuous dependent variables (in this case the relative weights of fatty acids in a given blubber sample). I identified particular fatty acids that most influenced the grouping of individuals using the factor structure matrix generated by DFA (Budge *et al.* 2006). DFA was also used to measure the ability of FA profiles to classify seals to demographic group, with each grouping variable having success rates between 0% and 100%. DFA requires at least as many samples as there are variables, and the reduction of the number of variables in relation to the number of samples increases the likelihood that the covariance matrices are homogenous (Budge *et al.* 2002, Ridoux *et al.* 2007). Therefore, I performed discriminant function analysis on 25 fatty acids that were selected from the larger subset of 31 dietary fatty acids, on the criterion that they were polyunsaturated, having at least two double bonds. Mammals cannot synthesize unsaturated fatty acids, and polyunsaturated FAs are contributed by diet (Budge *et al.* 2006). Categories with fewer than two representative samples were excluded from the analysis, since DFA cannot be performed on groups containing a single case. Therefore, although ten NAFO statistical areas were sampled, only 4 of these were included in the regional analysis, and the years 1994, 1997, 1999 and 2001 were excluded from the analysis of annual patterns.

I normalized the data using the following log transformation for proportional data (Budge *et al.* 2006):

$$X \text{ trans} = \ln (xi/cr)$$

Where:
xi = a given FA expressed as percent weight of total FA
X trans = transformed FA data
cr = percent weight of a reference FA

I chose 18:0 as a reference FA, since it is endogenously produced by the seal and therefore provides no information about diet, but was well quantified by gas chromatography (Budge *et al.* 2006, Table 2.3).

I investigated relationships among demographic groups using hierarchical tree clustering of the data, which allowed visual inspection of similarity among individuals. An advantage of tree clustering is that it allows investigation of grouping patterns in large datasets despite small within-group sample sizes, which discriminant function analysis does not (Budge *et al.* 2006, Smith *et al.* 1997). Opportunistic sampling led to uneven representation of individuals in different age, sex, temporal and regional groups (Table 2.1). I pooled samples collected in different months into seasons, since 1) seal diets were expected to shift with seasonal changes in prey distribution and abundance, and 2) this increased numbers of samples within a given time period. Seasons were defined as follows: *winter* = December 21-March 20; *spring* = March 21-June 20; *summer* = June 21-September 20; *fall* = September 21-December 20.

Results

Demographic summary of samples

Of the 45 seals sampled, 28 were yearlings (1-2 years old), and 17 were young-of-the-year pups (<1 year old). Bycaught adult gray seals are rarely sampled by fishery observers. It is logistically difficult to bring large animals onboard fishing vessels, and adult (>6 years old) seals are often cut loose from gear without being sampled. Adult seals are also more likely to break free from gear once they have been entangled (B. Lentell, NOAA Observer Program, NMFS/NEFSC, Woods Hole, MA, pers. comm.). Of those seals sampled, 17 were female, 26 were male, and two seals were not sexed during sampling/necropsy procedures. Thirty-two of the 45 seals sampled were caught in statistical areas 521 and 537 (Great South Channel and southern New England, Table 2.1, Figure 2.2). All samples were collected since 1994, and 36 of 45 seals were sampled between 2004 and 2007. Most (37 of 45) seals were sampled in spring and summer.

Hierarchical clustering of fatty acid profiles

Sex and age of seals accounted for two of the three closest groupings on the tree (Figure 2.3). The three smallest linkage distances were between 20.5 and 24 distance units, and defined groups of seals that were most similar. The closest grouping was comprised of 2 male yearling seals, and the third closest grouping included two female yearlings. In addition, the majority of female yearling seals (10 out of 12) clustered into a group defined by 45 distance units (Figure 2.3). The addition of region, season and year to the dendrogram did not result in clearer grouping patterns, suggesting that intraspecific variation in FA profiles played the most important role in group similarity. Overall, no clear seasonal, annual, or regional groupings emerged when individual seals were plotted on a dendrogram.

Discriminant function analysis

FA profiles clearly discriminated seals by age (Wilks-Lambda = 0.27, $F(25,19) = 2.07$, $p < 0.054$), with a 95.56% classification success rate (Figure 2.4). All seals were either young-of-the-year pups or yearlings. Age classification was influenced most by the 18:3n3 and 20:4n3 fatty acids (Figure 2.5). There was clear distinction between male and female seals (Figure 2.6), (Wilks-Lambda = 0.29, $F(25,17) = 1.65$, $p < 0.144$), and FA profiles classified seals to sex with a 95.35% success rate. Sex classification was dominated by 18:3n3 and 20:4n3 (Figure 2.7).

Seals were classified according to year (Wilks-Lambda = 0.003, F (125,59) = 1.06, p <0.412) with a 90.24% success rate. Years 2000, 2003, 2004, 2005 and 2006 were clearly separated on the 1st and 2nd discriminant functions (Figure 2.8), but 2007 overlapped with other years. DFA of seals with respect to year generated 5 discriminant functions, the first 3 of which explained 85% of the variance. The first discriminant function explained 42% of the variance, and was defined by 22:4n3. The second discriminant function accounted for 22% of the variance, and was primarily influenced by 16:4n3 (Figure 2.9).

Seals were classified according to region of capture (Wilks-Lambda = 0.04, F (75,33) = 0.90, p <0.648) with 94.87% success. Seals in all four statistical areas included in the analysis, 525 (Georges Bank), 521 (Great South Channel), 513 (western Gulf of Maine) and 537 (southern New England) separated well, with those captured in 537 in the upper right quadrant, 513 in the lower right quadrant, and 521 and 525 in the upper left quadrant (Figure 2.10). DFA of seals with respect to region generated 3 discriminant functions. The first, which explained 53% of the variance, was influenced primarily by 18:2n6. The second discriminant function explained 36% of the variance, and was mostly influenced by 18:3n6 (Figure 2.11).

Fatty acid profiles were least able to classify seals according to season (Wilks-Lambda = 0.09, F (75,51) = 0.86, p <0.736); but they were able to do so with an 86.67% success rate. Seals sampled in winter, summer and fall samples showed clear separation, with fall samples clustering in the upper right quadrant, winter in the lower right, and summer in the upper left quadrant (Figure 2.12). Spring samples separated less well and overlapped with other seasons. DFA with respect to season generated 3 discriminant functions. The 1st discriminant function explained 46% of the variance, and was defined by 18:2n6. The 2nd discriminant function explained 38% of the variance, and was primarily influenced by 20:2n6, 22:4n6 and 20:3n3 Figure 2.13).

Important prey taxa

The fatty acid 22:6n3 contributed the most by weight of any FA in seal blubber, and was also dominant in most prey species sampled by Budge *et al.* (2002) (Table 2.4 A-E). There was an approximate 2:1 ratio of the weights of 22:6n3 and 20:5n3 fatty acids in seal blubber (10.12/5.00 = 2.02), (Table 2.3) and this difference persisted across demographic groups (Figures 2.14-2.18). Two of 28 prey species had a similar ratio of these two FAs: alewife (*Alosa pseudoharengus*, 15.04/7.48 = 2.01, Table 2.4A) and smooth skate (*Malacoraja senta*, 20.87/10.02 = 2.08, Table 2.4D). In many cases, the most dominant FAs, and those with predictable ratios, were not the same as those FAs that were responsible for the majority of within-group variation. Fatty acid ratios in seal blubber did not match those of American lobster (*Homarus americanus,*7.69/17.04 = 0.45).

Comparison of diet estimated from fatty acids and hard parts

Results from fatty acid and stomach contents were similar to some extent. Sex differences in diet were detected in stomach samples (males consumed more silver hake, *Merluccius bilinearis*, than did females: $F_{1, 35} = 6.33$, p =.017). Sex differences, along with age differences, influenced grouping of seals by fatty acid profiles. Age differences were apparent in both fatty acid and hard part data. FAs grouped seals according to age with more confidence than any other group. Although analysis of 49 seal stomachs yielded no significant age differences in diet, stomach samples, on average, contained different prey types, and had a significantly higher number of prey taxa, than did scat samples ($F_{1,352} = 8.86$, $p = 0.003$). This could be an age-related effect because all stomachs but one were from young seals, whereas scats reflected the diet of adult seals and young seals. Significant regional differences in diet were detected in stomach samples (more red/white hake was recovered in stomachs collected in southern New England/New York Bight than in other areas, $F_{8, 28} = 6.83$, $p < 0.001$). The fatty acid profiles of seals from different NAFO areas separated well in canonical projections (Figure 2.10), although differences among these seals were not statistically significant.

Comparison of FAs in seal blubber and various prey species suggested that smooth skate and alewife are important in the diet. Skates were important prey items in scats, and were recovered in 24.5% of samples, more frequently than any other taxon (Table 2.5). However, only 7 of 49 stomachs showed evidence of skates (Table 2.6). I was unable to identify species of skates from hard part analysis. No alewife was recovered in scats or stomachs. Alewife, also known as river herring, is a clupeid. The only clupeid recovered in scats and/or stomachs was Atlantic herring (*Clupea harengus*), but did not make up an important part of the diet inferred from either sampling method (Tables 2.5 and 2.6).

Discussion

Hierarchical clustering of fatty acid profiles indicated that intraspecific differences in FA profiles, namely the age and sex of seals, played more important roles in group similarity than temporal or regional variation. Fatty acid profiles were best able to distinguish seals according to age. The difference in diet between first year pups and yearlings may be explained by the slightly greater foraging experience of the latter group. Young seals are more likely to engage in exploratory foraging behavior, have less developed prey preferences, and have larger and more variable home ranges than do adults (Austen *et al.* 2004, Sjöberg and Ball 2000). Gray seal pups are completely weaned at 3-4 weeks, have no parental care when they enter the sea, and must learn to hunt without parental influence. The yearlings in this study may have had more foraging experience, and learned to exploit profitable foraging grounds to a greater extent, than YOY pups. This would explain diet differences observed in both blubber and stomach samples of young seals. The higher number of prey taxa recovered in stomachs, as opposed to scats, suggests that young seals have a more diverse diet than that of adults.

The possibility exists, however, that the higher number of prey taxa in stomachs is not an age-related effect, but rather due to the fact that these seals were associating with commercial fishing vessels, whose gear captures a variety of both target species and bycatch. This situation may be analogous to a “buffet”, where a variety of food options are present, in contrast to seals hunting on their own in more homogenous prey assemblages that may be spatially separated. Seals taken in commercial fishing gear showed a higher proportion of economically important fish, such as hake, in the diet, whereas scat samples collected independent of commercial fisheries were dominated by sand lance, which is not economically important in the U.S.

The discrepancy between stomach and blubber analysis in reporting regional differences was likely due to the fact that stomachs and blubber represent seals' diet history on different time scales. Seal stomachs contain prey consumed in the last 12 hours (Grellier and Hammond 2006, Tollit *et al.* 2003). FA molecules in blubber reflect prey consumed weeks and months prior to sampling, with more recent prey information located in the blubber column region closest to the muscle layer, and less recent diet history contained closer to the skin layer (Thiemann *et al.* 2009). It is therefore not surprising that stomachs reflect prey differences according to region, whereas blubber fatty acids do so to a lesser extent. Blubber cores were taken from animals at sea, where seals are highly mobile and able to move between NAFO fishery statistical areas. It is therefore likely that seals consumed prey in overlapping statistical areas during the period of fatty acid deposition in the blubber layer (Budge *et al.* 2006). Prey in stomachs represent a very recent snapshot of diet, and may reflect separate prey assemblages encountered by seals in different NAFO regions (Bowen and Harrison 1996).

Seasonal, regional, age and sex differences were all detected in FA profiles to some extent. Although I was unable to separate the effects of region, age, sex and season on diet based on my data, gray seal foraging grounds have been shown to be dependent on season, age and sex of the seal (Breed *et al.* 2006, Sjöberg and Ball 2000). In Canada, male and female gray seals exploit separate foraging grounds in the months leading up to, and following, the breeding season (Breed *et al.* 2006), and in the Baltic, young seals have larger and more variable home ranges than adults (Sjöberg and Ball 2000).

Analysis of individual FAs in seals and fish suggest that skates and alewife are important in the diet of the gray seals sampled in this study. Skates are primarily demersal, but alewife are pelagic, and swim higher up in the water column (Bigelow and Schroeder 2002). Skates are important in the diet as measured from scats, and this result is not surprising. Although alewife was not recovered in scats or stomachs, it may be an important food item for several reasons. Demersal species dominate the diet of adult gray seals, whereas young seals include pelagic species, and shrimps, in their diet to a greater extent (Bowen and Harrison 1996) since they have less ability to dive to depths, and for long periods of time, than do adult seals (Austen *et al.* 2004, Bowen and Harrison 1996). Gray seals have been observed consuming alewife in weir traps in southern New England (O. Nichols, U. Mass. Dartmouth, North Dartmouth, MA, unpubl. data; E. Eldridge, Chatham, MA, pers. comm.). Alewives enter rivers on Cape Cod and in northern Massachusetts in the spring for the purpose of spawning, and are a potential seasonal prey item for seals. Alewife detected by blubber analysis may therefore be due to 1) free-swimming young seals targeting pelagic species, 2) seals preying upon pelagic species caught in fixed fishing gear, or 3) a combination of both of these factors.

The FAs responsible for most within-group variation were not identical to those that identified potential prey taxa. This is because those FAs that contributed to the most variation among seals were not necessarily the most abundant, and did not always occur in predictable ratios to other FAs.

The blubber fatty acids identified in this work provide basic information about diet variation among individual gray seals. Future studies should employ Quantitative Fatty Acid Signature Analysis (QFASA) to investigate particular prey species consumed by gray seals, and their relative importance in the diet. Results could be compared to those found by hard part analysis, since other studies have shown large discrepancies in diet estimated using these two methods (Beck *et al.* 2007a). Blubber samples collected from live seals, of known age and sex, at a variety of haul out locations in the U.S., and sampled repeatedly across time, would provide more comprehensive data on the temporal, regional and intraspecific influences on gray seal diet. Understanding this variation will allow better estimates of the predation impact of this species upon fish stocks, and add to our knowledge of the foraging ecology of this species.

Chapter 2: Tables

Seal ID (N = 45)	Season	Year	Sex	Age	Length (cm)	Statistical Area
3447	Fall	1994	UNK	Yearling	125	513
3429	Winter	1997	Female	YOY	98	521
6518	Fall	1999	Male	YOY	108	513
6523	Spring	2000	Male	Yearling	115	537
6525	Spring	2000	Male	YOY	104	537
6905	Spring	2000	Female	Yearling	111	537
6238	Summer	2001	Male	Yearling	138	616
5182	Spring	2003	Male	Yearling	118	537
5189	Summer	2003	Male	YOY	105	537
3271	Spring	2004	UNK	YOY	110	537
3941	Spring	2004	Female	Yearling	114	521
4119	Spring	2004	Male	Yearling	115	537
4120	Spring	2004	Female	Yearling	115	537
4121	Spring	2004	Male	YOY	106	537
4481	Spring	2004	Female	YOY	109	521
4482	Spring	2004	Female	YOY	107	521
5192	Spring	2004	Male	YOY	98	521
5406	Summer	2004	Female	Yearling	117	521
6101	Spring	2004	Female	YOY	98	521
6868	Spring	2004	Male	Yearling	114	521
3918	Spring	2005	Female	Yearling	112	537
3921	Spring	2005	Female	YOY	101	537
5138	Fall	2005	Female	Yearling	118	521
5616	Spring	2005	Female	Yearling	131	537
6867	Spring	2005	Male	Yearling	111	514
8526	Summer	2005	Male	YOY	108	562
8669	Spring	2005	Male	Yearling	114	537
5310	Fall	2006	Female	Yearling	124	537
6563	Summer	2006	Female	Yearling	120	513
8271	Fall	2006	Female	Yearling	113	513
8742	Winter	2006	Male	YOY	105	537
5136	Spring	2007	Female	Yearling	124	526
5846	Summer	2007	Male	Yearling	131	521
5850	Summer	2007	Male	Yearling	139	521
6140	Summer	2007	Male	Yearling	147	521
6209	Winter	2007	Male	Yearling	136	537
8204	Spring	2007	Female	Yearling	113	537
8205	Spring	2007	Male	YOY	94	537
8273	Spring	2007	Male	YOY	107	525
8321	Summer	2007	Male	Yearling	125	521
8361	Spring	2007	Male	Yearling	112	539
8407	Spring	2007	Male	YOY	108	525
8409	Spring	2007	Male	YOY	107	525
8855	Summer	2007	Male	Yearling	125	521
8966	Spring	2007	Male	Yearling	111	515

Table 2.1: Summary of seal blubber samples

Age	Age class	Length (cm)
0-1 yrs	Young-of-the-year pup (YOY)	≥105
1-2 yrs	Yearling	106-115
2-5 yrs	Subadult	116-160
≥ 6 yrs	Adult	> 160

Table 2.2: Age of seals inferred from straight length

FATTY ACID	MEAN WT.	SD	FATTY ACID	MEAN WT.	SD
12:0	0.11	± 0.02	**18:3n4**	0.18	± 0.04
13:0	0.02	± 0.00	**18:3n3**	0.63	± 0.17
i-14:0	0.02	± 0.00	**18:3n1**	0.10	± 0.02
14:0	3.61	± 0.47	**18:4n3**	1.06	± 0.22
14:1n9	0.07	± 0.02	**18:4n1**	0.18	± 0.06
14:1n7	0.07	± 0.01	**20:0**	0.05	± 0.02
14:1n5	1.07	± 0.22	**20:1n11**	2.31	± 0.69
i-15:0	0.16	± 0.02	**20:1n9**	6.74	± 1.96
ai-15:0	0.07	± 0.01	**20:1n7**	0.52	± 0.14
15:0	0.30	± 0.04	**20:2NMID1**	0.02	± 0.02
15:1n8	0.02	± 0.01	**20:2n9**	0.01	± 0.01
15:1n6	0.08	± 0.02	**20:2NMID2**	0.05	± 0.02
i-16:0	0.07	± 0.01	**20:2n6**	0.19	± 0.05
16:0	8.39	± 1.19	**20:3NMIT**	0.02	± 0.01
16:1n11	0.58	± 0.09	**20:3n6**	0.10	± 0.01
16:1n9	0.47	± 0.07	**20:4n6**	0.64	± 0.22
16:1n7	15.10	± 2.42	**20:3n3**	0.10	± 0.03
16:1n5	0.29	± 0.03	**20:4n3**	0.57	± 0.10
17:1(a)	0.07	± 0.02	***20:5n3***	*5.00*	*± 1.26*
i-17:0	0.20	± 0.04	**22:0**	0.02	± 0.01
16:2n6	0.08	± 0.02	**22:1n11**	1.49	± 1.18
ai-17:0	0.11	± 0.03	**22:1n9**	0.40	± 0.26
17:1(b)	0.23	± 0.05	**22:1n7**	0.04	± 0.02
16:2n4	0.41	± 0.11	**22:2NMID1**	0.01	± 0.01
17:0	0.16	± 0.04	**22:2NMID2**	0.01	± 0.01
16:3n4	0.25	± 0.11	**22:3NMIT**	0.00	± 0.01
17:1	0.38	± 0.08	**22:2n6**	0.03	± 0.01
16:3n3	0.01	± 0.00	**21:5n3**	0.40	± 0.06
16:4n3	0.12	± 0.05	**23:0**	0.02	± 0.01
16:4n1	0.36	± 0.15	**22:4n6**	0.19	± 0.09
18:0	0.98	± 0.22	**22:5n6**	0.21	± 0.06
18:1n13	0.09	± 0.02	**22:4n3**	0.13	± 0.03
18:1n11	5.82	± 1.93	**22:5n3**	4.68	± 0.58
18:1n9	17.00	± 2.60	**24:0**	0.00	± 0.00
18:1n7	4.57	± 0.53	***22:6n3***	*10.12*	*± 1.70*
18:1n5	0.50	± 0.06	**24:1**	0.10	± 0.03
18:2d5,11	0.08	± 0.03	**Total**	**100.00**	
18:2n7	0.11	± 0.03	**Sum of saturated**	**14.28**	
18:2n6	1.41	± 0.27	**Sum of unsat.**	**85.72**	
18:2n4	0.15	± 0.06	**MUFA**	**58.01**	
18:3n6	0.12	± 0.02	**PUFA**	**27.71**	

Table 2.3: Mean weights of 78 fatty acids identified by gas chromatography. Italicized values indicate FAs used to infer important prey taxa in the diet

	Am. Plaice (*n* = 99)	**Argentine** (*n* = 10)	**Butterfish** (*n* = 10)	**Capelin** (*n* = 56)	**Cod** (*n* = 84)	**Alewife** (*n* = 41)
Length (cm)	27.4 ± 8.5	26.2 ± 1.2	15.5 ± 1.9	13.3 ± 2.2	36.5 ± 6.7	22.8 ± 3.4
Mass (g)	217.8 ± 201.9	180.1 ± 27.0	73.1 ± 29.8	12.4 ± 5.9	481.1 ± 264.4	126.3 ± 48.2
Lipid content (%)	2.2 ± 1.3	6.6 ± 2.7	7.2 ± 3.1	8.3 ± 4.4	2.1 ± 1.0	12.6 ± 6.7
14:0	3.52 ± 1.46	6.56 ± 0.44	5.00 ± 0.96	6.26 ± 1.17	2.06 ± 0.84	5.17 ± 1.04
16:0	14.35 ± 2.03	11.90 ± 0.89	16.48 ± 1.00	12.48 ± 3.10	14.32 ± 1.79	16.83 ± 1.02
18:0	3.73 ± 1.15	2.13 ± 0.19	4.84 ± 0.77	1.14 ± 0.42	3.63 ± 0.95	2.87 ± 0.72
16:1n7	6.29 ± 3.88	4.77 ± 0.56	3.11 ± 0.74	9.96 ± 2.67	5.19 ± 3.10	3.85 ± 0.56
18:1n9	8.42 ± 1.62	7.40 ± 1.65	22.69 ± 5.37	7.26 ± 3.63	10.14 ± 1.67	15.46 ± 3.47
18:1n7	4.18 ± 1.09	2.04 ± 0.33	2.10 ± 0.32	2.87 ± 1.54	4.71 ± 1.33	3.28 ± 0.66
20:1n11	1.02 ± 0.79	0.65 ± 0.11	0.23 ± 0.22	0.46 ± 0.16	0.71 ± 0.30	0.83 ± 0.20
20:1n9	3.26 ± 2.02	13.52 ± 1.60	4.50 ± 1.27	12.42 ± 4.72	3.96 ± 2.49	5.91 ± 1.28
20:1n7	1.44 ± 0.86	0.56 ± 0.13	1.25 ± 0.31	0.74 ± 0.29	0.74 ± 0.45	0.56 ± 0.17
22:1n11	2.71 ± 2.61	17.67 ± 3.09	2.70 ± 2.65	15.34 ± 6.59	2.64 ± 2.30	5.80 ± 2.93
22:1n9	0.56 ± 0.42	1.69 ± 0.20	3.07 ± 0.84	1.40 ± 0.57	0.48 ± 0.28	0.75 ± 0.43
24:1	1.09 ± 0.44	0.43 ± 0.12	0.72 ± 0.28	0.91 ± 0.31	1.06 ± 0.68	0.53 ± 0.22
18:2n6	0.93 ± 0.32	0.96 ± 0.12	0.75 ± 0.23	1.19 ± 0.32	0.78 ± 0.20	1.36 ± 0.37
18:4n3	0.84 ± 0.63	1.77 ± 0.42	0.76 ± 0.42	1.34 ± 0.45	0.83 ± 0.47	1.63 ± 0.72
20:4n6	2.51 ± 1.18	0.70 ± 0.07	1.63 ± 0.39	0.34 ± 0.19	1.83 ± 0.81	0.86 ± 0.29
20:5n3	13.90 ± 2.76	7.61 ± 1.13	5.06 ± 0.84	7.39 ± 2.56	13.81 ± 2.23	*7.48 ± 0.87*
22:5n3	2.65 ± 0.76	1.40 ± 0.24	2.35 ± 0.20	0.74 ± 0.13	1.44 ± 0.30	1.64 ± 0.32
22:6n3	17.03 ± 5.76	9.60 ± 1.72	10.76 ± 2.26	9.65 ± 4.53	22.77 ± 7.50	*15.04 ± 3.13*

Table 2.4A: Fatty acid profiles of fish from the Scotian Shelf (adapted from Budge *et. al* 2002)

	Haddock (*n* = 54)	**Halibut** (*n* =8)	**Herring** (*n* = 74)	**Lobster** (*n* =9)	**Longhorn sculpin** (*n* = 20)	**Mackerel** (*n* = 10)
Length (cm)	27.0 ± 5.8	30.2 ± 4.3	26.0 ± 4.2	19.7 ± 0.8	25.0 ± 3.1	32.5 ± 2.2
Mass (g)	202.2 ± 133.2	245.0 ± 139.2	196.0 ± 91.1	243.7 ± 23.5	166.4 ± 72.0	280.5 ± 73.8
Lipid content (%)	1.4 ± 0.6	1.1 ± 0.3	7.7 ± 3.9	2.0 ± 0.6	1.4 ± 1.0	3.4 ± 2.0
14:0	1.97 ± 0.94	0.99 ± 0.28	5.33 ± 1.35	2.65 ± 0.51	2.63 ± 0.89	3.59 ± 1.19
16:0	14.39 ± 1.13	17.58 ± 0.56	13.65 ± 2.18	11.41 ± 0.67	12.46 ± 1.27	16.41 ± 0.95
18:0	4.08 ± 0.73	5.65 ± 0.61	1.39 ± 0.54	3.16 ± 0.28	3.78 ± 0.84	4.58 ± 1.03
16:1n7	3.07 ± 1.20	3.32 ± 1.45	6.24 ± 2.60	6.52 ± 0.43	6.71 ± 2.38	2.96 ± 0.79
18:1n9	8.82 ± 1.91	7.34 ± 1.18	7.25 ± 3.48	10.40 ± 1.50	11.26 ± 1.19	10.99 ± 2.57
18:1n7	4.13 ± 0.86	4.37 ± 0.77	2.34 ± 0.50	6.53 ± 0.73	4.77 ± 0.91	3.46 ± 0.58
20:1n11	0.72 ± 0.24	0.30 ± 0.25	0.96 ± 0.36	1.68 ± 0.37	0.63 ± 0.17	0.66 ± 0.23
20:1n9	3.10 ± 1.94	0.82 ± 0.28	11.09 ± 3.41	4.53 ± 1.55	3.87 ± 1.48	4.92 ± 1.94
20:1n7	0.83 ± 0.30	0.60 ± 0.32	0.50 ± 0.28	1.69 ± 0.20	0.46 ± 0.18	0.52 ± 0.12
22:1n11	1.65 ± 1.58	0.19 ± 0.22	17.27 ± 5.68	3.51 ± 2.26	1.88 ± 1.36	6.07 ± 3.44
22:1n9	0.49 ± 0.24	0.16 ± 0.06	1.23 ± 0.65	0.71 ± 0.21	0.41 ± 0.11	0.99 ± 0.36
24:1	1.17 ± 0.41	1.18 ± 0.34	0.75 ± 0.39	0.18 ± 0.05	1.20 ± 0.51	1.25 ± 0.21
18:2n6	0.76 ± 0.16	0.61 ± 0.15	1.15 ± 0.34	0.84 ± 0.08	1.27 ± 0.40	1.49 ± 0.17
18:4n3	0.75 ± 0.51	0.17 ± 0.08	1.51 ± 0.80	0.83 ± 0.18	0.67 ± 0.36	1.44 ± 0.70
20:4n6	2.54 ± 0.67	5.43 ± 0.84	0.42 ± 0.28	6.33 ± 1.17	3.00 ± 1.20	1.50 ± 0.68
20:5n3	14.77 ± 2.34	9.59 ± 1.04	7.77 ± 1.57	17.04 ± 1.10	13.78 ± 1.84	8.03 ± 1.21
22:5n3	1.90 ± 0.37	2.56 ± 0.27	0.83 ± 0.13	1.29 ± 0.20	1.66 ± 0.32	1.58 ± 0.27
22:6n3	24.77 ± 4.69	30.60 ± 4.38	12.46 ± 6.89	7.69 ± 1.06	19.86 ± 3.14	19.34 ± 5.89

Table 2.4B: Fatty acid profiles of fish from the Scotian Shelf (adapted from Budge *et. al* 2002)

	Ocean pout (*n* = 18)	**Pollock** (*n* = 25)	**Red hake** (*n* =7)	**Redfish** (*n* = 49)	**Rock crab** (*n* = 10)
Length (cm)	26.6 ± 6.1	24.8 ± 9.8	29.3 ± 5.1	27.6 ± 9.2	8.1 ± 0.6
Mass (g)	81.0 ± 57.7	221.1 ± 256.5	183.7 ± 102.8	405.6 ± 339.3	184.4 ± 44.5
Lipid content (%)	2.0 ± 1.0	3.0 ± 1.9	1.7 ± 0.8	6.3 ± 2.9	0.8 ± 0.2
14:0	2.46 ± 1.06	2.89 ± 1.37	1.32 ± 0.40	3.74 ± 0.74	1.69 ± 0.55
16:0	12.95 ± 1.20	14.53 ± 2.32	15.08 ± 1.14	9.39 ± 1.84	10.44 ± 0.72
18:0	4.69 ± 1.08	4.26 ± 0.44	5.87 ± 0.45	2.43 ± 0.51	3.18 ± 0.27
16:1n7	6.14 ± 2.73	3.53 ± 0.97	2.87 ± 1.37	7.63 ± 2.23	5.93 ± 0.78
18:1n9	10.61 ± 3.16	10.77 ± 1.98	12.13 ± 2.63	8.66 ± 3.34	8.16 ± 1.39
18:1n7	5.79 ± 1.15	3.51 ± 0.58	5.59 ± 1.34	3.33 ± 0.63	7.45 ± 1.83
20:1n11	1.32 ± 0.66	0.71 ± 0.32	0.52 ± 0.15	1.07 ± 0.43	1.37 ± 0.35
20:1n9	1.42 ± 0.26	4.40 ± 1.76	1.94 ± 0.58	14.91 ± 3.05	3.85 ± 1.49
20:1n7	1.65 ± 0.82	0.40 ± 0.16	0.46 ± 0.19	1.37 ± 0.63	1.84 ± 0.62
22:1n11	0.53 ± 0.24	2.68 ± 1.45	0.81 ± 0.33	15.91 ± 3.70	3.63 ± 2.01
22:1n9	0.29 ± 0.09	0.49 ± 0.23	0.26 ± 0.06	3.02 ± 1.74	0.61 ± 0.23
24:1	1.10 ± 0.60	1.01 ± 0.38	1.29 ± 0.46	0.87 ± 0.41	0.30 ± 0.08
18:2n6	0.86 ± 0.11	1.00 ± 0.18	0.79 ± 0.20	0.90 ± 0.22	1.00 ± 0.13
18:4n3	0.43 ± 0.26	1.35 ± 0.39	0.44 ± 0.23	1.07 ± 0.41	0.42 ± 0.13
20:4n6	4.06 ± 1.29	1.11 ± 0.44	2.59 ± 0.96	0.57 ± 0.39	4.05 ± 1.11
20:5n3	15.07 ± 2.76	11.03 ± 2.19	9.90 ± 3.16	7.39 ± 1.81	20.74 ± 2.19
22:5n3	1.98 ± 0.51	1.00 ± 0.36	2.25 ± 0.44	0.79 ± 0.14	2.06 ± 0.40
22:6n3	14.32 ± 4.58	25.58 ± 8.39	25.16 ± 7.13	8.23 ± 3.10	10.35 ± 1.74

Table 2.4C: Fatty acid profiles of fish from the Scotian Shelf (adapted from Budge *et. al* 2002)

	Sand lance (*n* = 71)	**Sea raven** (*n* =6)	**Shrimp** (*n* = 46)	**Silver hake** (*n* = 38)	**Smooth skate** (*n* =5)
Length (cm)	18.5 ± 5.0	27.2 ± 5.5	11.5 ± 1.0	22.8 ± 6.9	29.7 ± 8.2
Mass (g)	14.5 ± 10.1	389.9 ± 238.8	10.5 ± 4.1	88.9 ± 74.4	120.7 ± 91.1
Lipid content (%)	5.6 ± 4.3	0.8 ± 0.3	2.6 ± 0.7	2.2 ± 1.4	1.4 ± 0.4
14:0	5.43 ± 1.49	1.20 ± 0.74	2.89 ± 0.43	2.34 ± 0.96	1.66 ± 0.60
16:0	13.44 ± 1.69	13.88 ± 1.85	11.42 ± 0.94	16.80 ± 1.25	16.65 ± 2.16
18:0	2.04 ± 0.81	5.31 ± 1.55	1.93 ± 0.33	3.72 ± 1.06	4.23 ± 1.16
16:1n7	6.23 ± 2.12	6.71 ± 3.77	8.74 ± 1.59	3.20 ± 1.54	7.60 ± 2.52
18:1n9	5.88 ± 1.59	13.29 ± 1.20	11.76 ± 2.63	11.29 ± 1.81	10.68 ± 0.48
18:1n7	2.47 ± 0.64	7.28 ± 0.69	6.83 ± 1.93	3.23 ± 0.76	6.99 ± 0.26
20:1n11	0.49 ± 0.16	0.48 ± 0.27	1.40 ± 1.03	1.02 ± 0.32	0.49 ± 0.18
20:1n9	7.50 ± 3.02	1.77 ± 0.87	4.85 ± 1.45	5.16 ± 2.36	1.08 ± 0.39
20:1n7	0.45 ± 0.23	0.74 ± 0.32	1.53 ± 0.32	0.33 ± 0.12	0.86 ± 0.41
22:1n11	9.39 ± 4.20	0.50 ± 0.49	6.74 ± 2.35	4.16 ± 3.07	0.24 ± 0.19
22:1n9	1.11 ± 1.06	0.24 ± 0.05	1.56 ± 0.71	0.54 ± 0.36	0.30 ± 0.07
24:1	1.34 ± 0.33	0.72 ± 0.16	0.30 ± 0.21	1.48 ± 0.73	0.27 ± 0.09
18:2n6	1.49 ± 0.50	0.91 ± 0.31	1.00 ± 0.18	1.05 ± 0.22	1.50 ± 0.29
18:4n3	1.98 ± 1.17	0.48 ± 0.42	0.71 ± 0.29	0.70 ± 0.38	0.90 ± 0.50
20:4n6	0.59 ± 0.31	4.40 ± 1.63	1.66 ± 0.72	1.45 ± 0.51	3.09 ± 0.48
20:5n3	12.96 ± 1.87	12.44 ± 1.53	15.26 ± 1.30	9.66 ± 2.56	*10.02 ± 2.24*
22:5n3	1.03 ± 0.32	2.32 ± 1.00	0.74 ± 0.21	1.11 ± 0.23	1.75 ± 0.25
22:6n3	16.17 ± 4.90	18.73 ± 3.57	11.37 ± 1.99	23.64 ± 6.28	*20.87 ± 3.20*

Table 2.4D: Fatty acid profiles of fish from the Scotian Shelf (adapted from Budge *et. al* 2002)

	Thorny skate (*n* = 12)	**White hake** (*n* = 46)	**Winter flounder** (*n* = 25)	**Winter skate** (*n* = 15)	**Yellowtail flounder** (*n* = 92)
Length (cm)	33.0 ± 3.0	32.9 ± 5.3	27.0 ± 6.6	35.6 ± 4.0	26.8 ± 6.1
Mass (g)	297.1 ± 64.4	281.1 ± 142.8	274.8 ± 189.8	262.2 ± 112.3	189.8 ± 138.6
Lipid content (%)	1.1 ± 0.2	1.3 ± 0.8	1.9 ± 0.8	1.5 ± 0.6	2.7 ± 1.3
14:0	1.77 ± 0.56	1.49 ± 0.61	1.96 ± 0.69	1.58 ± 1.09	2.72 ± 0.87
16:0	16.82 ± 0.65	14.39 ± 1.05	15.04 ± 0.86	16.94 ± 2.20	14.01 ± 1.53
18:0	4.04 ± 0.59	5.37 ± 0.92	4.51 ± 0.85	3.98 ± 0.90	3.56 ± 0.96
16:1n7	6.57 ± 1.74	3.59 ± 1.52	5.21 ± 2.92	4.30 ± 1.20	6.47 ± 2.90
18:1n9	12.63 ± 1.63	12.08 ± 2.82	7.31 ± 1.61	9.30 ± 0.73	9.75 ± 2.57
18:1n7	6.40 ± 0.54	5.69 ± 1.08	3.61 ± 0.86	5.24 ± 0.96	4.25 ± 0.75
20:1n11	0.73 ± 0.19	0.72 ± 0.35	0.55 ± 0.27	0.59 ± 0.35	0.76 ± 0.32
20:1n9	1.92 ± 0.49	3.18 ± 2.37	1.27 ± 0.30	2.10 ± 2.10	1.34 ± 0.38
20:1n7	1.03 ± 0.15	0.66 ± 0.24	2.52 ± 1.57	0.81 ± 0.36	1.65 ± 0.74
22:1n11	0.66 ± 0.59	1.75 ± 1.80	0.23 ± 0.09	1.19 ± 2.18	0.49 ± 0.28
22:1n9	0.45 ± 0.11	0.36 ± 0.22	0.35 ± 0.11	0.37 ± 0.15	0.25 ± 0.11
24:1	0.31 ± 0.09	0.90 ± 0.46	0.61 ± 0.49	0.54 ± 0.27	0.69 ± 0.41
18:2n6	1.41 ± 0.10	0.80 ± 0.17	0.60 ± 0.17	1.34 ± 0.24	1.03 ± 0.24
18:4n3	0.65 ± 0.31	0.43 ± 0.27	0.48 ± 0.28	0.64 ± 0.41	0.95 ± 0.57
20:4n6	3.46 ± 0.74	2.29 ± 0.94	3.58 ± 0.99	3.24 ± 1.22	2.55 ± 1.25
20:5n3	8.30 ± 1.45	9.61 ± 1.54	14.43 ± 2.14	7.78 ± 1.91	15.02 ± 3.32
22:5n3	2.35 ± 0.25	2.69 ± 0.61	3.82 ± 0.97	2.93 ± 0.75	3.31 ± 0.97
22:6n3	21.89 ± 2.14	24.83 ± 5.90	20.10 ± 4.26	26.06 ± 4.61	18.73 ± 4.84

Table 2.4E: Fatty acid profiles of fish from the Scotian Shelf (adapted from Budge *et. al* 2002)

Common name	Scientific name	MNI	% RA	% FO	% Biomass	Biomass (kg)
Sand lance	*Ammodytes spp.*	4198	66.3	14.0	53.3	138.8
Winter flounder	*Pseudopleuronectes americanus*	162	2.6	6.9	19.0	49.6
Atlantic cod	*Gadus morhua*	25	<1.0	2.0	6.4	16.6
Skates	Rajidae	159	2.5	24.5	5.7	14.8
Red/white hake	*Urophycis spp.*	530	13.5	9.4	3.3	8.6
Atlantic herring	*Clupea harengus*	93	1.5	2.3	3.7	9.6
Windowpane flounder	*Scopthalmus aquosus*	118	1.9	7.1	2.2	5.6
Squid	*Loligo pealeii*	219	3.4	6.2	1.4	3.6
Cusk eel	Ophidiidae	159	2.5	5.2	<1.0	0.5
Sculpin	*Myoxocephalus spp.*	132	2.1	2.5	4.0	10.3
Shrimp/crab	Crustacea	32	<1.0	1.7	<1.0	0.1
Fourspot flounder	*Paralichthys oblongus*	22	<1.0	1.9	<1.0	2.1
Yellowtail flounder	*Limanda ferruginea*	20	<1.0	1.9	<1.0	1.1
Silver hake	*Merluccius bilinearis*	22	<1.0	2.0	<1.0	1.5
Gulfstream flounder	*Citharichthys arctifrons*	22	<1.0	2.0	<1.0	0.3
n/a	*Merluccius spp.*	13	<1.0	1.1	<1.0	0.2
Atlantic mackerel	*Scomber scombrus*	13	<1.0	1.1	<1.0	0.2
Unidentified flatfish	*Pleuronectiformes*	21	<1.0	3.0	<1.0	0.1
Unidentified gadids	Gadiformes	14	<1.0	3.0	<1.0	0.1
Ocean pout	*Macrozoarces americanus*	6	<1.0	<1.0	<1.0	<0.1
Lumpfish	*Cyclopterus lumpus*	4	<1.0	<1.0	*	*
Blue mussel	*Mytilus edulis*	4	<1.0	1.0	*	*
Hagfish	*Petromyzon marinus*	3	<1.0	<1.0	*	*
Tautog	*Tautoga onitis*	3	<1.0	<1.0	*	*
Spiny dogfish	*Squalus acanthias*	2	<1.0	<1.0	*	*
Striped bass	*Morone saxatilis*	2	<1.0	<1.0	*	*
Eel	*Anguilla rostrata*	1	<1.0	<1.0	*	*
Scup	*Stenotomus chrysops*	1	<1.0	<1.0	*	*
Wolffish	*Anarhichas spp.*	1	<1.0	<1.0	*	*
Unknown	Unknown	13	<1.0	1.0	*	*
TOTAL		**6013**	**100.0**	**100.0**	**100.0**	**263.6**

Table 2.5: Prey in 252 seal scats
MNI = Minimum number of individuals; RA = Relative abundance; FO = Frequency of occurrence
* Biomass not estimated

Common name	Scientific name	MNI	%RA	%FO	% Biomass	Biomass (kg)
Red/white hake	*Urophycis spp.*	301	30.3	22.1	32.5	29.9
Silver hake	*Merluccius bilinearis.*	69	7.0	10.4	29.7	26.7
Winter flounder	*Psuedopleuronectes americanus*	13	1.3	4.1	15.1	13.9
Pollock	*Pollachus viriens*	12	1.0	1.0	2.3	2.3
Fourspot flounder	*Paralichthys oblongus*	34	3.4	7.6	7.7	7.1
Gulfstream flounder	*Citharichthys arctifrons*	128	12.9	7.6	3.1	2.8
Redfish	*Sebastes sp.*	14	1.4	2.1	2.3	2.1
Atlantic cod	*Gadus morhua*	10	1.0	3.5	1.7	1.5
Squid	*Loligo pealeii*	16	1.6	3.5	1.6	1.5
Shrimp/crab	Crustacea	306	30.8	4.1	1.3	1.2
Yellowtail flounder	*Limanda ferruginea*	17	1.7	3.5	0.9	0.8
Ocean pout	*Zoarces americanus*	8	0.8	3.5	0.6	0.5
Skates	Rajidae	7	0.7	4.8	<0.1	0.5
Sand lance	*Ammodytes spp.*	15	1.5	1.4	<0.1	0.5
Atlantic herring	*Clupea harengus*	4	<0.1	2.8	<0.1	0.4
Windowpane flounder	*Scophthalmus aquosus*	4	<0.1	2.1	<0.1	0.2
Cusk eel	*Lepophidium cervinum*	8	0.8	2.1	<0.1	0.1
Unidentified gadid	Gadidae	5	0.5	2.1	*	*
n/a	*Merluccius spp.*	4	<0.1	2.1	*	*
Unidentified flatfish	Pleuronectes	2	<0.1	0.7	*	*
Sculpin	*Myoxocephalus spp.*	1	<0.1	0.7	*	*
Tautog	*Tautoga onitis*	5	0.5	2.8	*	*
American eel	*Anguilla rostrata*	4	<0.1	2.8	*	*
Unknown	n/a	3	<0.1	2.1	*	*
Hagfish	*Myxine glutinosa*	1	<0.1	0.7	*	*
Atlantic silverside	*Menidia menidia*	1	<0.1	0.7	*	*
	TOTAL	**992**	**100.0**	**100.0**	**100.0**	**102.4**

Table 2.6: Prey in 46 seal stomachs
MNI = Minimum number of individuals; RA = Relative abundance; FO = Frequency of occurrence
* Biomass not estimated

Chapter 2: Figures

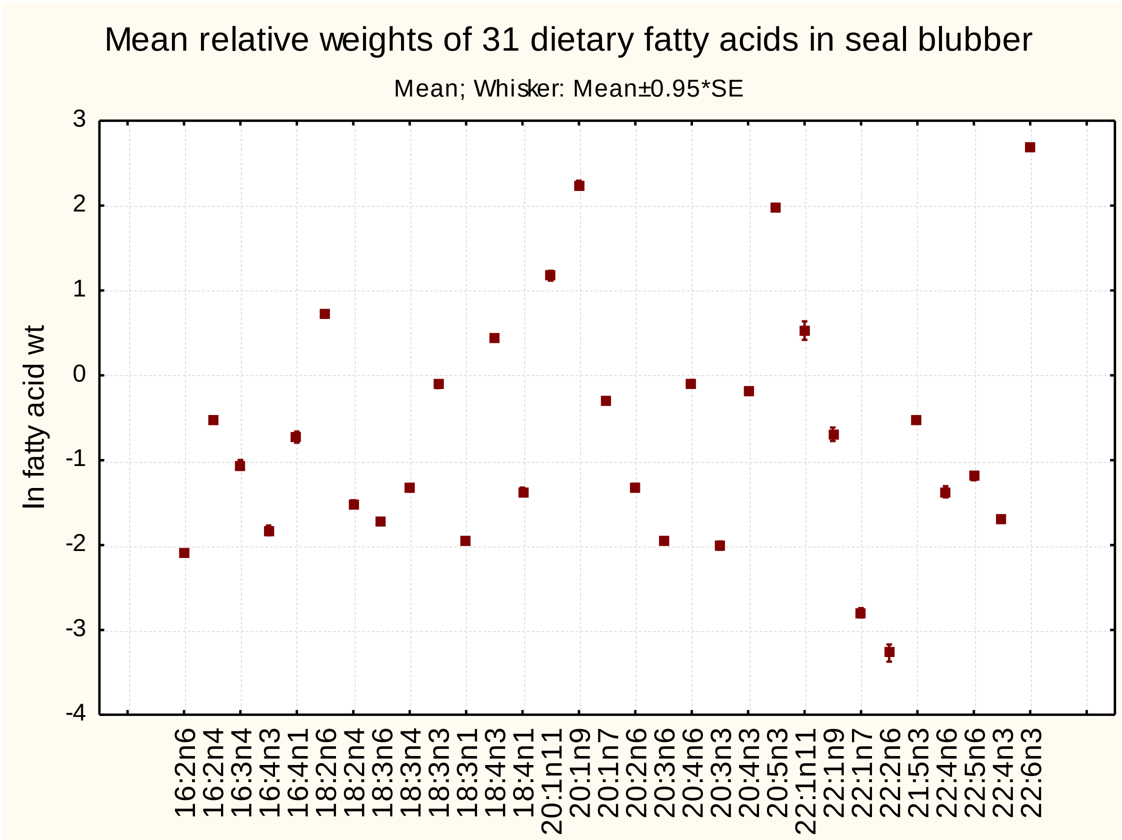

Figure 2.1: Mean and standard error of 31 dietary fatty acids in seal blubber, by weight

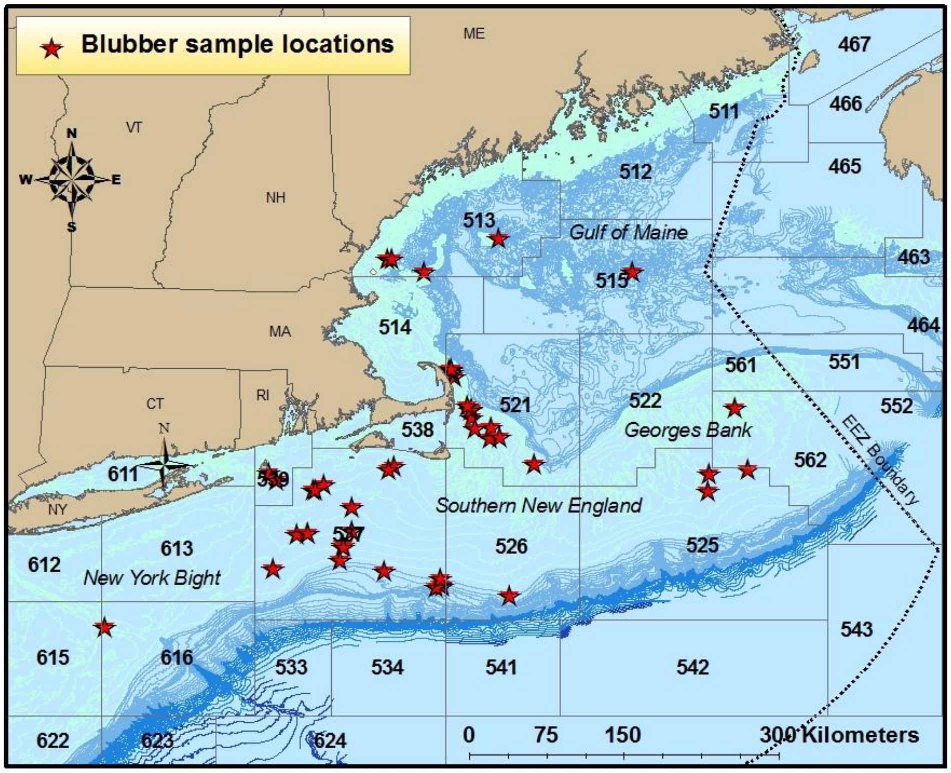

Figure 2.2: Location of seal bycatch specimens from which blubber samples were extracted

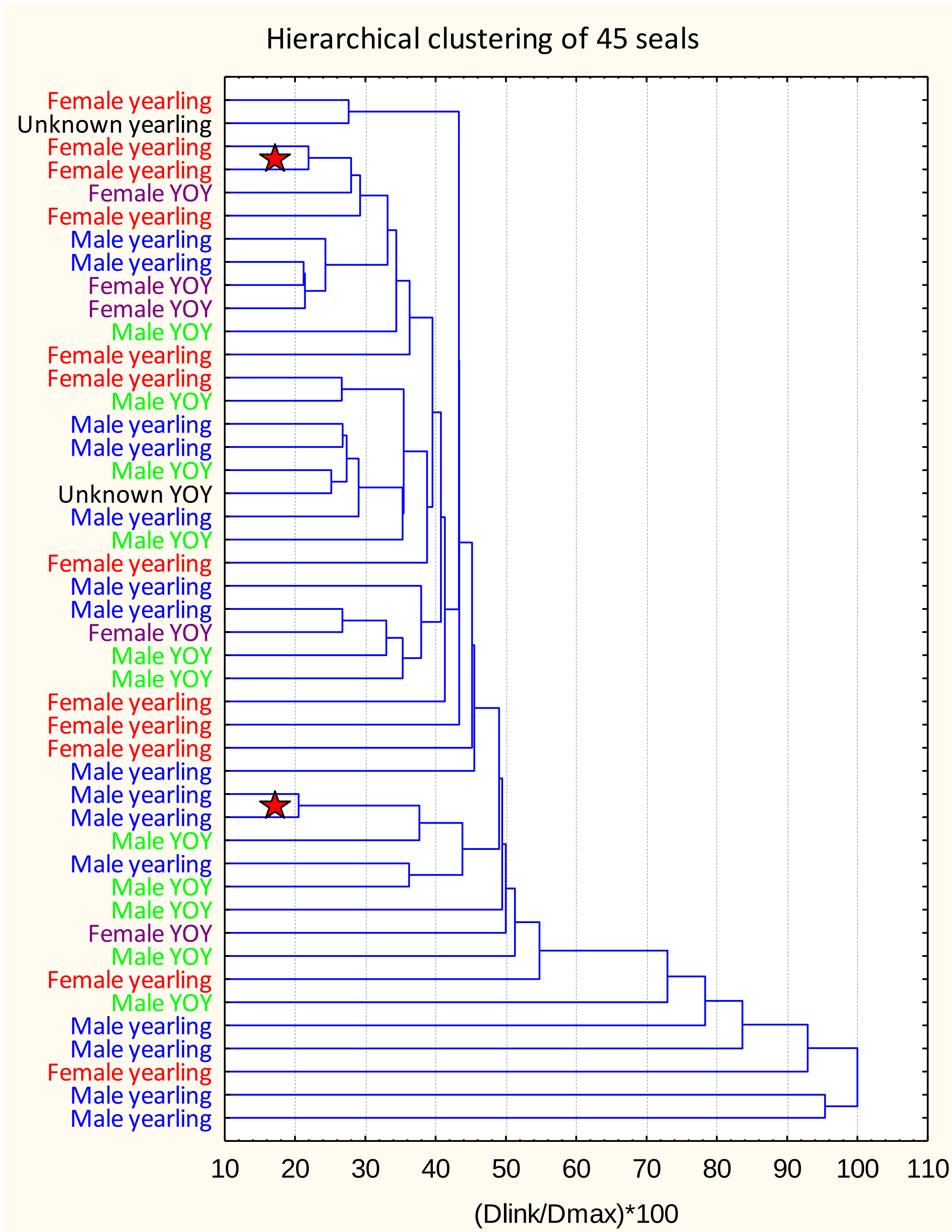

Figure 2.3: Dendrogram of fatty acid clustering (by closest Euclidean distance of data points), according to age and sex of seals

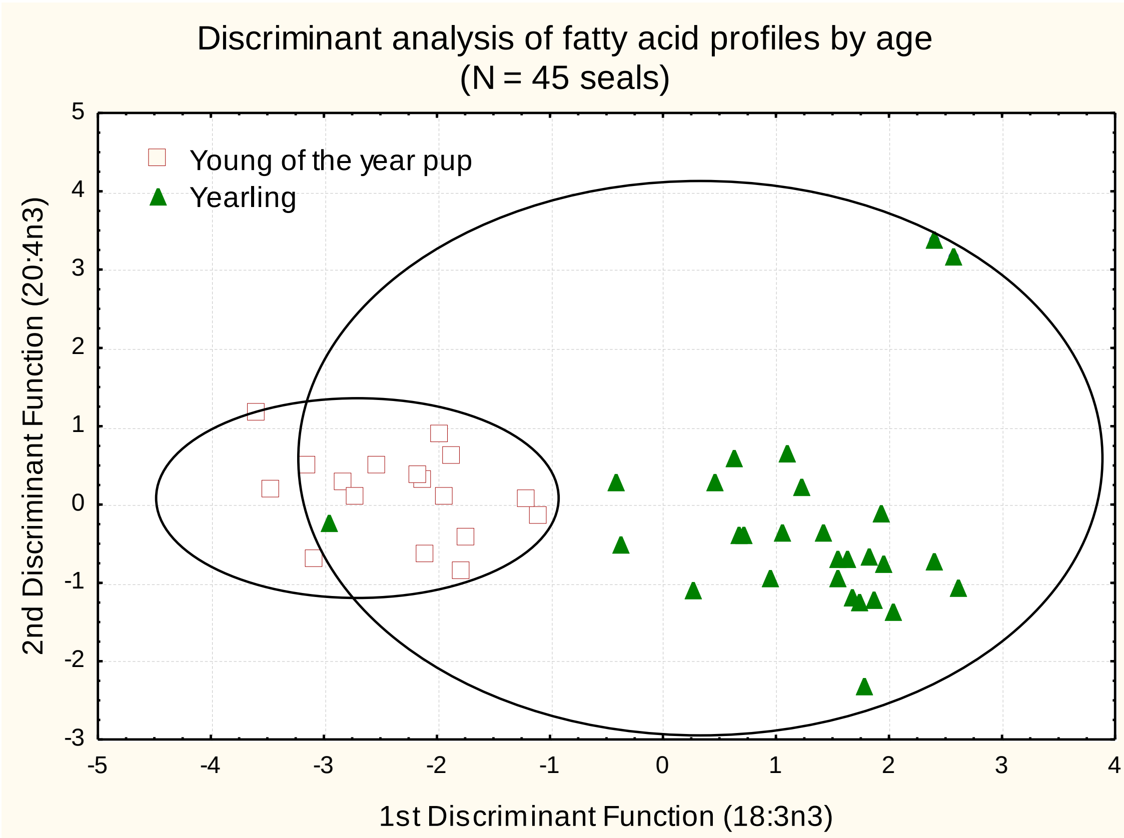

Figure 2.4: Canonical plot of fatty acids by age of seals
"Young of the year pups" >1 yr old, "yearlings" between 1 and 2 yrs old

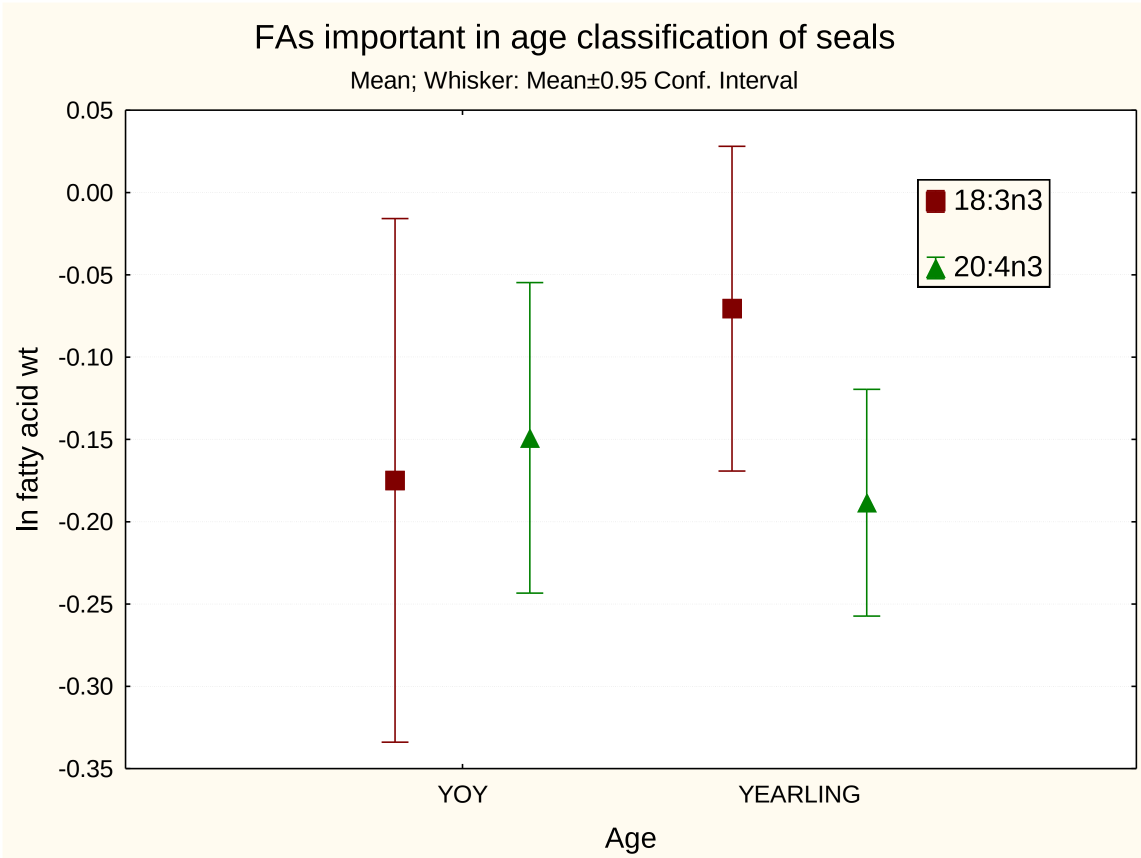

Figure 2.5: Fatty acids most influential in classifying seals to age

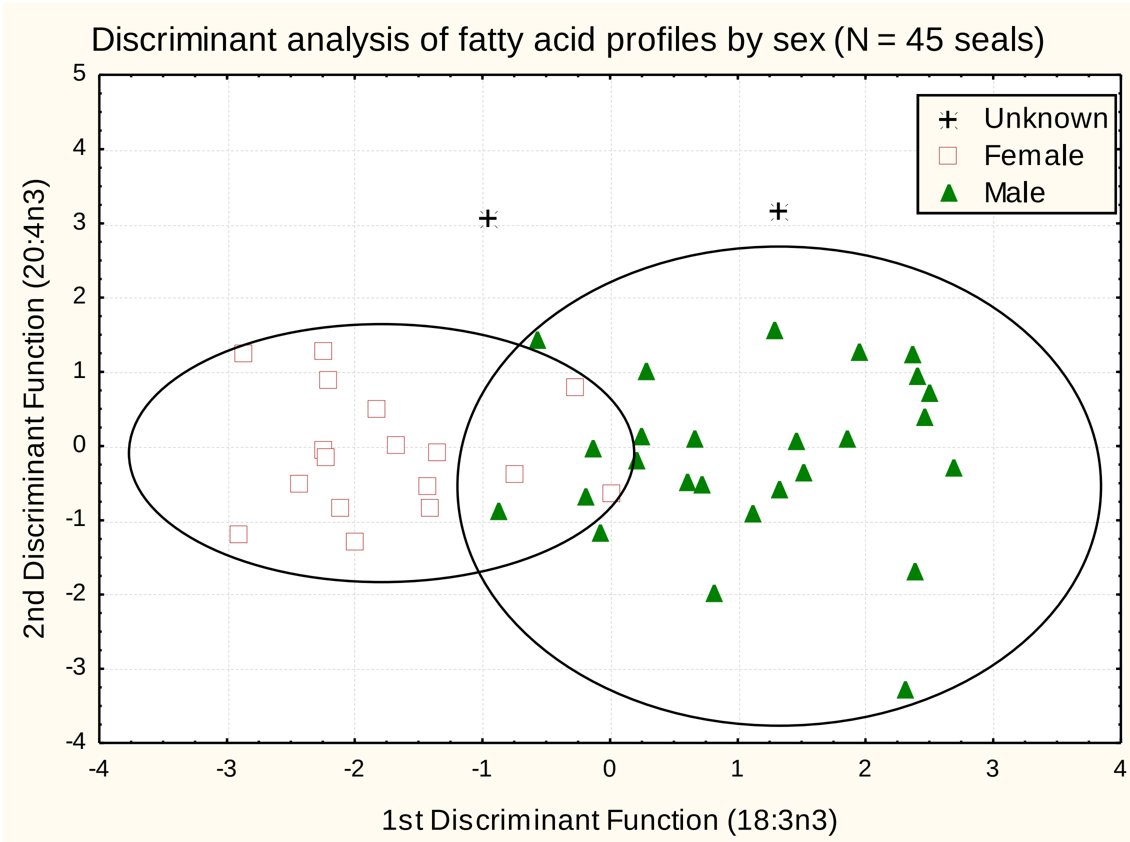

Figure 2.6: Canonical plot of fatty acids by sex of seals

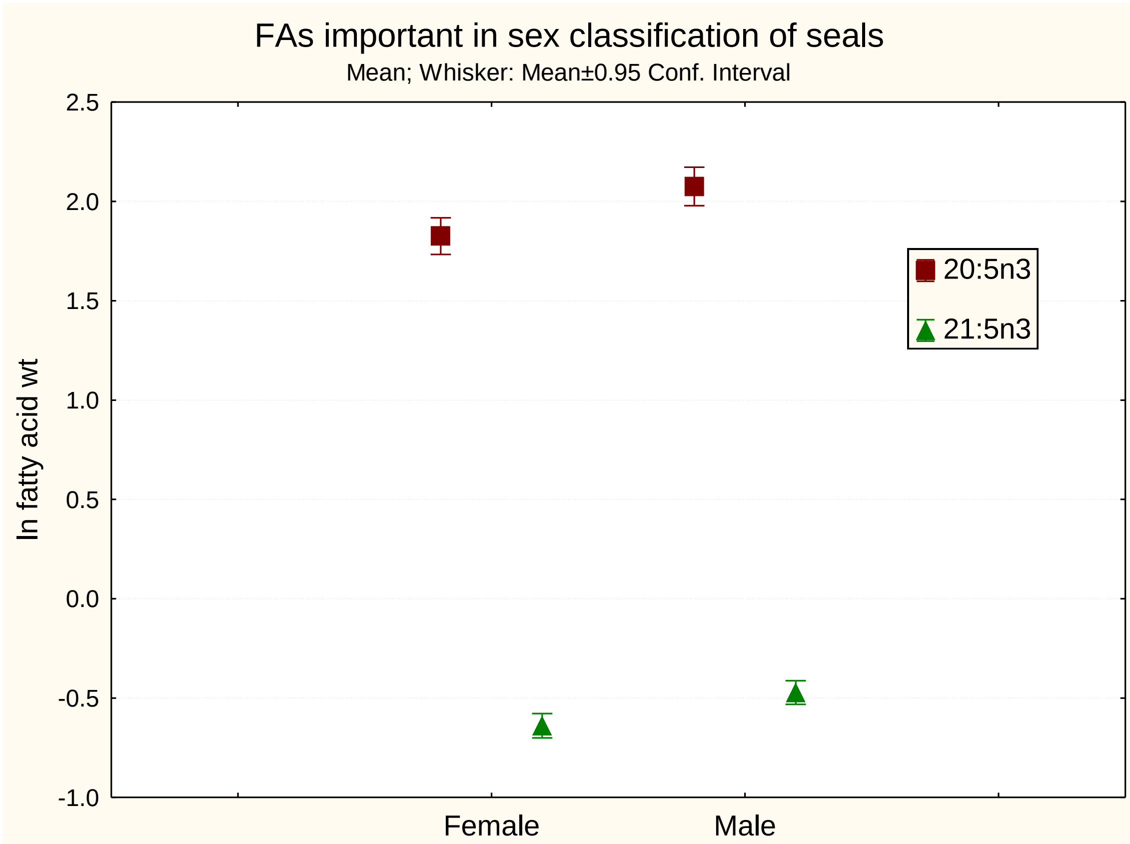

Figure 2.7: Variation in fatty acids most influential in classifying seals to sex

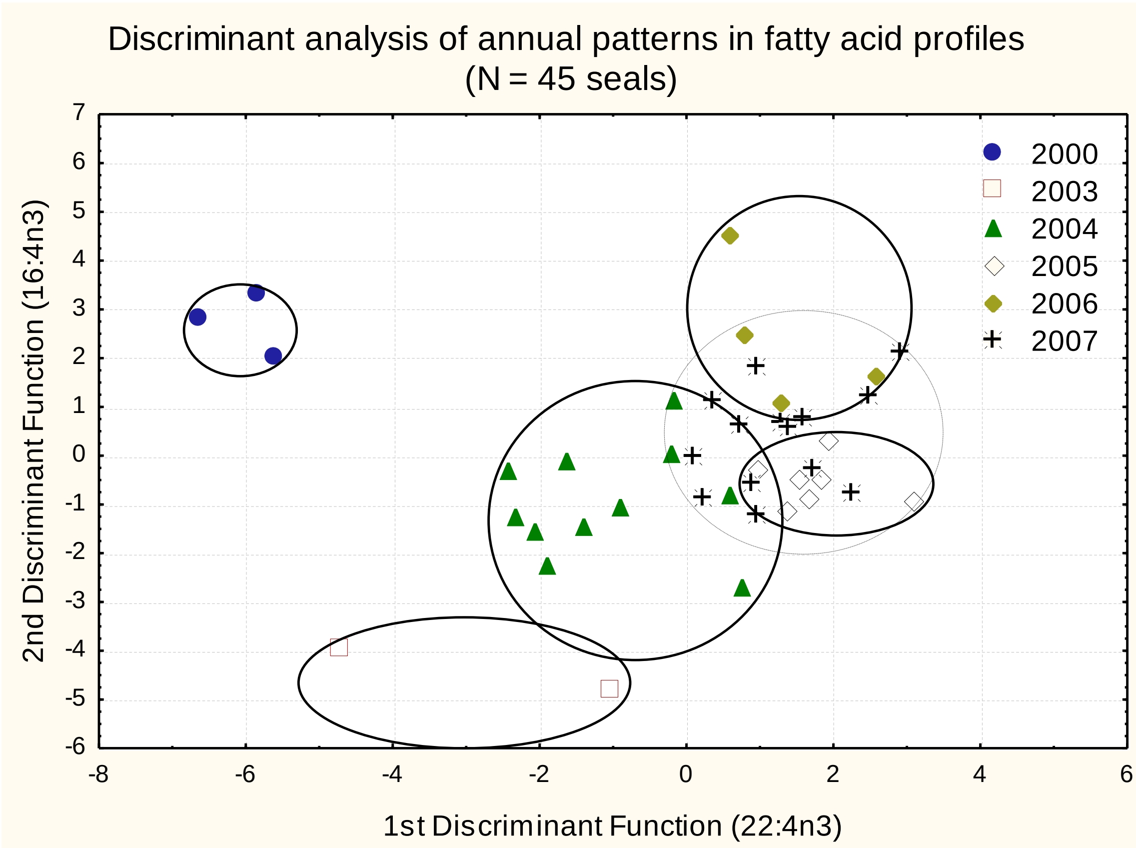

Figure 2.8: Canonical plot of fatty acids by year

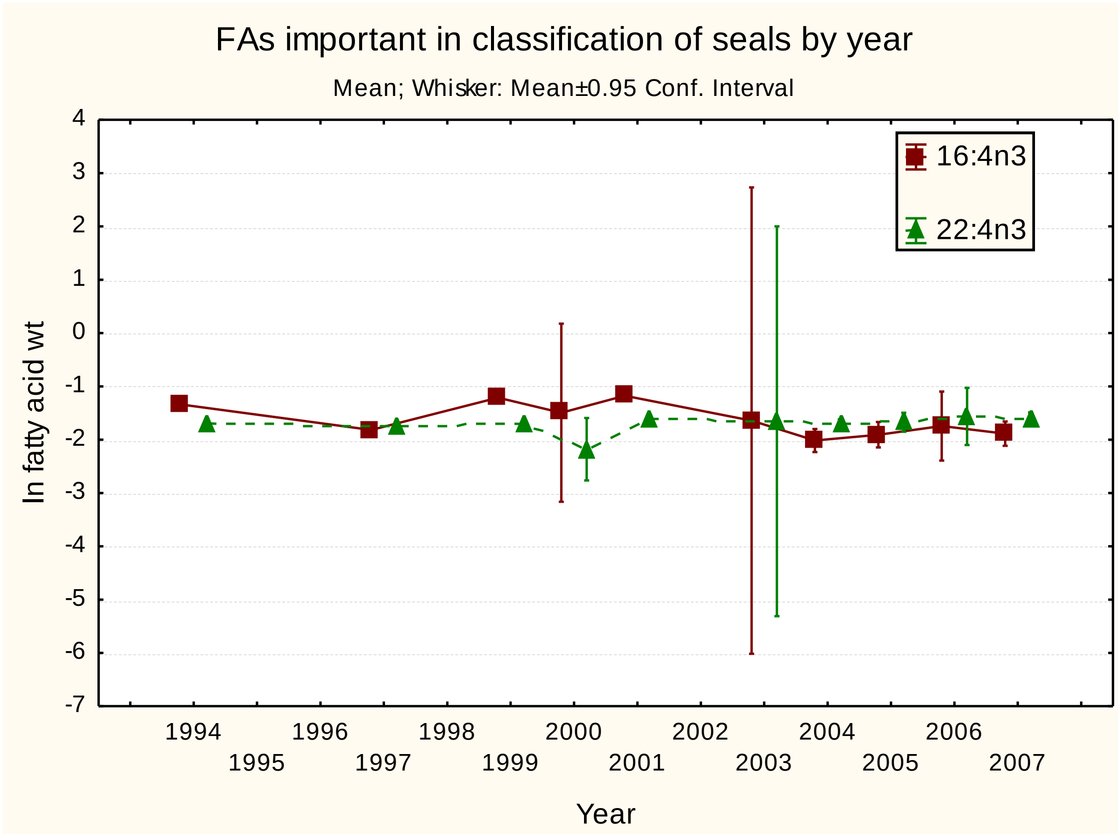

Figure 2.9: Annual variation in fatty acids most influential in classifying seals to year

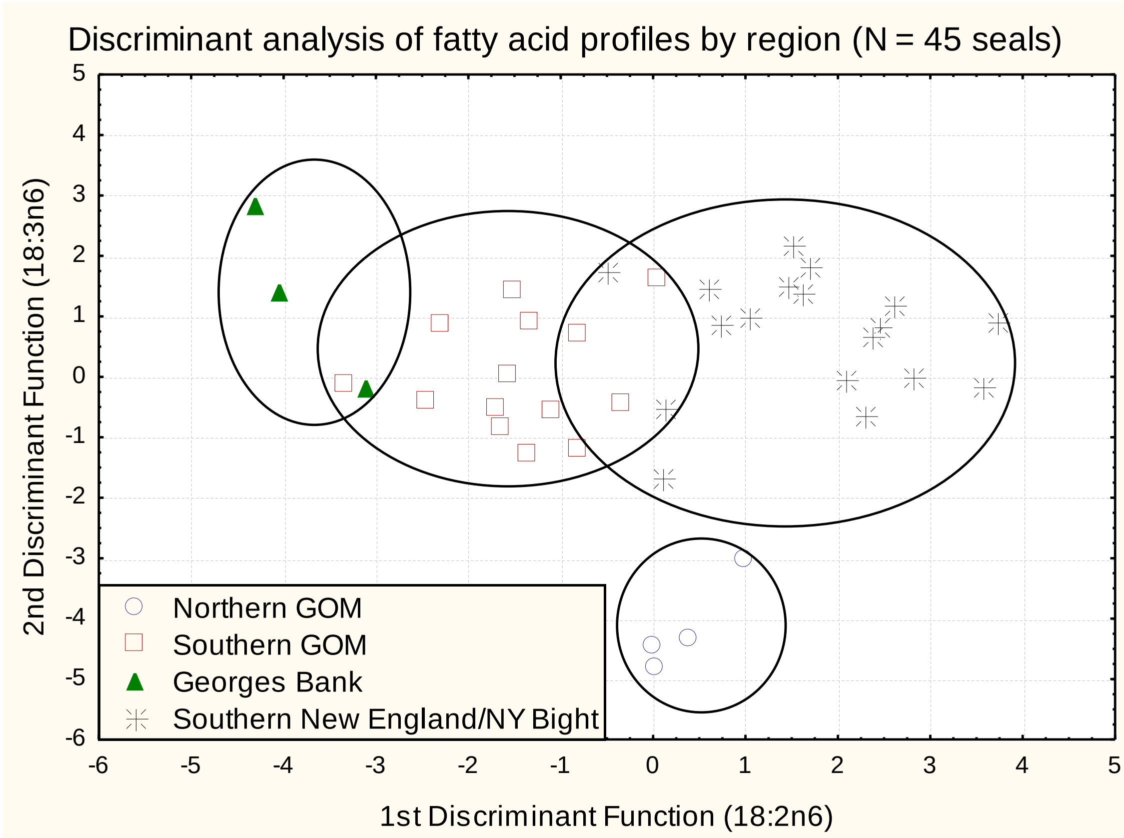

Figure 2.10: Canonical plot of fatty acids by region of seal capture
GOM = Gulf of Maine

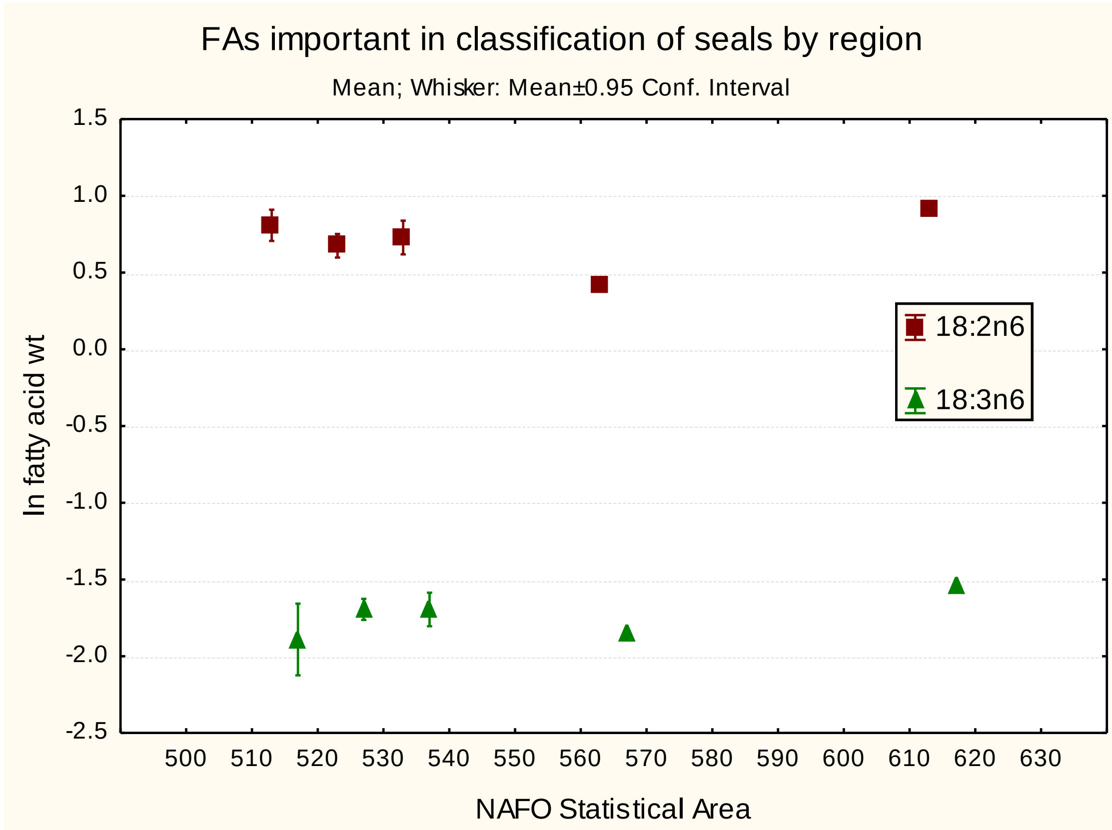

Figure 2.11: Regional variation in fatty acids most influential in classifying seals to area
See Figure 2.2 for Statistical Areas

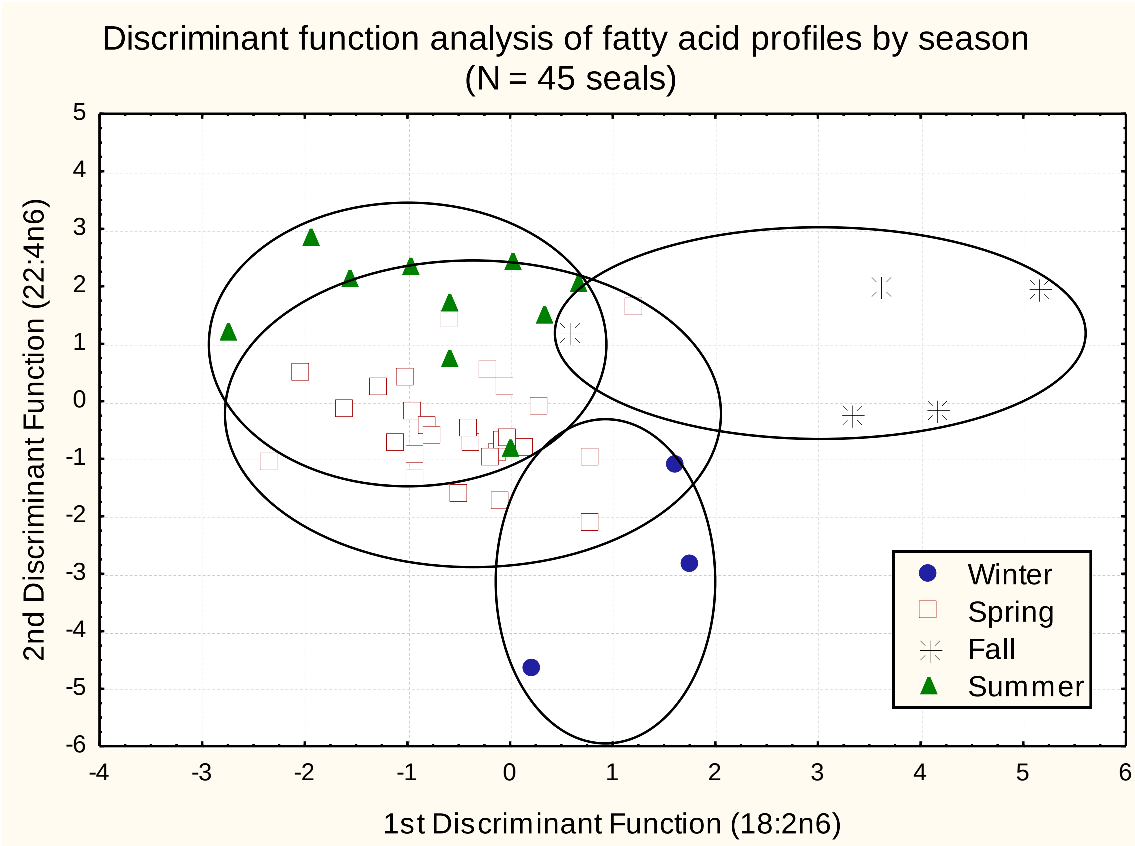

Figure 2.12: Canonical plot of fatty acids by season

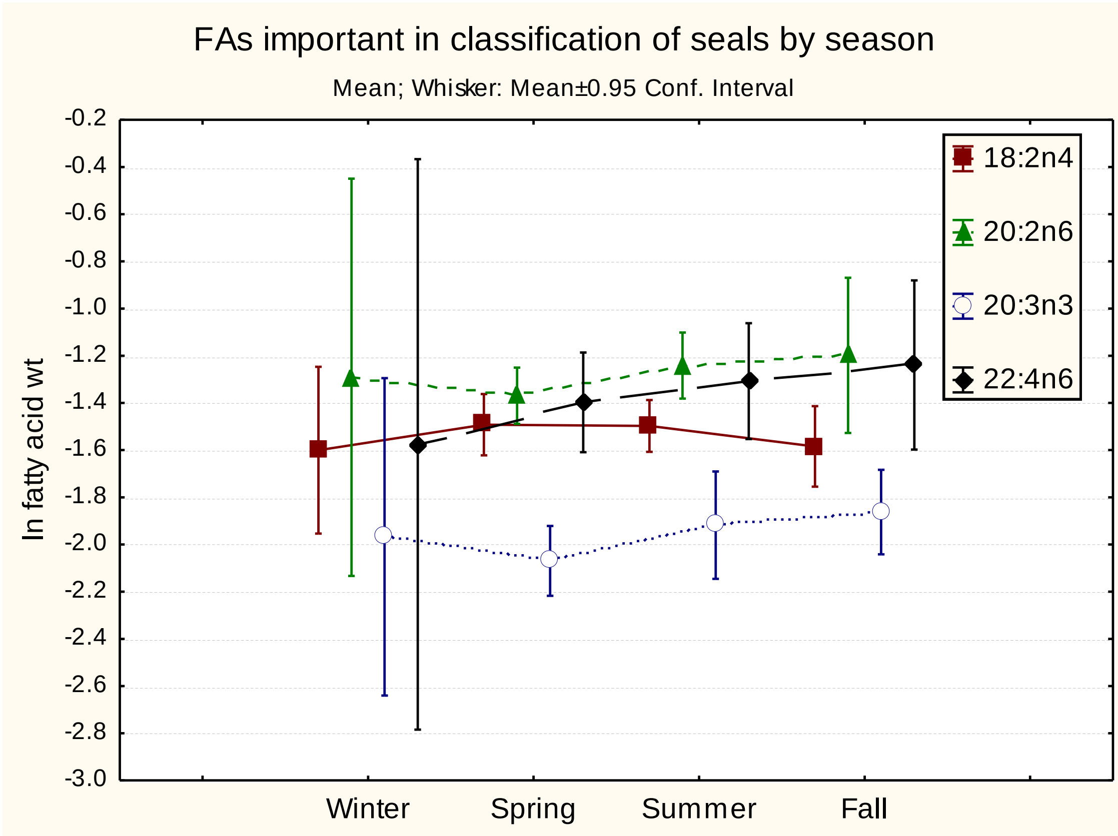

Figure 2.13: Seasonal variation in fatty acids most influential in classifying seals to season

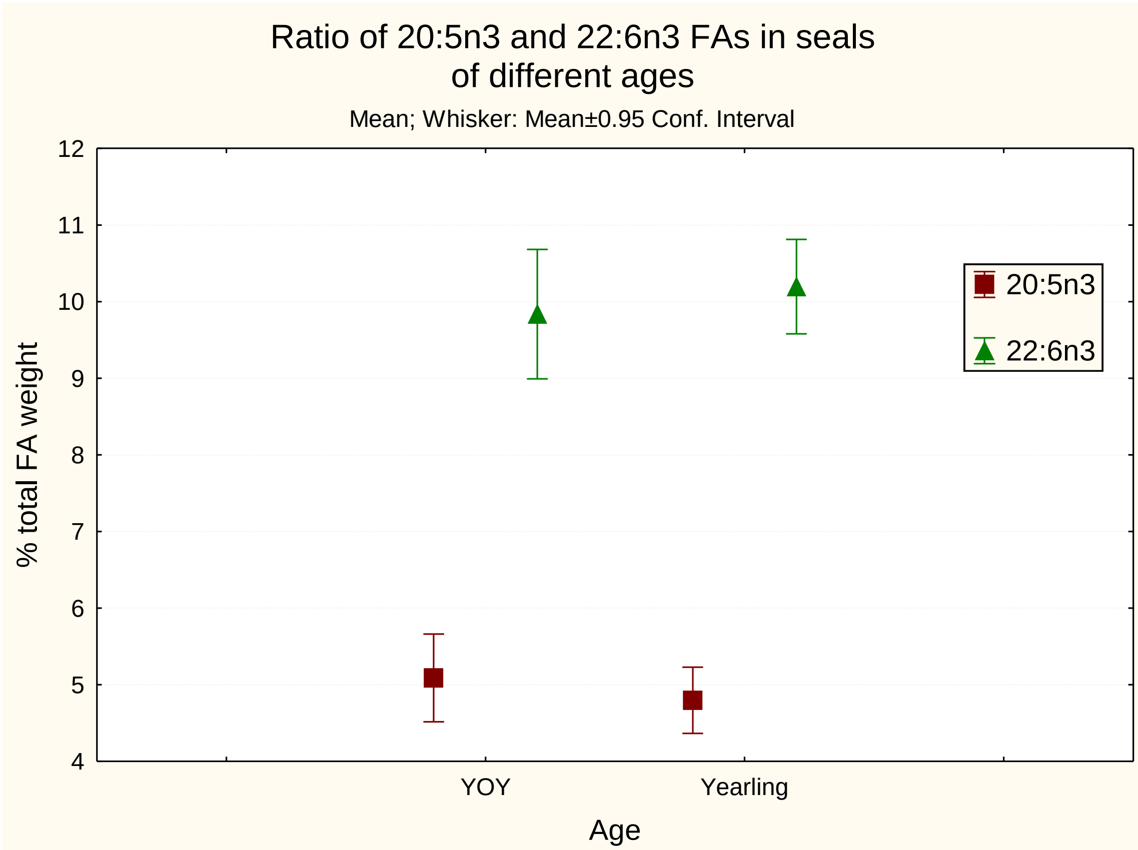

Figure 2.14: Ratios of 20:5n3 and 22:6n3 fatty acids are consistent in young of the year pups and yearlings. These FA ratios are similar to those in smooth skate (*Malacoraja senta)* and alewife (*Alosa pseudoharengus*)

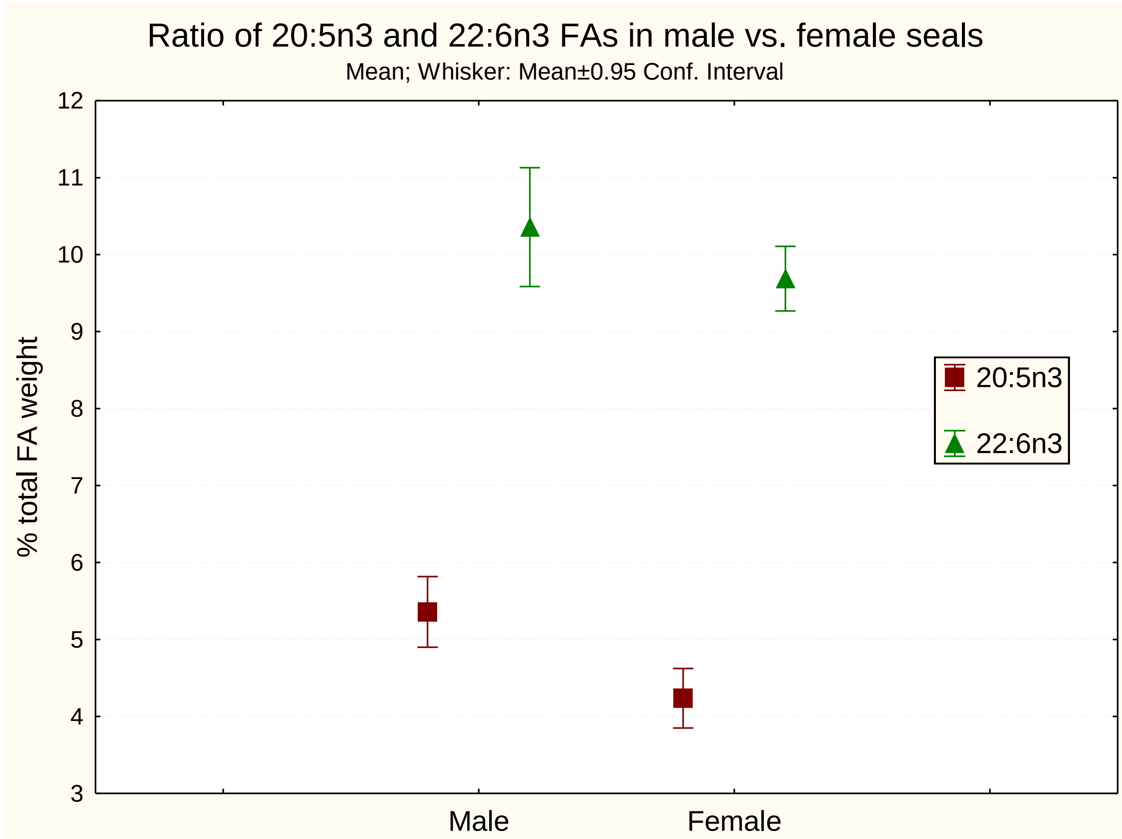

Figure 2.15: Ratios of 20:5n3 and 22:6n3 fatty acids are consistent in male and female seals. These FA ratios are similar to those in smooth skate (*Malacoraja senta)* and alewife (*Alosa pseudoharengus*)

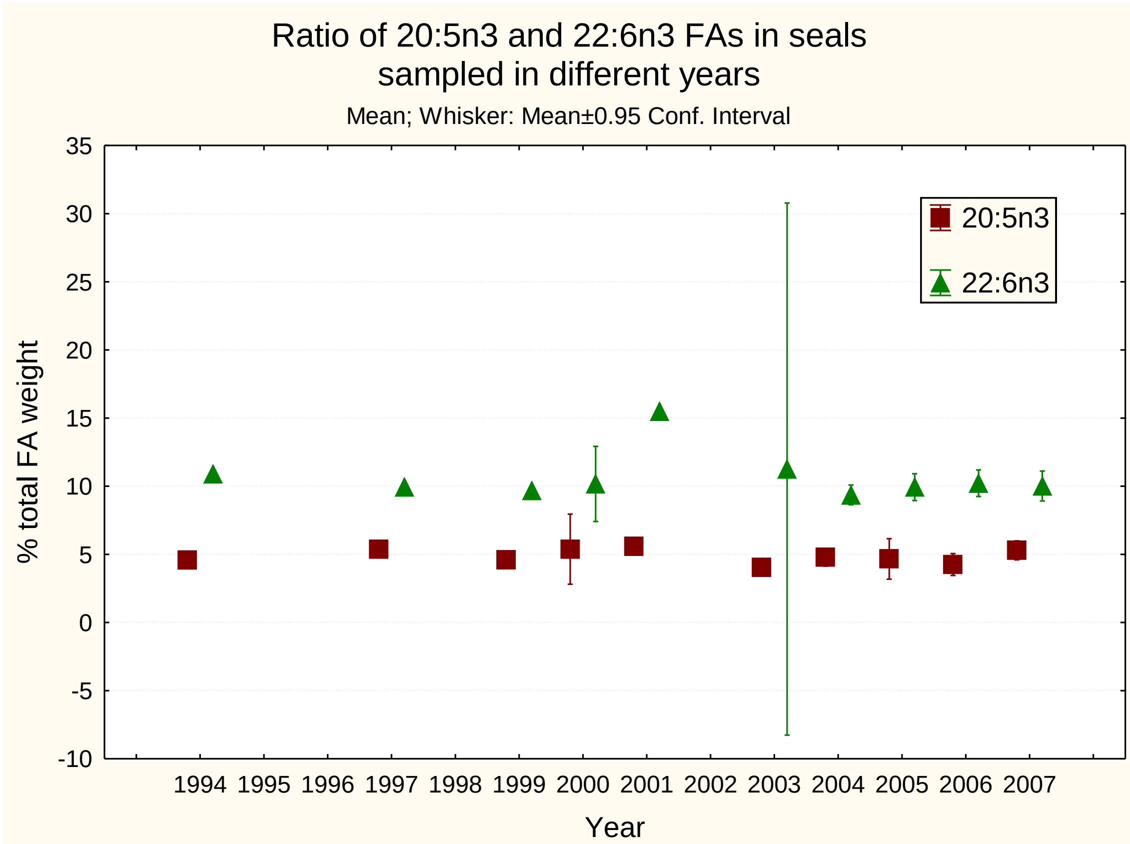

Figure 2.16: Ratios of 20:5n3 and 22:6n3 fatty acids are consistent in seals collected in most years. These FA ratios are similar to those in smooth skate (*Malacoraja senta)* and alewife (*Alosa pseudoharengus*)

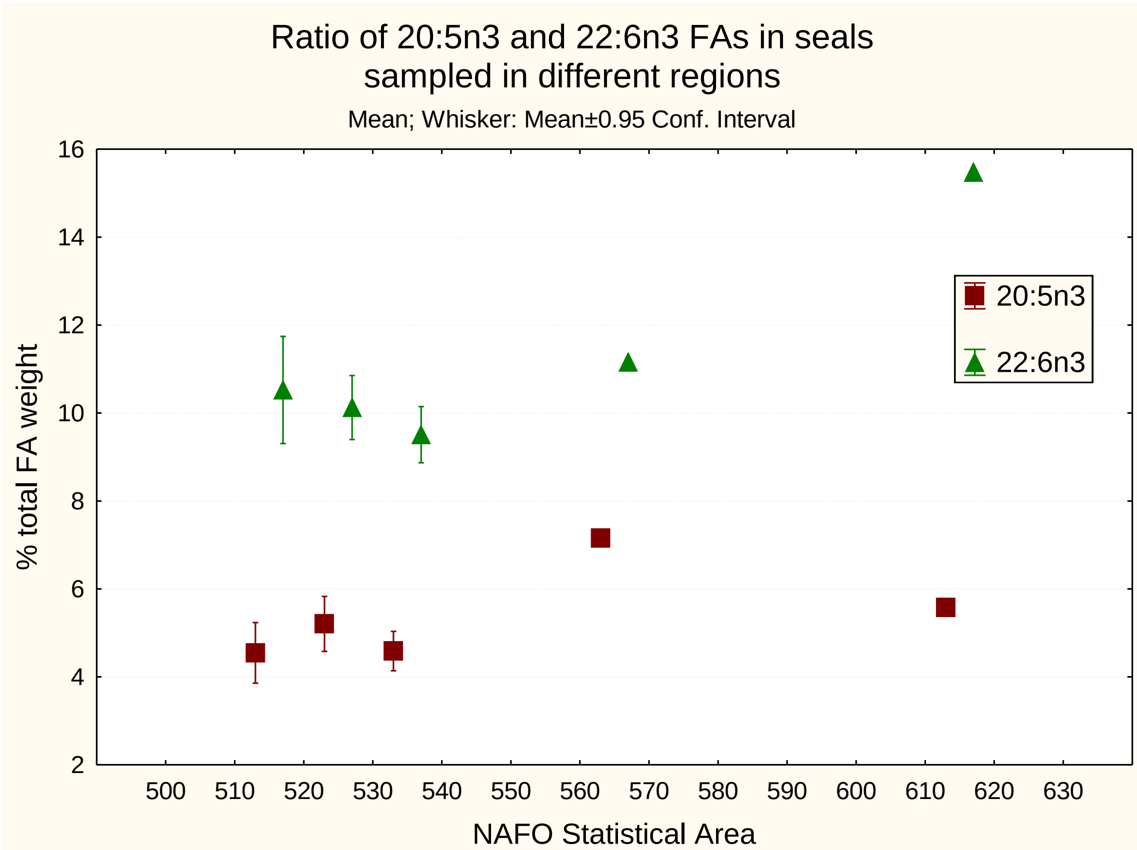

Figure 2.17: Ratios of 20:5n3 and 22:6n3 fatty acids are consistent in seals collected in most regions. These FA ratios are similar to those in smooth skate (*Malacoraja senta)* and alewife (*Alosa pseudoharengus*)

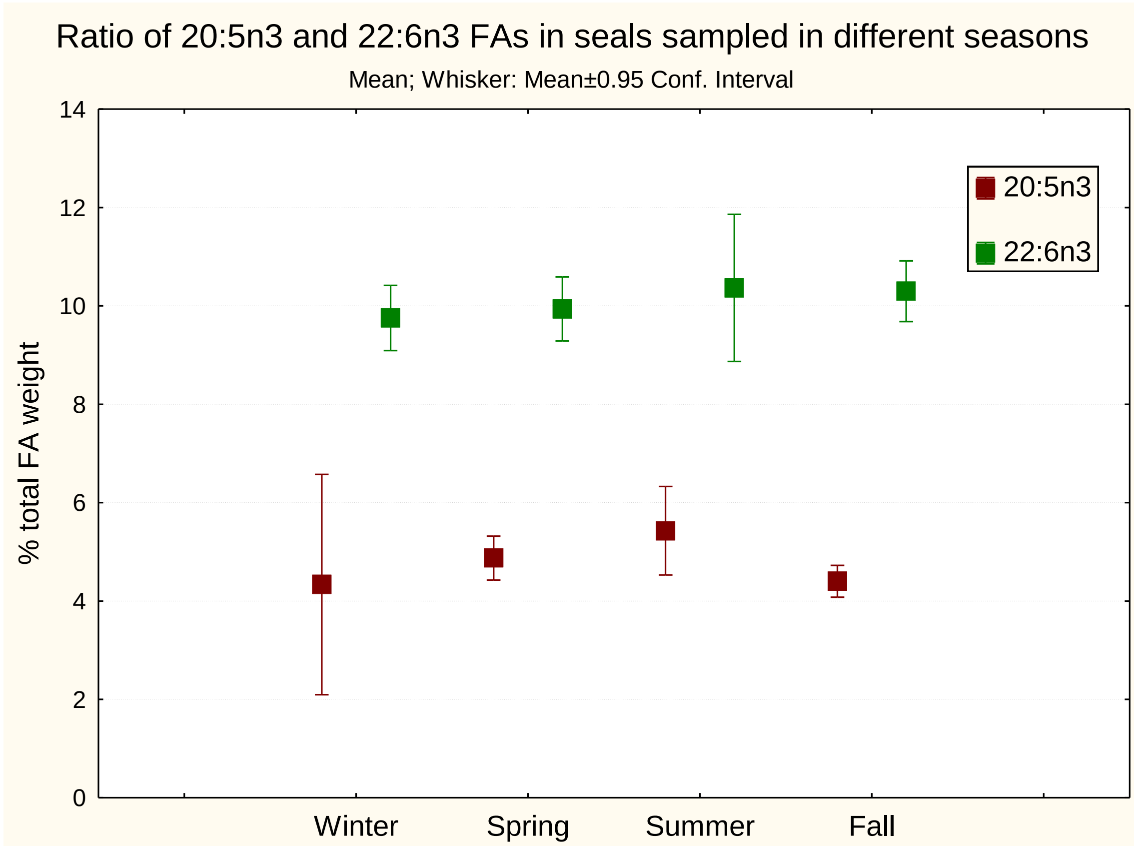

Figure 2.18: Ratios of 20:5n3 and 22:6n3 fatty acids are consistent in seals collected in different seasons. These FA ratios are similar to those in smooth skate (*Malacoraja senta)* and alewife (*Alosa pseudoharengus*)

Chapter 3: Gray seal diet, foraging behavior and habitat use in relation to the distribution and abundance of their prey

Introduction

Gray seals (*Halichoerus grypus*) require terrestrial and marine habitat. They must come on land to molt, breed and rest (Bonner 1994). Gray seal use of habitat is influenced by several factors, including distribution and abundance of their prey (Bowen *et al.* 2002, Sjöberg and Ball 2000, Thompson *et al.* 1991), physical factors such as bathymetry, underwater topography, and sediment type (McConnell *et al.* 1999) and the distribution of conspecifics (Poland *et al.* 2008, Pomeroy *et al.* 2005). Disturbance also plays a role in seals' choice of haul out (i.e. resting, pupping) sites: major gray seal colonies are typically located on relatively remote, uninhabited islands and coastal areas (Amos *et al.* 1993, Baker *et al.* 1995). A seal haul out site is an area where seals come out on land. Haul out sites to which large numbers of animals return on a regular basis are referred to as a colonies, and colonies where pupping occurs regularly are referred to as breeding colonies.

The coast of the northeastern United States represents the southernmost extreme of the gray seal's northwest Atlantic distribution. Their distribution extends north to the Gulf of St. Lawrence in Canada (Waring *et al.* 2007) and south to New England (Waring *et al.* 2007), although sightings of this species occur as far south as Virginia (Waring *et al.* 2007) and pupping occurs occasionally on the shores of Long Island, NY (R. DiGiovanni, Riverhead Foundation, Riverhead NY, pers. comm.). There are five major gray seal colonies in the U.S.: two in Nantucket Sound, in southern New

England, and three in the Gulf of Maine (GOM).The three GOM colonies are located at Green Island (44^{o}0’ N, 69^{o}59’ W), Seal Island (43^{o} 5’ N, 68^{o}44’ W) and Mount Desert Rock (43^{o}96’ N, 68^{o}13’ W) (Renner 2005, Waring *et al.* 2007). These islands are rocky, relatively inaccessible, and located 10-30 kilometers from shore. It is therefore difficult to collect seal scat samples from these areas on a consistent basis, and there is little information about the diet of seals occupying these sites. Seal and Green Islands are only surveyed during the pupping season (December-February), and the numbers of animals present during other months is unknown (Waring *et al.* 2007).

The two major sites in Nantucket Sound are Monomoy (41^{o}36’ N, 69^{o}59’ W) and Muskeget (40^{o}20’ N, 70^{o}16’ W) Islands (Figure 3.1). Muskeget is located approximately 6 km west of Nantucket Island, and is the largest gray seal breeding colony in the U.S. (Waring *et al.* 2007). Monomoy Island is located 30 km northeast of Muskeget. Both islands are surrounded by areas of shallow, sandy bottom and swift currents, and have continually changing shorelines (Rough 1995). The eastern shore of Monomoy faces the open Atlantic, whereas Muskeget is protected by Nantucket Island to the south and east, Cape Cod to the north, and Martha’s Vineyard and the mainland to the west (Figure 3.1). It should be noted that a land bridge was formed between Monomoy and a barrier beach (South Beach, Chatham MA) during a fall 2006 storm, and Monomoy is therefore technically no longer an island.

Monomoy and Muskeget support year-round aggregations of gray seals, but the number of animals present at haul out sites changes seasonally. For example, between

2004 and 2008, a maximum of 6,000 (Muskeget) to 8,000 (Monomoy) gray seals were observed during the spring molting season, but in late summer an average of about 300 animals was observed at each site (pers. obs.). The reason for these large fluctuations is unknown, but movement to colonies further north, or extended foraging trips (Sjöberg and Ball 2000) are two plausible reasons.

Based on remote tracking of gray seals in the North Sea, McConnell *et al.* (1999) suggested that satellite telemetry be combined with dietary analysis to better understand seals' predation impact on fish stocks. Seal foraging decisions will obviously impact their diet, and govern habitat use (Middlemas *et al.* 2006). Prey consumption varies with region (Bowen and Harrison 1996) and gray seals differ in their use of foraging grounds, and target different prey, based on sex and season (Beck *et al.* 2003, Breed *et al.* 2006). Consumption models require knowledge of diet, age and sex structure of the population, seals energy budgets, and energy content of prey (Hammill and Stenson 2000). Therefore, data on seal movements in relation to prey inform seal-fishery interaction models, as well as wildlife management decisions affecting these animals (McConnell *et al.* 1999).

Gray seals foraging on the Scotian Shelf appear to shift their diet based on prey availability (Bowen and Harrison 1994, Bowen *et al.* 2003). However, it is not known if the diet of gray seals in their U.S. range is determined primarily by prey availability, or if these seals use other prey selection criteria, such as prey size, body shape, energy content, schooling behavior, or swimming speed (Stephens *et al.* 2007). Seal movements and diet are influenced by prey selection criteria: for example, if seals passively sample available prey, they will use space differently, and exploit different foraging grounds, than if they actively select certain prey items based on value (Bowen *et al.* 2002).

Since gray seals can travel long distances between haul out sites and in search of food, their movements at sea must be followed remotely (Austen *et al.* 2004, Beck *et al.* 2003, Breed *et al.* 2006, McConnell *et al.* 1999, Thompson *et al.* 1991, Thompson *et al.* 1996). Satellite-relay data loggers provide data on seal movements, and the pattern of satellite fixes provides an indirect measure of feeding activity (Robinson *et al.* 2007). While satellite tagging has not been conducted on adult wild caught gray seals in the U.S., marine mammal rescue centers have deployed tags on rehabilitated seals (overwhelmingly young-of-the-year pups). Further, researchers at the University of Massachusetts, Boston, have deployed satellite tags on two healthy young-of-the-year gray seal pups, captured at breeding colonies in Maine (S. Wood, U. Mass. Boston, unpubl. data).

I combined gray seal diet information, available data on satellite-tracked seals, and fishery independent prey surveys, to answer the following questions: 1) Do gray seals consume species that are most abundant in the marine environment? 2) Do seals at sea forage in areas with high abundance of certain prey types? 3) Are gray seal colonies located in or near areas of high abundance of certain prey types?

Methods

Data sources

Gray seal diet composition was estimated from scats collected at haul out sites in Nantucket Sound (see chapter 1). I obtained fishery independent information on the distribution and abundance of seal prey from long-term research bottom trawl surveys conducted by the National Marine Fisheries Service, Northeast Fisheries Science Center (NEFSC) and Massachusetts Division of Marine Fish (Azarovitz *et al.* 1989). These surveys provide the best available index of the distribution and abundance trends for fish and squids in this region (Despres *et al.* 1988). Both state and federal surveys are conducted each spring and fall. The NEFSC surveys cover the region from Cape Hatteras to Nova Scotia, primarily in federal waters (>5.6 km from shore) (DeLong and Collie 2004), and DMF surveys are conducted in Massachusetts state waters, within 5.6 km from shore (Figure 3.2). I used these data to construct an index of the distribution and abundance of fish and squids available to gray seals throughout their U.S. foraging range. Data on gray seal movements, derived from satellite tags, is available at (http://whale.wheelock.edu/).

Diet in relation to prey availability

To compare the diet of gray seals to the availability of their prey, I ranked the most important species recovered in scat samples, and compared these to those found in bottom trawl surveys (Bowen and Harrison 1994). The “importance” of a given species in the diet was defined by the percentage of the total weight it contributed to the diet. The “importance” of a given species in trawls was defined by the percentage that species contributed to the total weight of all catch. I chose the years 2004 -2006 to perform diet-trawl comparisons, since 82% of scat samples were collected in these years (Table 3.1). I used samples collected in all seasons to reconstruct diet, even though trawl surveys were only conducted in spring and fall. Fall trawl surveys were used as a proxy for winter prey distribution, and spring surveys were used as a proxy for summer prey distribution (Overholtz and Link 2007). Scats collected at a given site likely contain prey obtained within a radius of approximately 80km, based on passage rates and swimming speed (Bowen and Harrison 1994). Therefore, trawl survey data was restricted to those stations falling within this radius of Monomoy and Muskeget Islands ($40^{o}30'$ - $42^{o}70'$ N, $69^{o}00'$ - $71^{o}26'$ W). Diet data was also available from stomach contents of bycaught seals, but these were not used for diet/trawl comparison, since most stomach samples came from animals caught outside of the 80 km foraging radius represented at scat collection sites (Figure 3.3).

I ranked the 10 most important prey types in diet, measured by percent of total ingested wet mass, for each time period. To calculate the top 10 species recovered in trawl surveys, I divided the total weight of each prey taxon collected during the course a cruise by the total weight of all taxa collected during that cruise, thus creating a relative measure of prey abundance. This index was assumed to be a measure of prey availability. This is not an unreasonable assumption, since seals are highly mobile, diving mammals that have the potential to exploit the entire water column. I compared diet in scats to species rankings from both inshore and offshore trawl surveys, since together these provided coverage of the 0-80 km foraging range reflected in scat contents. Data from inshore and offshore surveys were treated separately because trawls were conducted by different vessels, using slightly different gear.

Several prey taxa were grouped in the diet, and were therefore compared as a group to particular species in trawl survey data. Red hake (*Urophycis chuss*) and white hake (*Urophycis tenuis*) could not be distinguished by hard parts, and were grouped together into the *Urophycis* genus. *Urophycis* ranks in diet were then compared to separate red and white hake ranks in trawl data. To map abundance and distribution for this taxon, I combined trawl survey data for both species, so distribution maps reflected red and white hake together. Skate species could likewise not be distinguished in the diet, and were grouped into the family Rajidae. Diet ranks for "skates" were compared to ranks for different skate species recovered in trawls. Sculpin (*Myoxocephalus spp*.) species could not be distinguished in diet analysis. I used longhorn sculpin (*Myoxocephalus octodecemspinosus*) for comparison to trawl surveys, since this is the dominant sculpin species in the study area (Bigelow and Schroeder 2002).

Seal foraging at sea in relation to prey distribution

Satellite fixes for 12 young-of-the-year gray seals were entered into a Geographic Information System (GIS, ArcView 6.3, ESRI). Data were made available online through the Satellite Tagging Observation Program (STOP), and the Whalenet website (http://www.whale.wheelock.edu). Satellite fixes posted on the site have been filtered for location quality (Mike Williamson, pers. comm.), and include location classes of 0-3.

Locations classes of 0 have a spatial resolution of at least 5,000 meters, and get progressively more accurate from 1 to 3. Most tags had satellite uplinks that occurred every 24 hours.

I used two measures to infer foraging activity from satellite tracks. Using the principle of area restricted search (ARS), I hypothesized that increased turning rates were suggestive of feeding behavior. Turning rates were calculated as the quotient of step length (the distance between two satellite fixes) and the absolute value of the turn angle at the end of that step (measured from forward direction to turn direction). ARS behavior was distinguished from transiting behavior (Robinson *et al.* 2007). Transiting behavior was defined by an animal traveling in a relatively straight line, with even spatial intervals between satellite fixes, which suggested it was moving at a constant rate (Thompson *et al.* 2003). Although not a behavior in itself, central place foraging (CPF) patterns were also used to infer feeding activity. Central place foraging occurs when an animal conducts repeated foraging bouts from a centrally located nest or colony (Orians and Pearson 1979). CPF was defined by repeated returns to the same haul out site following short-term transiting bouts (<2 days) (Sjöberg and Ball 2000).

In order to link foraging behavior at sea with prey, I selected seals that had active tags during the periods when seasonal trawl surveys were conducted. Of 12 tagged gray seals, 6 had tags that were active and transmitting during the same months, and occurred in the same area as, a trawl survey was conducted (Table 3.2). Since I had no diet information for the seals instrumented with tags, I mapped the distribution and abundance of seven prey taxa known to be important in the diet of gray seals: Atlantic cod (*Gadus morhua*), sand lance (*Ammodytes spp*.), longfin inshore squid (*Loligo pealeii*) winter flounder (*Pseudopleuronectes americanus*), fawn cusk-eel (*Lepophidium cervinum*), skates (family Rajidae) and hake (*Urophycis spp*.). Together these taxa comprised more than 87% of biomass of gray seal diet inferred from scat analysis. Although two species of sand lance occur in the gray seal's U.S. range, northern sand lance (*Ammodytes dubius*) and American sand lance (*Ammodytes americanus*), these species could not be distinguished in diet analysis, and were pooled into the *Ammodytes* genus. Likewise, skates could not be identified to species and were grouped in the family Rajidae. Trawl surveys only record catch of northern sand lance, not American sand lance, and therefore only the former species was used to map sand lance distribution.

There are various possible spatial scales at which to analyze seal movements in relation to prey distribution. I chose the fishery statistical areas defined by the Northwest Atlantic Fisheries Organization (NAFO) (Figure 3.1) to investigate seals' use of space at sea. I chose these spatial units because 1) they were originally created based on stock distribution areas of commercially important species, and were "designed to correspond with the natural divisions of fish populations and barriers to migrations" (Halliday and Pinhorn 1990); 2) NAFO areas provide a spatial structure relevant to commercial fishing effort, catch and landings, of interest when relating seal foraging behavior to commercial fisheries, and 3) fine-scale foraging activity such as diving could not be inferred from daily satellite fixes, so I examined foraging behavior on a larger spatial scale, relevant to the swimming speed of gray seals, and distances they can travel in days and weeks (approximately 0.9 m s^{-1}) (Bowen and Harrison 1994, McConnell *et al.* 1992). I created a standardized index of prey abundance for each prey taxon within each statistical area. This index was calculated as the number of individuals from a given taxon caught per station, during a particular research cruise, averaged across all stations within a given statistical area. This index takes into account catch per unit effort (number of stations sampled) within a given fishery statistical area, and allows the comparison of statistical areas containing different numbers of sampling stations. It should be pointed out that fishery statistical areas, although useful spatial references for seal behavior, are not in themselves related to the strata in bottom trawl survey design (Despres *et al.* 1988). Therefore, statistical areas likely do not contain even proportions of sampling stations.

Colors representing gradients of prey abundance were assigned to each statistical area using Jenks natural breaks. Breaks were based on natural groupings inherent in the data, and best grouped similar values while maximizing differences between classes (ArcView 9.2 Manual, ESRI, Redlands, CA, 2006). Jenks breaks were chosen as a classification scheme, rather than equal-sized breaks or quantiles, because catch data in most prey groups were not normally distributed, and showed large and uneven jumps in data values (Longley *et al.* 2005). Red signified statistical areas with the highest relative abundance of a given species, and dark blue signified areas that were sampled, but had a catch of zero for that species. Exceptions to this were the six areas at the southern and eastern boundaries of the study area: 533, 534, 541, 542, 543 and 463

(Figure 3.2). These were not sampled by NMFS or DMF surveys at any time between 1998 and 2008, the time period for which seals were satellite tracked and diet samples were collected. These statistical areas were colored dark blue on prey distribution maps for convenience, but it should be noted that these regions had an abundance of zero not because species of interest did not occur there, but because they were not sampled.

Prey distribution around major haul out sites

In order to relate gray seal colony locations to prey distribution, I mapped the distribution of the most important prey taxa by weight in the diet of gray seals (see chapter 1). These were: Atlantic cod (*Gadus morhua*), sand lance (*Ammodytes spp*.), longfin inshore squid (*Loligo pealeii*) winter flounder (*Pseudopleuronectes americanus*), fawn cusk-eel (*Lepophidium cervinum*), skates (family Rajidae) hake (*Urophycis spp*.) and windowpane flounder (*Scophthalmus aquosus*). Together these comprised over 90% of the wet mass consumed, based on scat analysis (Table 3.3). I compared these distribution patterns to the locations of five major U.S. gray seal colonies. Prey distribution was calculated using the methods outlined above. I averaged species abundance in trawls from 1998 to 2008 in order to observe general spatial patterns in prey abundance and distribution in relation to seal colonies. I pooled these data because colony locations are not ephemeral, persist across many years, and gray seals demonstrate considerable haul out and breeding site fidelity (Pomeroy *et al.* 2000).

Results

Diet in relation to prey availability

Species important in the diet (Table 3.4) were also important, to some extent, in trawl surveys. At least 2, and as many as 6, of the top 10 species in diet were also among the top ranked trawl species in surveys between 2004 and 2006. Diet matched up slightly better with fall surveys, with an average of 4.2 species in common, than with spring surveys, with an average of 4 species in common (Table 3.5A-C). Diet ranks matched up slightly better with offshore than inshore survey data (offshore 4.3 species in common; inshore 3.8 species). The top ranked species in diet was also among the top 10 species in surveys in 9 out of 12 cruises. The most abundant taxon in trawls was spiny dogfish (*Squalus acanthias*). However, only two dogfish were recovered in the diet, out of a total of 2,569 prey individuals (Table 3.3). Three species, haddock (*Melanogrammus aeglefinus*), pollock (*Pollachus viriens*) and Acadian redfish (*Sebastes fasciatus*) were consistently among the top 10 species in trawls, but were not recovered at all in scat samples (Tables 3.3 and 3.5A-C). Although neither pollock nor haddock was recovered in scats, 14 unidentified gadid individuals were recovered. The remains of these gadids were so eroded as to preclude identification. Even so, the percent frequency of occurrence of this group was only 3%, and the percent relative abundance and wet mass in the diet were <1%. Therefore this group did not comprise an important prey taxon by any measure. Atlantic cod was among the top 10 most abundant species in 10 out of 12 bottom trawl surveys conducted between 2004 and 2006. This is somewhat surprising in the context of the recent collapse of this stock and its apparent failure to rebuild (O'Brien 1999).

Seal foraging at sea in relation to prey distribution

In several cases, foraging behavior was clear within the context of prey distribution. In fall 2004, seal # 39382 (“Solange”) engaged in CPF primarily in statistical area 465, returning to a single haul out site off the coast of southern Nova Scotia (43°50’ N, 66°00’ W) (Figure 3.4). A total of 60 trips were made from the same location, and each trip lasted > 2 days (Figure 3.4). All trips were made within 100 km of the haul out site, and 97% were made within 80 km (Table 3.6). This region had high abundance of winter flounder, cod, and red/white hake (Figures 3.5-3.7). During spring 2005, seal # 39393 (“Stephanie”) displayed ARS behavior in statistical area 525 (Georges Bank). The animal’s turning rate increased markedly in this region in relation to other statistical areas (Figure 3.8), and 67% of the animal’s turn angles were greater than 45° (Table 3.7). Georges Bank, along with adjacent area 562 (at the eastern edge of the EEZ), had the highest abundance of squid in the survey area (Figure 3.9). Cusk eel and skates were also highly abundant in these regions (Figures 3.10 and 3.11). In fall 2007, seal # 39391 exhibited CPF in statistical area 513, with repeated trips to a single haul out site in coastal Maine (43°66’ N, 70°04’ W) (Figure 3.12). Of a total of 61 trips from this site, all were made within 24 hours, and all were within 40 km of the haul out site (Figure 3.12). Seventy-four percent of these trips were made within 20 km of the haul out site (Table 3.6). This region was most abundant in winter flounder (Figure 3.13), and also had high abundance of red/white hake (Figure 3.14) and cod (Figure 3.15). During September-October 2002, seal # 01657 ("Louise") exhibited CPF in statistical area 513 (Figure 3.16). Of a total of 48 trips from the site, each conducted within 24 hours, 99% fell within 10 km of the haul out site (Table 3.6). This area in the western Gulf of Maine encompasses the southern Maine coast, and entire New Hampshire coast (Figure 3.17). In fall 2002, trawl surveys reported the highest abundance of northern sand lance in the regions corresponding to areas 513 and 465 (Scotian Shelf waters) (Figure 3.17).

Prey distribution around major haul out sites

The three major gray seal colonies in the GOM (Seal Island, Green Island, and Mount Desert Rock) are located in areas with highest relative abundance of Atlantic cod (Figure 3.18), and areas that have high abundance of sand lance, red/white hake, and winter flounder (Figures 3.19-3.21). The two largest colonies in southern New England, Monomoy and Muskeget Islands, are located near areas that have the highest abundance of windowpane flounder, skates and squid (Figures 3.22-3.24), and relatively high abundance of sand lance, red/white hake, winter flounder and cusk eel (Figures 3.19-3.21, 3.25).

Sand lance and winter flounder made up majority of the diet by weight, even though the areas of highest abundance of these species were located outside the daily foraging range of animals hauled out at these sites. Marked differences were apparent in the prey assemblages around SNE and GOM colonies, particularly in the case of windowpane flounder, skates, squid and cusk eel. These taxa are present near the GOM colonies, but are much less abundant than they are further south (Bigelow and Schroeder 2002, Bowman *et al.* 2000, Neuman *et al.* 2001) (Figures 3.22-3.25).

Discussion

Gray seals include abundant species in their diet, such as skates, winter flounder, cod and sculpin (*Myoxocephalus spp*.). However, seal diet could not be directly predicted from species abundance, and this is therefore not the only criterion for prey selection. Haddock, pollock and Acadian redfish were abundant in the areas where seals forage, but did not appear in the diet. A similar situation occurred on the Scotian Shelf, home to the largest gray seal colony in the world, Sable Island (Bowen and Harrison 1994). Gray seal diet at this colony, inferred from scats, contained a small amount of Acadian redfish (1.3% of diet by weight, although different diet analysis methods put this number at 30%; see Beck *et al.* 2007), some pollock (0.2%) and no haddock, even though these ranked in the top eight most abundant species in trawl surveys conducted by the Canadian Department of Fisheries and Oceans (Bowen and Harrison 1994). This suggests that gray seals do not target prey based solely on availability, but use some other prey preference criteria.

In addition to availability, gray seal diet may be constrained by dietary resource partitioning. The harbor seal, also a year-round resident in the Gulf of Maine, is more abundant than gray seals. The most recent estimate of the number of harbor seals in the U.S. is close to 100,000, more than 10 times the maximum estimated number of gray seals (Gilbert *et al.* 2005, Waring *et al.* 2007). Acadian redfish, pollock and haddock, three abundant prey species not found in gray seal diets, are found in those of harbor seals (Kopec 2009). Acadian redfish comprises up to 58% of the diet of harbor seals, although this varies interannually; pollock up to 6.3%, and haddock comprises between 1 and 4 percent of the diet by weight (Kopec 2009). Both gray and harbor seals appear to be increasing in number in the U.S. (Gilbert *et al.* 2005, Waring *et al.* 2007), and resource partitioning between the two, if it were occurring, would reduce interspecific competition, particularly in a marine environment where many fish stocks are declining (Page *et al.* 2006).

Satellite tracking suggested that young seals were foraging in areas with high abundance of winter flounder and sand lance (Figures 3.5, 3.13 and 3.17). These two species together comprised over 72% of the gray seal diet by weight (Table 3.3), and available satellite telemetry data appear to agree with findings from scat analysis. However, caution should be used in interpreting these results, because of the extremely small sample size of tagged seals, and because all of the tagged seals were young-of-the-year pups. YOY pups are known to have different foraging patterns (Sjöberg and Ball 2000) and diet composition (Bowen and Harrison 1996) than those of adults.

Sand lance and winter flounder, the most important diet items by weight, were most abundant in regions outside the daily foraging range of scat sampling sites. If gray seals target prey based solely on abundance, one would expect to see windowpane flounder, squid, and cusk eel comprise a larger proportion of the diet in scats collected in southern New England, since these species are more abundant around colonies in this area (Figures 3.22, 3.24, 3.25). As it is, squid, windowpane flounder and cusk eel comprised 1.4%, 2.2%, and 0.1% of the diet by weight, respectively.

Central place foraging was observed in three seal tracks. The radius of these foraging bouts varied among seals, but all were within 100 km of the haul out site (Table 3.6). One animal conducted most of its bouts between 40 and 80km, one entirely within 40km, and a third never strayed from a 20 km radius of the haul out site. This finding suggests that prey in scats are a good indication of diet, since they contain prey taken in an 80 km foraging radius. This result is also in agreement with McConnell *et al.* (1999), who found that most gray seal foraging bouts were conducted within a 40 km radius of haul out sites.

There were clear differences in prey distribution around GOM and SNE seal colonies (Figures 3.18-3.25). Prey abundance varied between SNE and GOM colonies, particularly in the case of windowpane flounder, skates, squid, and cusk eel. These taxa are present near the GOM colonies, but are more abundant further south (Figures 3.22-3.25). Unfortunately there is little diet data from scats collected at GOM sites. Comparison of diet between the two sites would be instructive, not only to further test the hypothesis that seals target abundant prey, but to obtain more comprehensive diet information for gray seals in United States waters.

Gray seals in this study foraged inshore, close to haul out sites, as well as in offshore areas such as Georges Bank. Telemetry data corresponded with diet data: sand lance, gadids and flounder were important in the diet, and at-sea feeding activity occurred in areas with high abundance of these prey taxa. In order to map relative foraging intensity inshore and offshore, and to better understand seal predation impacts on fish stocks, a useful next step would be to instrument a large number of seals, from all sex and age classes, with satellite-tracked tags and time-depth recorders. This would reveal foraging grounds commonly used by seals, and take into account sex and age variation in foraging behavior.

Chapter 3: Tables

	Winter	**Spring**	**Summer**	**Fall**
2004	1	31	13	28
2005	6	9	10	21
2006	22	45	21	44
2007	13	21	7	7
2008	6	0	0	0
Total: 305 seal scat samples				

Table 3.1: Overview of scat sample collection

Seal name	Tag #	Sex	Location released	Organization/Researcher	Duration of Tag Activity
*Stephanie	39393	Female	ME	2,3	2/2/05-9/23/05
*Solange	39382	Female	ME	2,3	5/12/04-12/25/04
Wade	39383	Male	ME	4	5/5/03-7/2/03
*Valentine	39384	Male	ME	4	5/5/03-10/8/03
*Louise	01657	Female	ME	4,5	5/8/02-3/14/03
Sputnik	27569	Male	NY	1	7/2/01-8/19/01
Gray	27568	Male	ME	3,4	5/24/01-9/2/01
McHenry	27584	Male	MA	3	11/24/98-12/20/98
Casino	27583	Male	MA	6	5/18/98-8/4/98
*Ernie	39389	Male	MA	1	8/5/07-2/28/08
*39391	39391	Male	NY	1	6/21/07-3/14/08
Bubba	39392	Male	NY	1	4/15/08-5/11/08

Table 3.2: Gray seals satellite-tagged in U.S. waters, 1998-2008
1. Riverhead Foundation, Riverhead, NY; 2. Stephanie Wood, U. Mass Boston; 3. New England Aquarium, Boston, MA; 4. Marine Animal Lifeline, Westbrook, ME; 5. Marine Environmental Research Institute, Blue Hill, Maine; 6. Marine Mammal Stranding Center, Brigantine, NJ.
* Seal whose tagging period coincided with research trawl surveys

Common name	Scientific name	MNI	% RA	% FO	% Wet wt	(kg)
Sand lance	*Ammodytes spp.*	4198	66.3	14.0	53.3	138.8
Winter flounder	*Pseudopleuronectes americanus*	162	2.6	6.9	19.0	49.6
Atlantic cod	*Gadus morhua*	25	<1.0	2.0	6.4	16.6
Skates	Rajidae	159	2.5	24.5	5.7	14.8
Red/white hake	*Urophycis spp.*	530	13.5	9.4	3.3	8.6
Atlantic herring	*Clupea harengus*	93	1.5	2.3	3.7	9.6
Windowpane flounder	*Scopthalmus aquosus*	118	1.9	7.1	2.2	5.6
Squid	*Loligo pealeii*	219	3.4	6.2	1.4	3.6
Cusk eel	Ophidiidae	159	2.5	5.2	<1.0	0.5
Sculpin	*Myoxocephalus spp.*	132	2.1	2.5	4.0	10.3
Shrimp/crab	Crustacea	32	<1.0	1.7	<1.0	0.1
Fourspot flounder	*Paralichthys oblongus*	22	<1.0	1.9	<1.0	2.1
Yellowtail flounder	*Limanda ferruginea*	20	<1.0	1.9	<1.0	1.1
Silver hake	*Merluccius bilinearis*	22	<1.0	2.0	<1.0	1.5
Gulfstream flounder	*Citharichthys arctifrons*	22	<1.0	2.0	<1.0	0.3
n/a	*Merluccius spp.*	13	<1.0	1.1	<1.0	0.2
Atlantic mackerel	*Scomber scombrus*	13	<1.0	1.1	<1.0	0.2
Unidentified flatfish	*Pleuronectiformes*	21	<1.0	3.0	<1.0	0.1
Unidentified gadids	Gadiformes	14	<1.0	3.0	<1.0	0.1
Ocean pout	*Macrozoarces americanus*	6	<1.0	<1.0	<1.0	<0.1
Lumpfish	*Cyclopterus lumpus*	4	<1.0	<1.0	*	*
Blue mussel	*Mytilus edulis*	4	<1.0	1.0	*	*
Hagfish	*Petromyzon marinus*	3	<1.0	<1.0	*	*
Tautog	*Tautoga onitis*	3	<1.0	<1.0	*	*
Spiny dogfish	*Squalus acanthias*	2	<1.0	<1.0	*	*
Striped bass	*Morone saxatilis*	2	<1.0	<1.0	*	*
Eel	*Anguilla rostrata*	1	<1.0	<1.0	*	*
Scup	*Stenotomus chrysops*	1	<1.0	<1.0	*	*
Wolffish	*Anarhichas spp.*	1	<1.0	<1.0	*	*
Unknown	Unknown	13	<1.0	1.0	*	*
TOTAL		**6013**	**100.0**	**100.0**	**100.0**	**263.6**

Table 3.3: Prey in 252 scats
MNI = Minimum number of individuals; RA = Relative abundance; FO = Frequency of occurrence.
* Weight not estimated

2004				
Prey taxon	**Spring % wt**	**Spring Rank**	**Fall % wt**	**Fall Rank**
Cod	3.0	6	0.0	
Sand lance	24.0	2	1.0	9
Skates	0.0		26.0	2
Red/White Hake	10.0	4	3.0	4
Windowpane Flounder	3.0	7	2.0	6
Squid	13.0	3	1.0	8
Cusk Eel	0.0		0.0	
Herring	0.0		2.0	7
Silver Hake	2.0	8	0.0	
Sculpin	3.0	5	4.0	3
Winter Flounder	57.0	1	57.0	1
Yellowtail Flounder	0.0		0.0	
Gulfstream Flounder	0.0		3.0	5
Fourspot flounder	1.0	9	1.0	10
Mackerel	1.0	10	0.0	

2005				
Prey taxon	**Spring % wt**	**Spring Rank**	**Fall % wt**	**Fall Rank**
Cod	24.0	2	0.0	
Sand lance	1.0	7	18.0	3
Skates	1.0	10	25.0	2
Red/White Hake	11.0	3	7.0	4
Windowpane Flounder	11.0	4	5.0	5
Squid	1.0	8	1.0	10
Cusk Eel	0.0		1.0	8
Herring	0.0		2.0	7
Silver Hake	0.0		0.0	
Sculpin	4.0	5	4.0	6
Winter Flounder	46.0	1	36.0	1
Yellowtail Flounder	3.0	6	0.0	
Gulfstream Flounder	0.0		0.0	
Fourspot flounder	1.0	9	0.0	
Mackerel	0.0		1.0	9

2006				
Prey taxon	**Spring % wt**	**Spring Rank**	**Fall % wt**	**Fall Rank**
Cod	1.0	10	36.0	1
Sand lance	30.0	2	21.0	2
Skates	0.0		18.0	3
Red/White Hake	1.0	7	3.0	5
Windowpane Flounder	4.0	5	3.0	6
Squid	2.0	6	3.0	7
Cusk Eel	0.0		1.0	8
Herring	12.0	3	1.0	10
Silver Hake	0.0		0.0	
Sculpin	1.0	8	0.0	
Winter Flounder	47.0	1	15.0	4
Yellowtail Flounder	0.0		1.0	9
Gulfstream Flounder	1.0	9	0.0	
Fourspot Flounder	4.0	4	0.0	
Mackerel	0.0		0.0	

Table 3.4: Ranked species in gray seal diet (based on scat sampling), 2004-2006

SPECIES	INSHORE SURVEY % WT	INSHORE SURVEY RANK	SPRING DIET RANK	SPECIES	OFFSHORE SURVEY % WT	OFFSHORE SURVEY RANK	SPRING DIET RANK
LITTLE SKATE	20.2	1		ACADIAN REDFISH	53.7	1	
SPINY DOGFISH	16.8	2		LITTLE SKATE	17.5	2	
ATLANTIC COD	14.8	3	6	SPINY DOGFISH	11.9	3	
SCULPIN	12.1	4	5	ATLANTIC COD	10.1	4	6
WINTER FLOUNDER	10.2	5	1	SCUP	8.6	5	
SCUP	8.6	6		SCULPIN	8.3	6	5
OCEAN POUT	5.8	7		WINTER FLOUNDER	7.0	7	1
AMERICAN PLAICE	4.1	8		OCEAN POUT	4.0	8	
YELLOWTAIL FL.	3.8	9		YELLOWTAIL FL.	3.8	9	
SPIDER CRAB	3.7	10		SPIDER CRAB	3.7	10	

SPECIES	INSHORE SURVEY % WT	INSHORE SURVEY RANK	FALL DIET RANK	SPECIES	OFFSHORE SURVEY % WT	OFFSHORE SURVEY RANK	FALL DIET RANK
SPINY DOGFISH	90.1	1		SPINY DOGFISH	83.5	1	
WINTER SKATE	3.5	2	2	WINTER SKATE	4.8	2	2
LITTLE SKATE	2.6	3	2	ATLANTIC HERRING	1.9	3	7
WINTER FL.	1.1	4	1	ACADIAN REDFISH	1.7	4	
SCUP	0.9	5		SCUP	1.5	5	
ATLANTIC COD	0.5	6		HADDOCK	1.5	6	
YELLOWTAIL FL.	0.4	7		LITTLE SKATE	1.4	7	2
ATL. ROCK CRAB	0.3	8		ATLANTIC COD	1.4	8	
AMERICAN PLAICE	0.3	9		LONGFIN SQUID	1.1	9	8
SMOOTH DOGFISH	0.3	10		SMOOTH DOGFISH	1.0	10	

Table 3.5A: Comparison of important species in seal diets vs. trawl surveys (2004)

SPECIES	INSHORE SURVEY % WT	INSHORE SURVEY RANK	SPRING DIET RANK	SPECIES	OFFSHORE SURVEY %WT	OFFSHORE SURVEY RANK	SPRING DIET RANK
LITTLE SKATE	36.8	1	10	POLLOCK	17.1	1	
WINTER FLOUNDER	10.5	2	1	LITTLE SKATE	15.5	2	10
ATLANTIC COD	9.0	3	2	ATLANTIC COD	14.6	3	2
SPINY DOGFISH	8.3	4		WINTER FLOUNDER	9.6	4	1
SPIDER CRAB	7.8	5		WINTER SKATE	9.2	5	10
WINTER SKATE	7.6	6	10	SCULPIN	7.9	6	5
SCULPIN	6.3	7	5	WHITE HAKE	7.8	7	3
OCEAN POUT	5.2	8		AMERICAN PLAICE	7.4	8	
YELLOWTAIL FL.	5.0	9	6	HADDOCK	7.0	9	
HADDOCK	3.5	10		SEA RAVEN	4.0	10	

SPECIES	INSHORE SURVEY % WT	INSHORE SURVEY RANK	FALL DIET RANK	SPECIES	OFFSHORE SURVEY % WT	OFFSHORE SURVEY RANK	FALL DIET RANK
SPINY DOGFISH	92.1	1		SPINY DOGFISH	87.7	1	
SCUP	1.9	2		ATLANTIC HERRING	3.1	2	7
LITTLE SKATE	1.8	3	2	POLLOCK	2.2	3	
WINTER SKATE	1.1	4	2	WINTER SKATE	1.5	4	2
SMOOTH DOGFISH	1.0	5		ACADIAN REDFISH	1.1	5	
WINTER FLOUNDER	0.7	6	1	WINTER FLOUNDER	1.1	6	1
BUTTERFISH	0.4	7		ATLANTIC COD	1.0	7	
SUMMER FL.	0.4	8		LITTLE SKATE	0.9	8	2
AMERICAN PLAICE	0.3	9		SMOOTH DOGFISH	0.7	9	
ATLANTIC HERRING	0.2	10	7	ALEWIFE	0.6	10	

Table 3.5B: Comparison of important species in seal diets vs. trawl surveys (2005)

	INSHORE SURVEY		SPRING DIET		OFFSHORE SURVEY		SPRING DIET
SPECIES	% WT	RANK	RANK	SPECIES	% WT	RANK	RANK
LITTLE SKATE	26.3	1		SPINY DOGFISH	19.3	1	
SPINY DOGFISH	14.6	2		ATLANTIC COD	14.8	2	10
SCUP	12.3	3		POLLOCK	10.5	3	
WINTER FLOUNDER	10.0	4	1	LITTLE SKATE	9.8	4	
WINTER SKATE	8.6	5		ALEWIFE	8.7	5	
ATLANTIC COD	7.2	6	10	ATLANTIC HERRING	8.4	6	3
SCULPIN	6.6	7	8	SCULPIN	8.3	7	8
YELLOWTAIL FL.	6.3	8		WINTER SKATE	8.2	8	
OCEAN POUT	4.7	9		HADDOCK	7.3	9	
AMERICAN PLAICE	3.5	10		AMERICAN LOBSTER	4.8	10	

	INSHORE SURVEY		FALL DIET		OFFSHORE SURVEY		FALL DIET
SPECIES	% WT	RANK	RANK	SPECIES	% WT	RANK	RANK
SPINY DOGFISH	77.8	1		SPINY DOGFISH	76.1	1	
LITTLE SKATE	9.9	2	3	ATLANTIC HERRING	6.4	2	10
SCUP	2.9	3		ACADIAN REDFISH	3.6	3	
WINTER SKATE	2.6	4	3	BUTTERFISH	3.2	4	
WINTER FLOUNDER	2.2	5	4	WINTER SKATE	2.4	5	3
SUMMER FL	1.2	6		HADDOCK	2.0	6	
AMERICAN LOBSTER	1.2	7		WINTER FLOUNDER	1.7	7	4
AMERICAN PLAICE	0.8	8		ATLANTIC COD	1.6	8	1
BUTTERFISH	0.7	9		LITTLE SKATE	1.6	9	3
LONGFIN SQUID	0.7	10	7	LONGFIN SQUID	1.5	10	7

Table 3.5C: Comparison of important species in seal diets vs. trawl surveys (2006)

RANGE FROM HAUL OUT SITE	NUMBER OF FORAGING TRIPS		RANGE FROM HAUL OUT SITE	NUMBER OF FORAGING TRIPS
	"LOUISE"	"39391"		"SOLANGE"
5 KM	37	20	20 KM	27
10 KM	10	7	40 KM	2
15 KM	0	9	60 KM	12
20 KM	1	9	80 KM	17
25 KM	0	6	100 KM	2
30 KM	0	9		
35 KM	0	0		
40 KM	0	1		

Table 3.6: Foraging distances for three seals in the Gulf of Maine

SATELLITE FIX	SEAL	DATE	STAT AREA	LAT	LONG	STEP LENGTH (M)	TURN ANGLE (ABS VAL)	TURN RATE (Δ IN TURN ANGLE/ METER)
1	39393	01.04.05	525	41.21	-67.97	265.45	9.81	0.04
2	39393	02.04.05	525	40.98	-67.84	372.79	52.75	0.14
3	39393	03.04.05	525	40.92	-67.47	173.49	7.54	0.04
4	39393	04.04.05	525	40.88	-67.30	55.76	16.83	0.30
5	39393	05.04.05	525	40.85	-67.26	132.64	92.94	0.70
6	39393	06.04.05	525	40.74	-67.33	144.93	132.97	0.92
7	39393	07.04.05	525	40.88	-67.36	250.06	163.18	0.65
8	39393	08.04.05	525	40.63	-67.38	218.67	77.63	0.36
9	39393	09.04.05	525	40.60	-67.60	165.01	7.79	0.05
10	39393	10.04.05	525	40.61	-67.77	133.00	9.26	0.07
11	39393	11.04.05	525	40.63	-67.90	14.76	141.74	9.60
12	39393	12.04.05	525	40.64	-67.88	69.89	170.91	2.45
13	39393	13.04.05	525	40.61	-67.95	175.60	56.34	0.32
14	39393	14.04.05	525	40.72	-68.09	101.77	104.60	1.03
15	39393	15.04.05	525	40.63	-68.13	313.90	46.95	0.15
16	39393	16.04.05	525	40.52	-68.42	181.08	2.23	0.01
17	39393	17.04.05	525	40.45	-68.59	89.82	124.30	1.38
18	39393	18.04.05	525	40.53	-68.57	98.60	138.31	1.40
19	39393	19.04.05	525	40.47	-68.65	96.08	140.86	1.47
20	39393	20.04.05	525	40.47	-68.56	135.28	44.09	0.33
21	39393	21.04.05	525	40.56	-68.45	15.00	168.57	11.24
22	39393	22.04.05	525	40.55	-68.46	116.62	120.96	1.04
23	39393	23.04.05	525	40.54	-68.35	357.22	146.24	0.41
24	39393	24.04.05	525	40.76	-68.62	205.28	23.40	0.11
25	39393	25.04.05	525	40.95	-68.72	733.40	47.64	0.06
26	39393	26.04.05	521	41.14	-69.42	398.61	61.97	0.16
27	39393	27.04.05	521	41.53	-69.51	460.49	72.78	0.16
28	39393	28.04.05	521	41.57	-69.97	26.93	10.46	0.39
29	39393	29.04.05	521	41.58	-69.99	600.52	151.06	0.25
30	39393	30.04.05	521	41.72	-69.41	519.25	15.64	0.03

Table 3.7: Turning rates of seal “Stephanie”, Spring 2005

Chapter 3: Figures

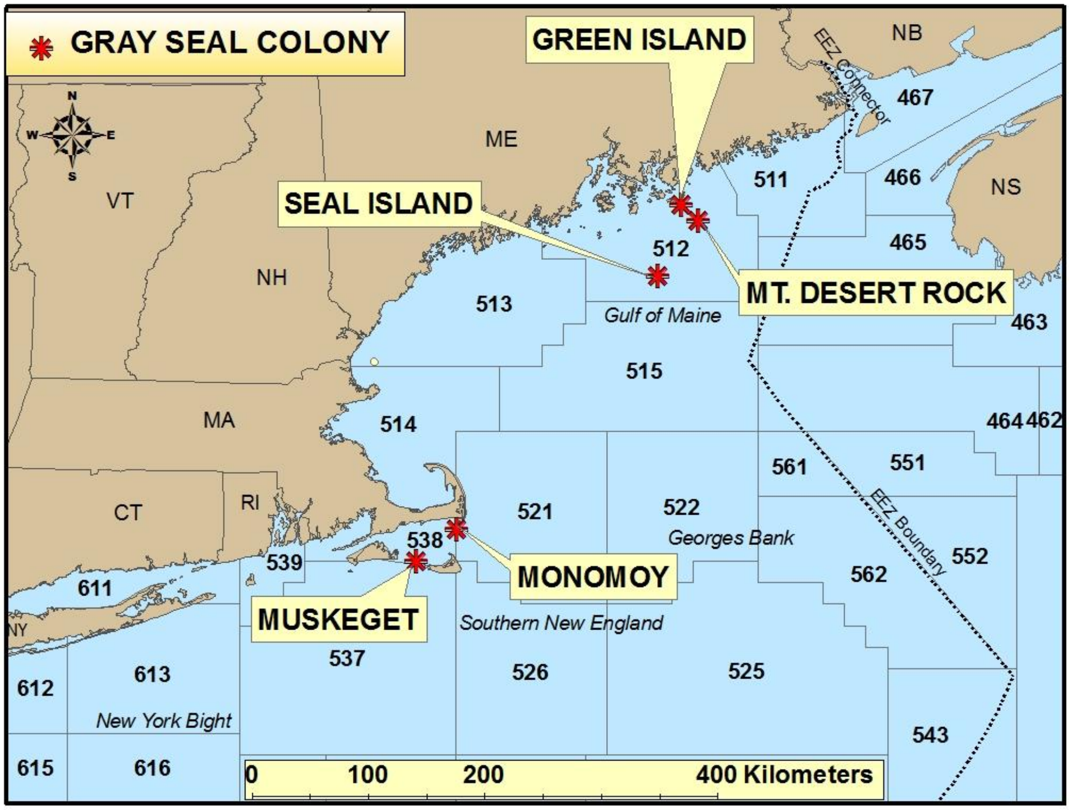

Figure 3.1: Five major gray seal colonies in U.S. waters, based on aerial surveys from 1999-2001

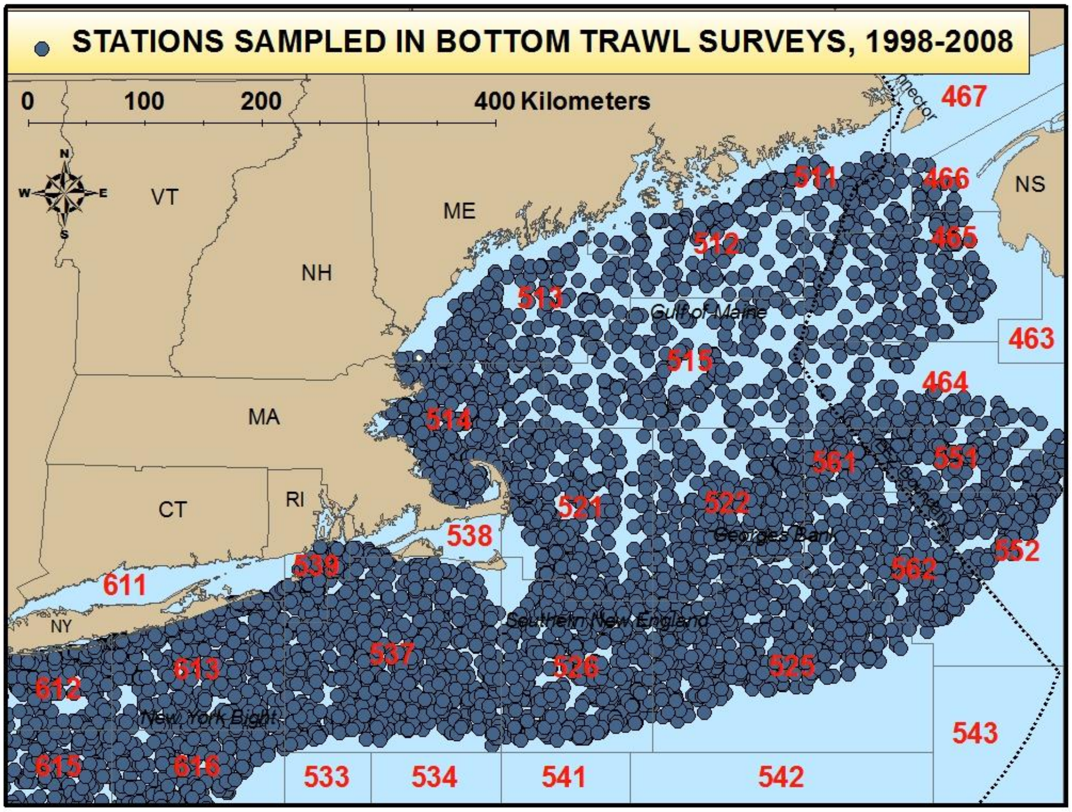

Figure 3.2: Locations of stations sampled during seasonal state and federal bottom trawl surveys, 1998-2008. Red numbers indicate Northwest Atlantic Fisheries Organization (NAFO) fishery statistical areas

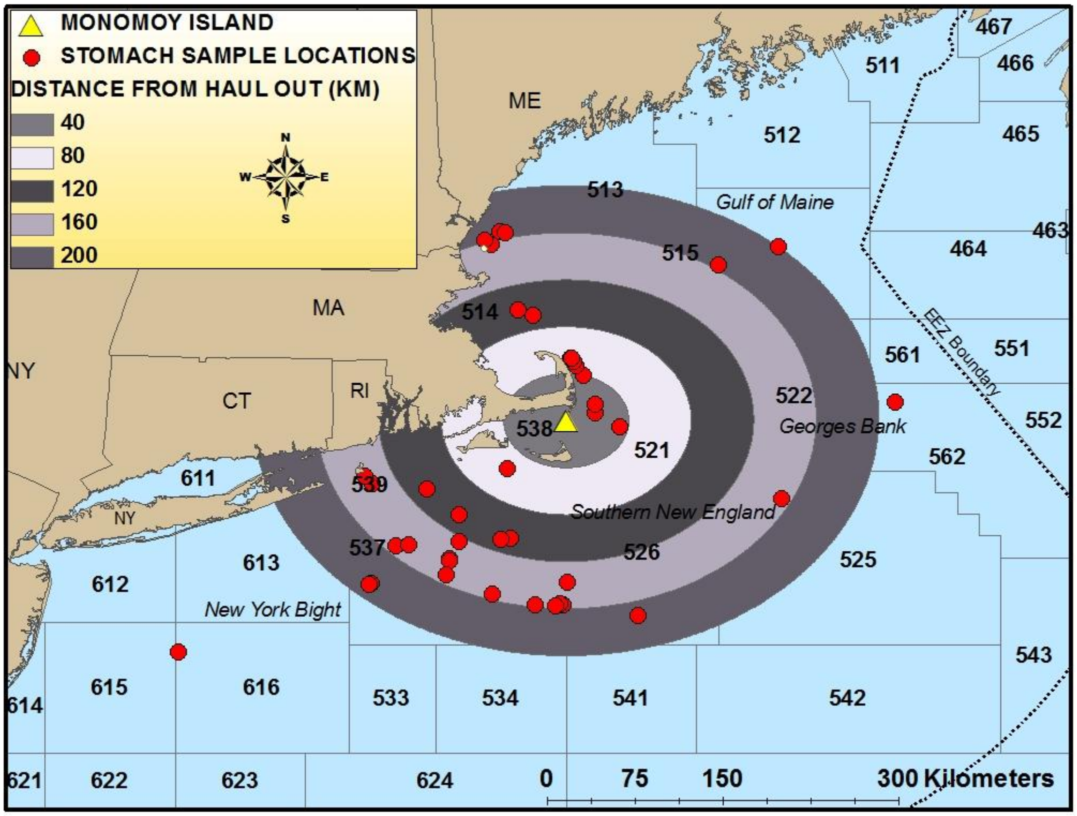

Figure 3.3: Distance between scat collection site and stomach sample locations

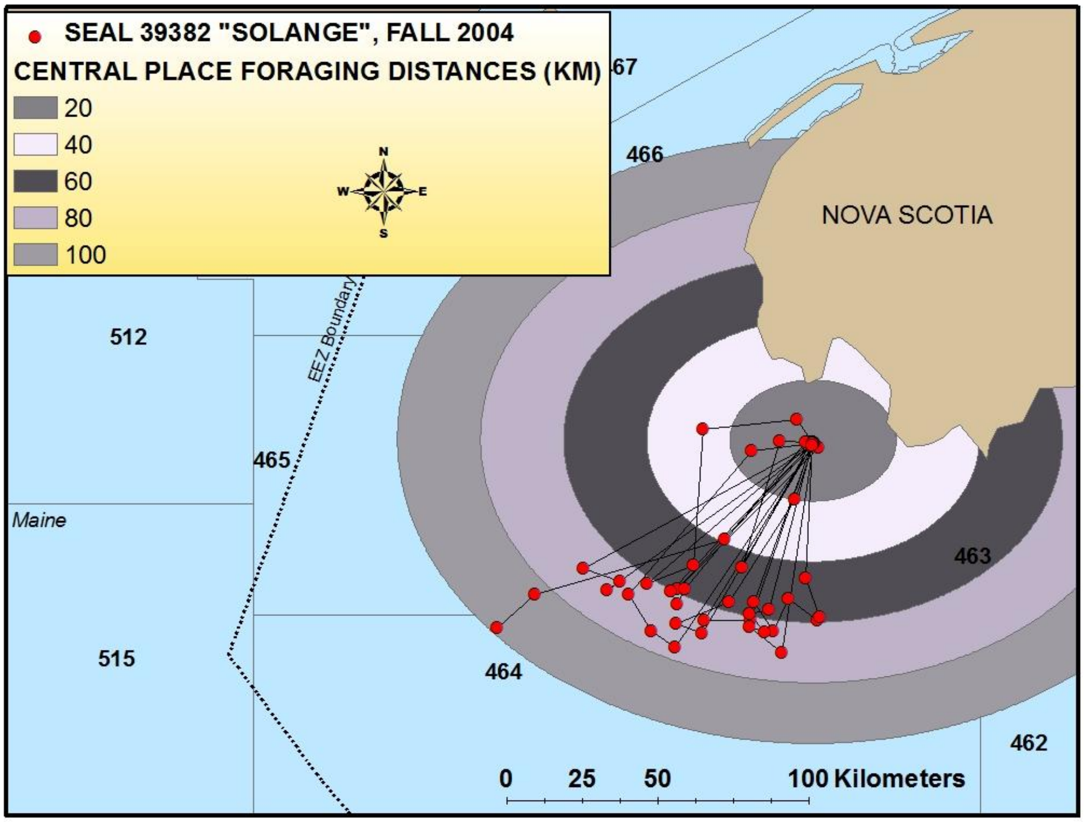

Figure 3.4: Central place foraging, and range of foraging trips, for seal "Solange"

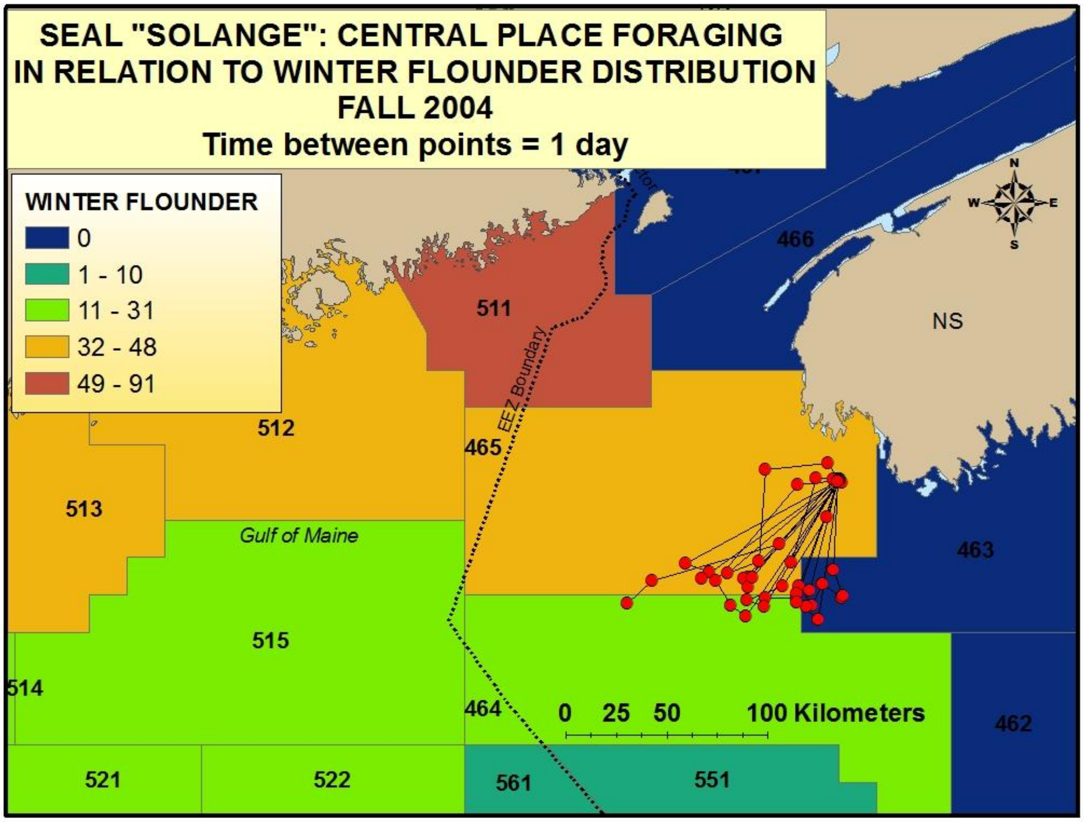

Figure 3.5: Central place foraging activity of seal "Solange" in relation to winter flounder (*Pseudopleuronectes americanus*) distribution. Color block gradients indicate mean number of individuals caught per station in a given statistical area

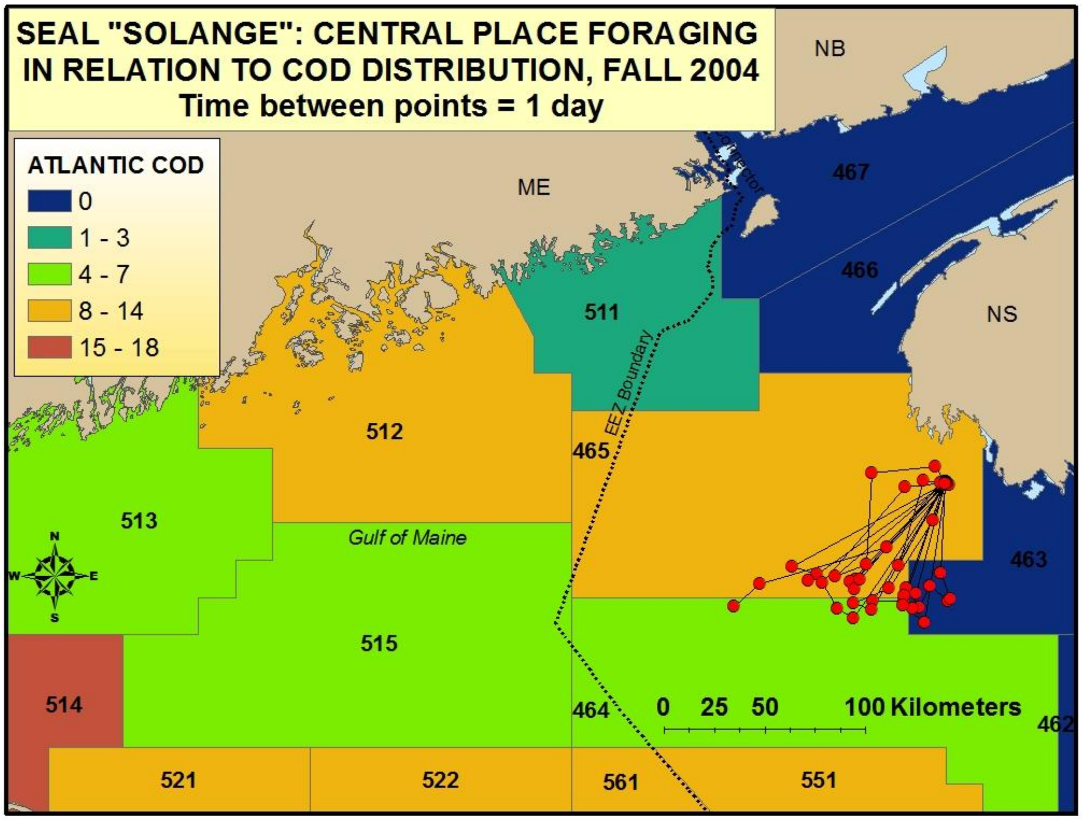

Figure 3.6: Central place foraging activity of seal "Solange" in relation to Atlantic cod (*Gadus morhua*) distribution. Color block gradients indicate mean number of individuals caught per station in a given statistical area

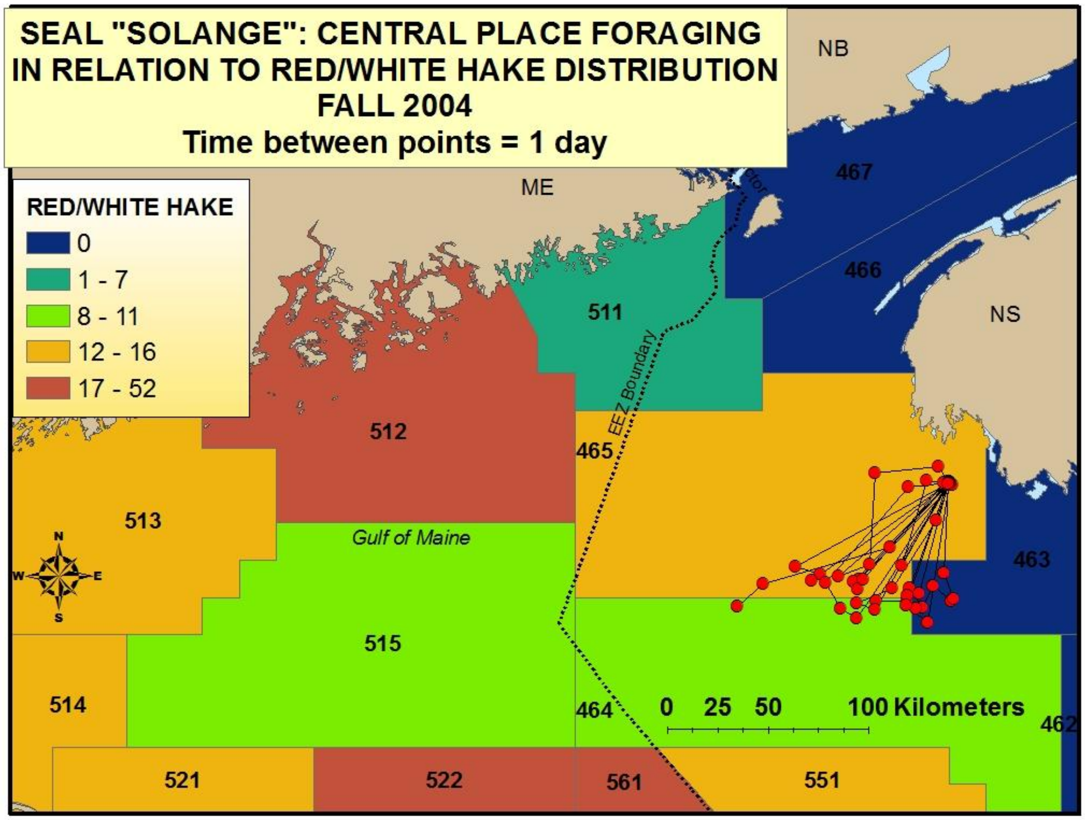

Figure 3.7: Central place foraging activity of seal "Solange" in relation to red/white hake (*Urophycis spp*.) distribution. Color block gradients indicate mean number of individuals caught per station in a given statistical area

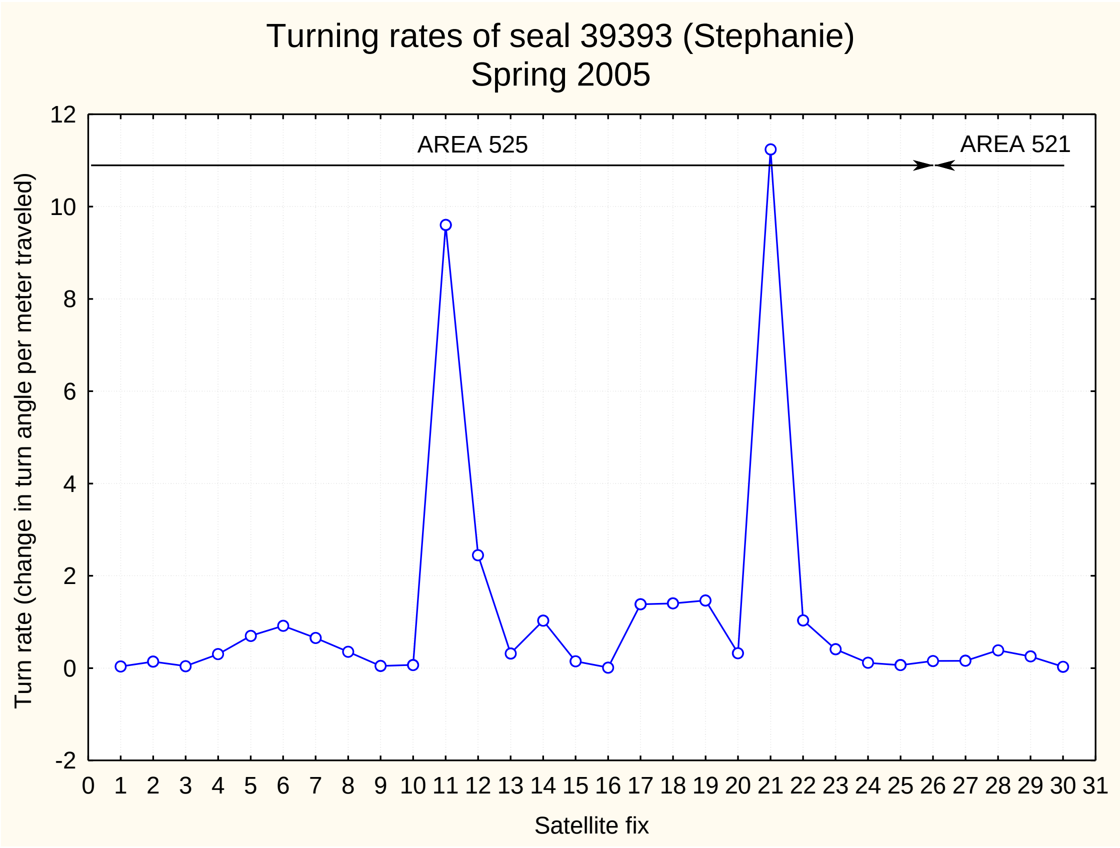

Figure 3.8: Increased turning rates of seal "Stephanie" on Georges Bank

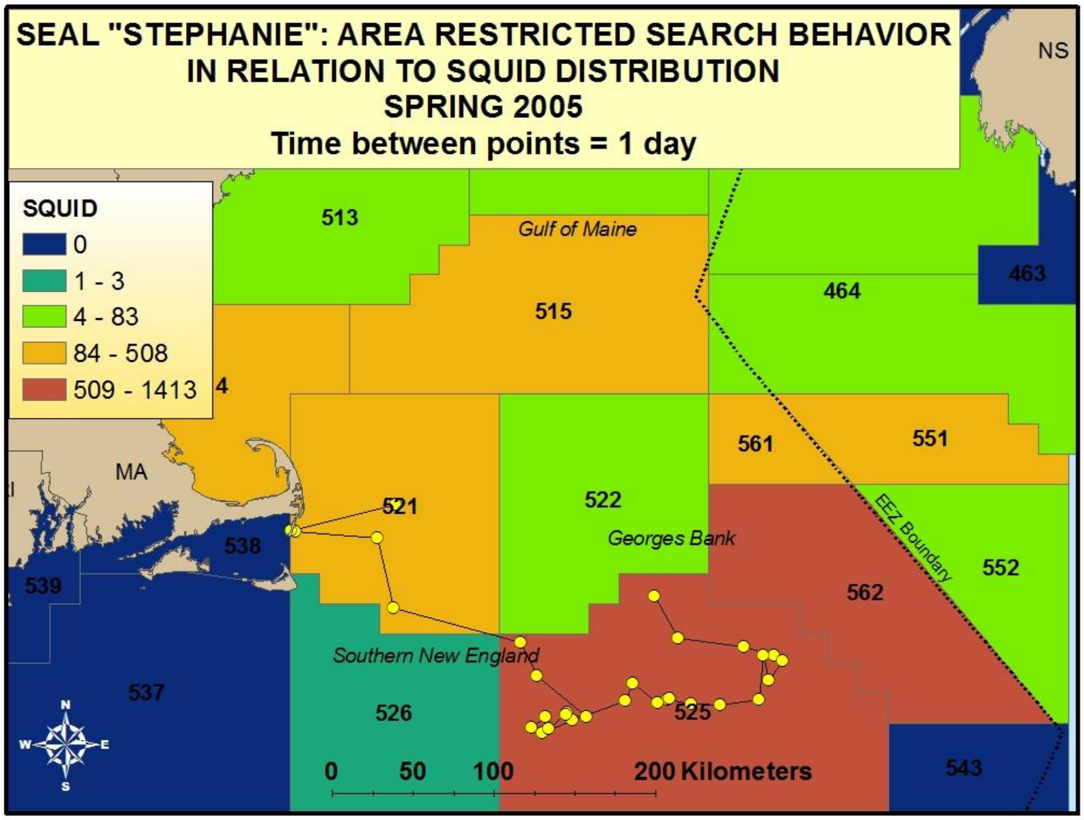

Figure 3.9: Area restricted search behavior of seal "Stephanie" in relation to squid (*Loligo pealeii*) distribution. Color block gradients indicate mean number of individuals caught per station in a given statistical area

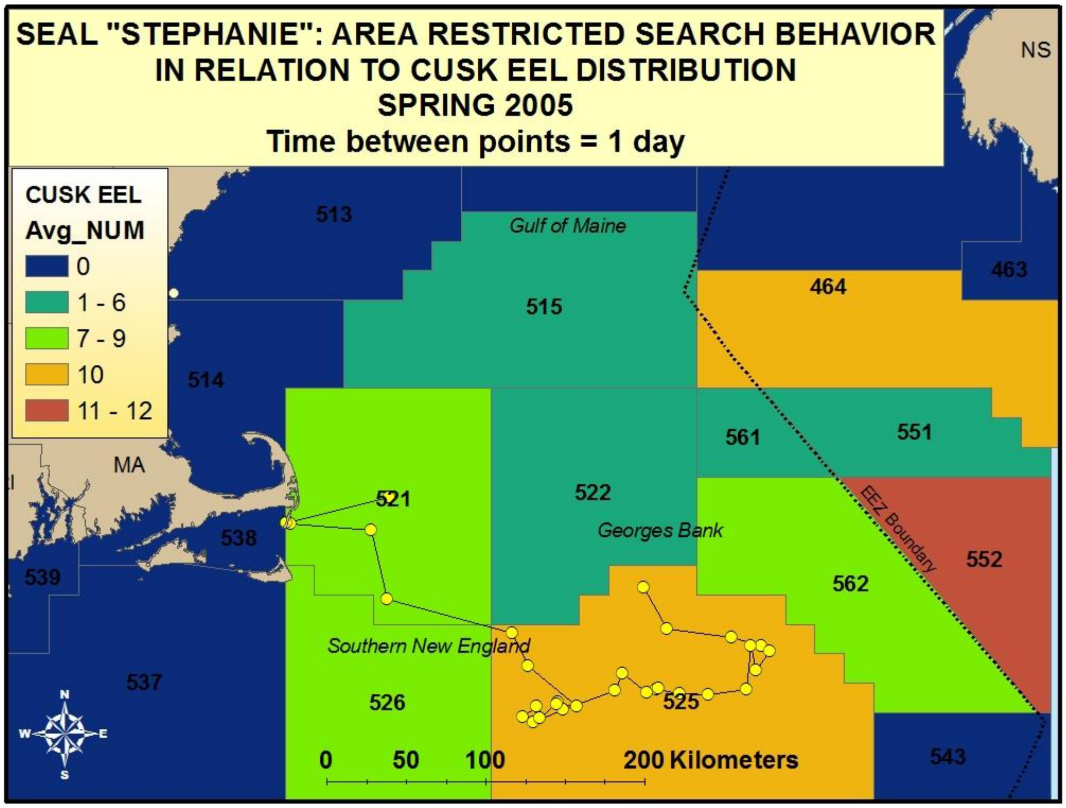

Figure 3.10: Area restricted search behavior of seal "Stephanie" in relation to cusk eel (*Lepophidium cervinum*) distribution. Color block gradients indicate mean number of individuals caught per station in a given statistical area

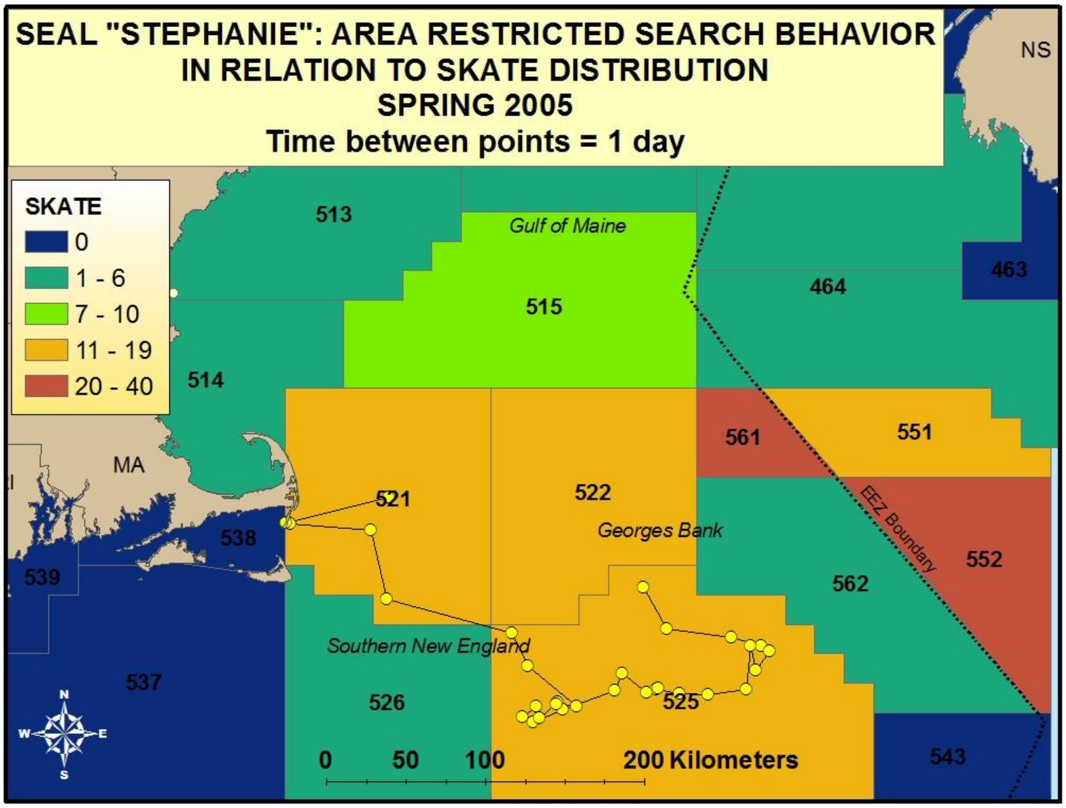

Figure 3.11: Area restricted search behavior of seal "Stephanie" in relation to skates (family Rajidae) distribution. Color block gradients indicate mean number of individuals caught per station in a given statistical area

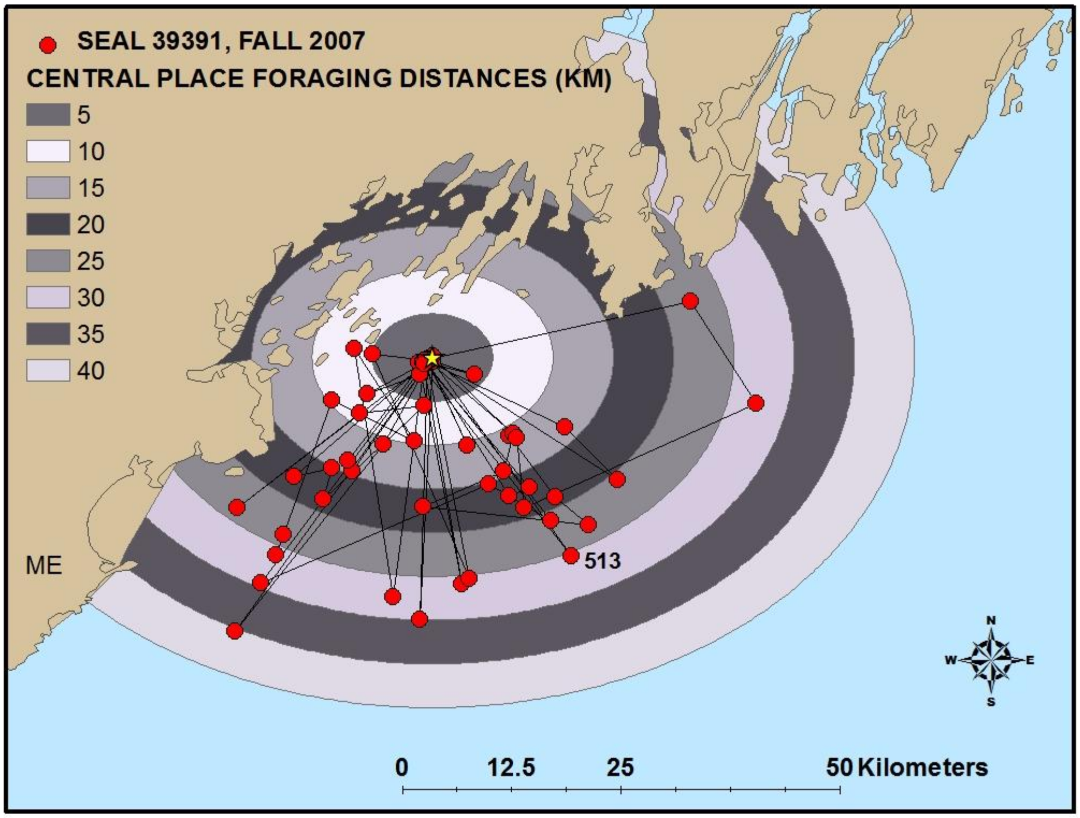

Figure 3.12: Central place foraging, and range of foraging trips, for seal “39391”

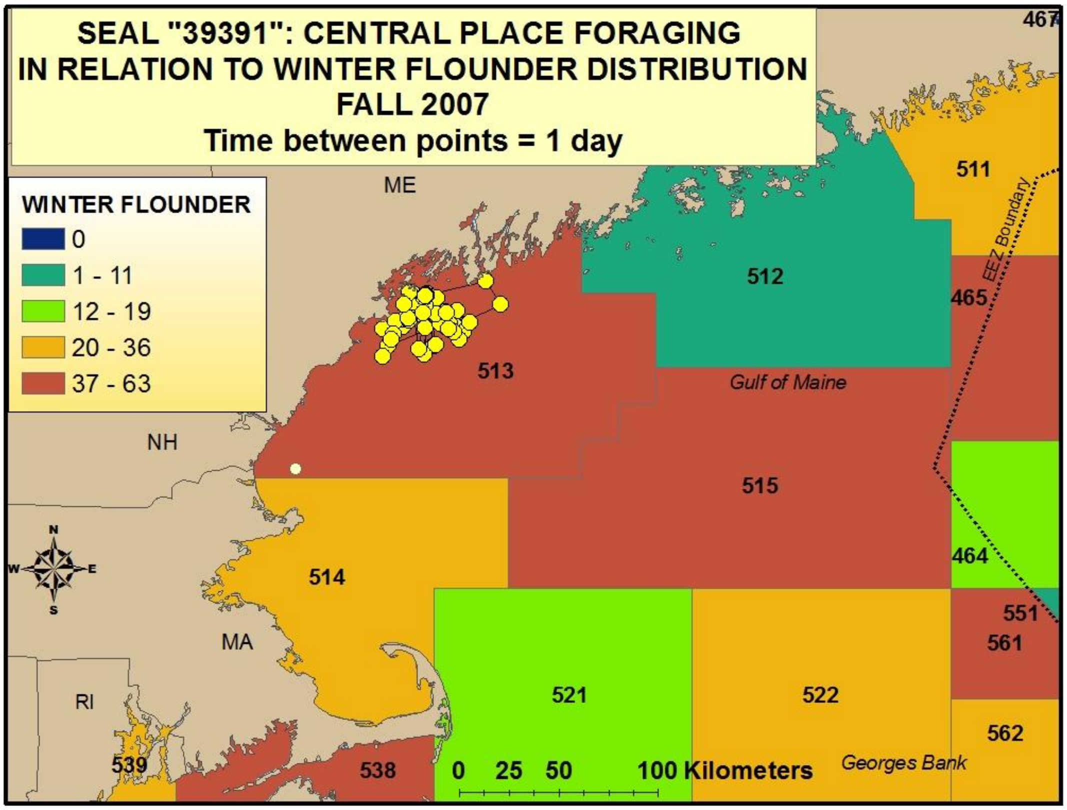

Figure 3.4: Central place foraging activity of seal “39391” in relation to winter flounder (*Pseudopleuronectes americanus*) distribution. Color block gradients indicate mean number of individuals caught per station in a given statistical area

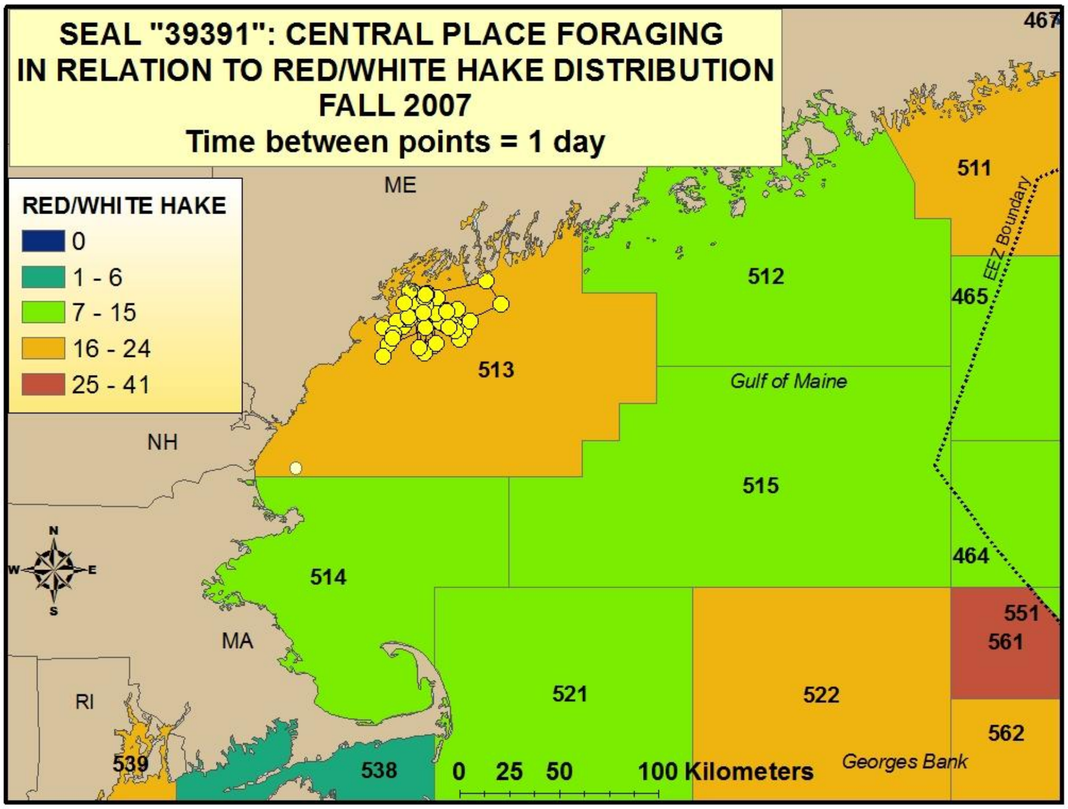

Figure 3.14: Central place foraging activity of seal "39391" in relation to red/white hake (*Urophycis spp.*) distribution. Color block gradients indicate mean number of individuals caught per station in a given statistical area

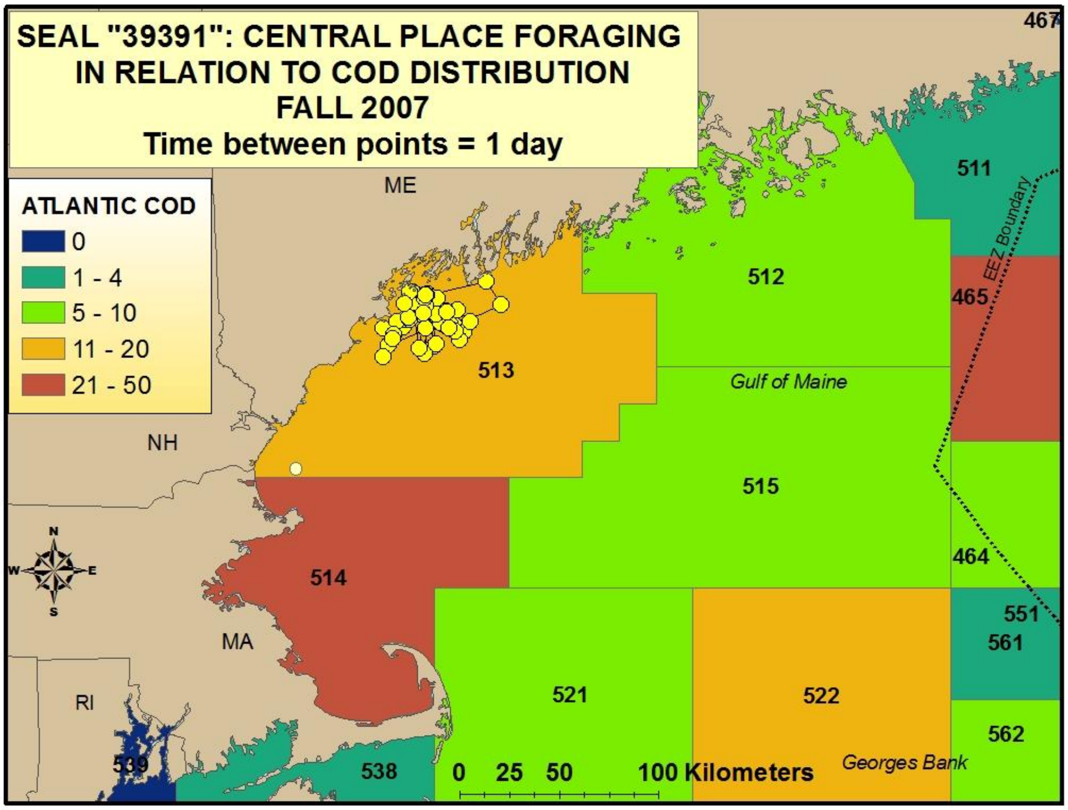

Figure 3.15: Central place foraging activity of seal "39391" in relation to Atlantic cod (*Gadus morhua*) distribution. Color block gradients indicate mean number of individuals caught per station in a given statistical area

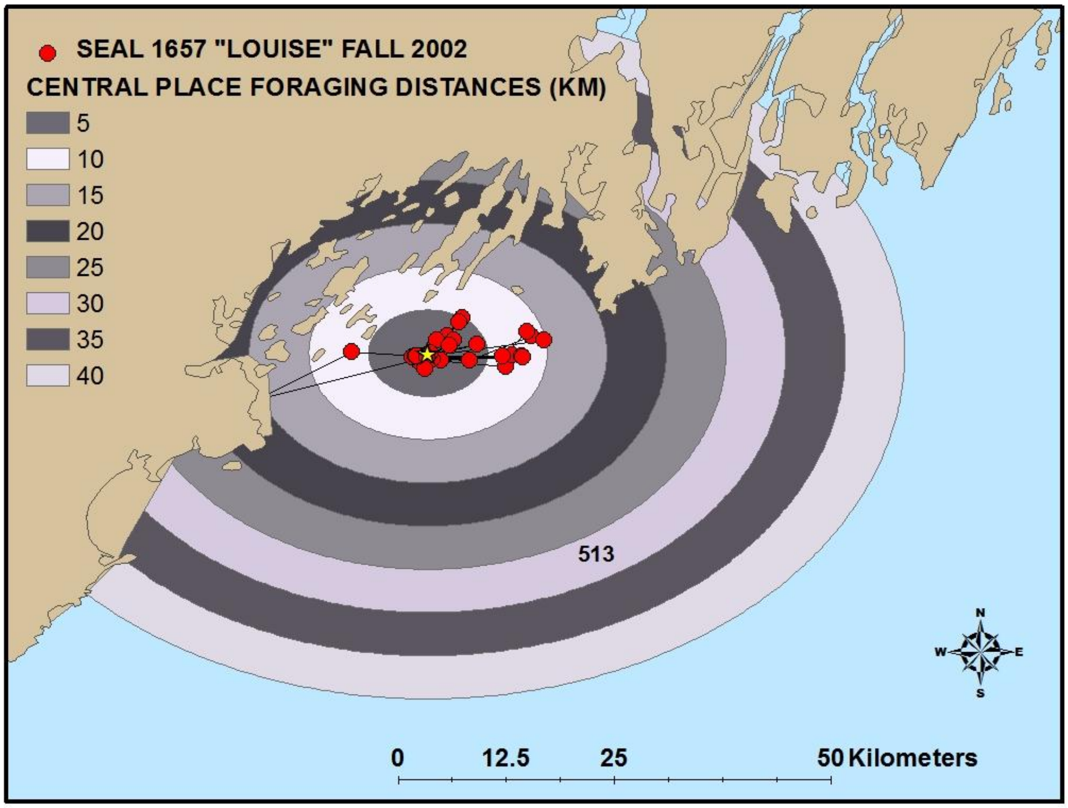

Figure 3.16: Central place foraging, and range of foraging trips, for seal "Louise"

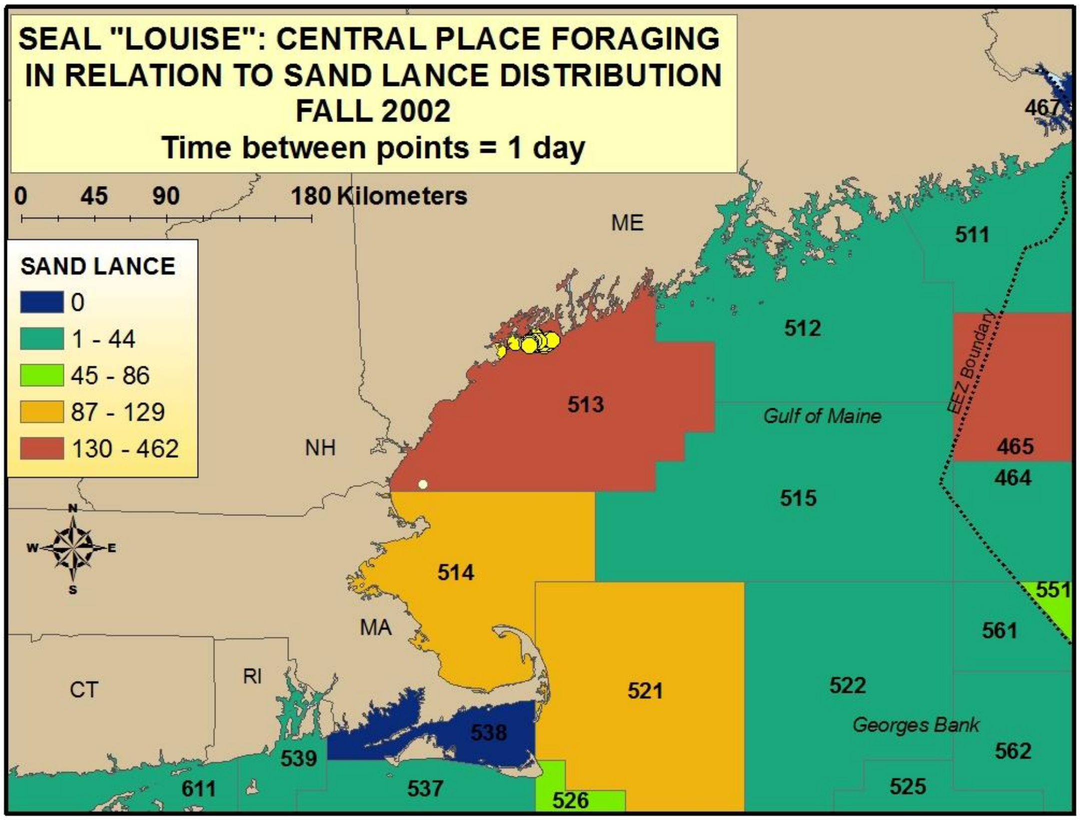

Figure 3.17: Central place foraging activity of seal "Louise" in relation to sand lance (*Ammodytes spp.*) distribution. Color block gradients indicate mean number of individuals caught per station in a given statistical area

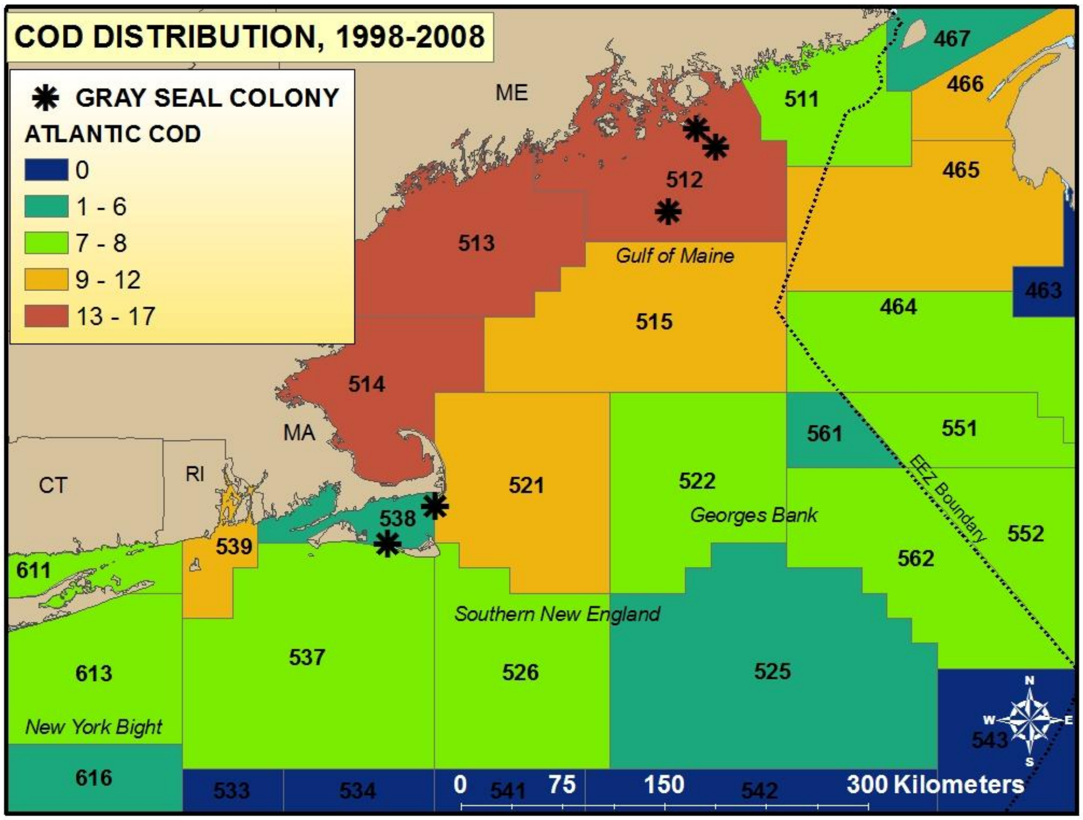

Figure 3.18: Distribution of Atlantic cod (*Gadus morhua*) near U.S. seal colonies. Color block gradients indicate mean number of individuals caught per station in a given statistical area

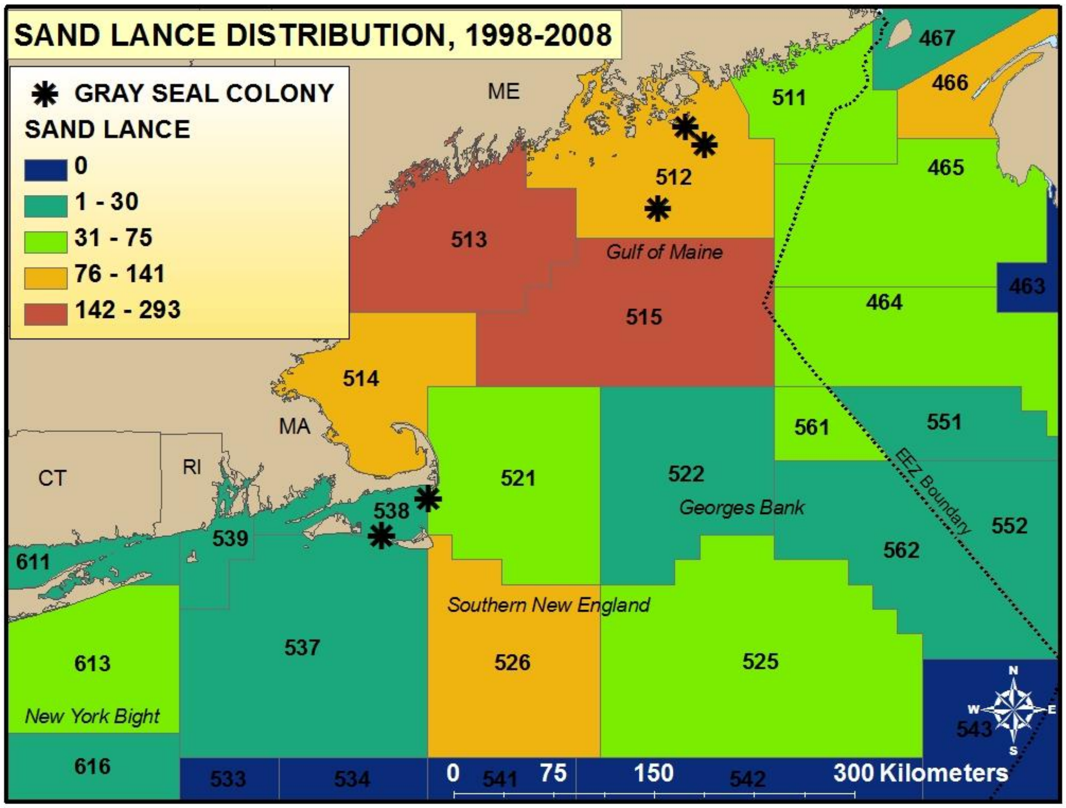

Figure 3.19: Distribution of sand lance (*Ammodytes spp*.) near U.S. seal colonies. Color block gradients indicate mean number of individuals caught per station in a given statistical area

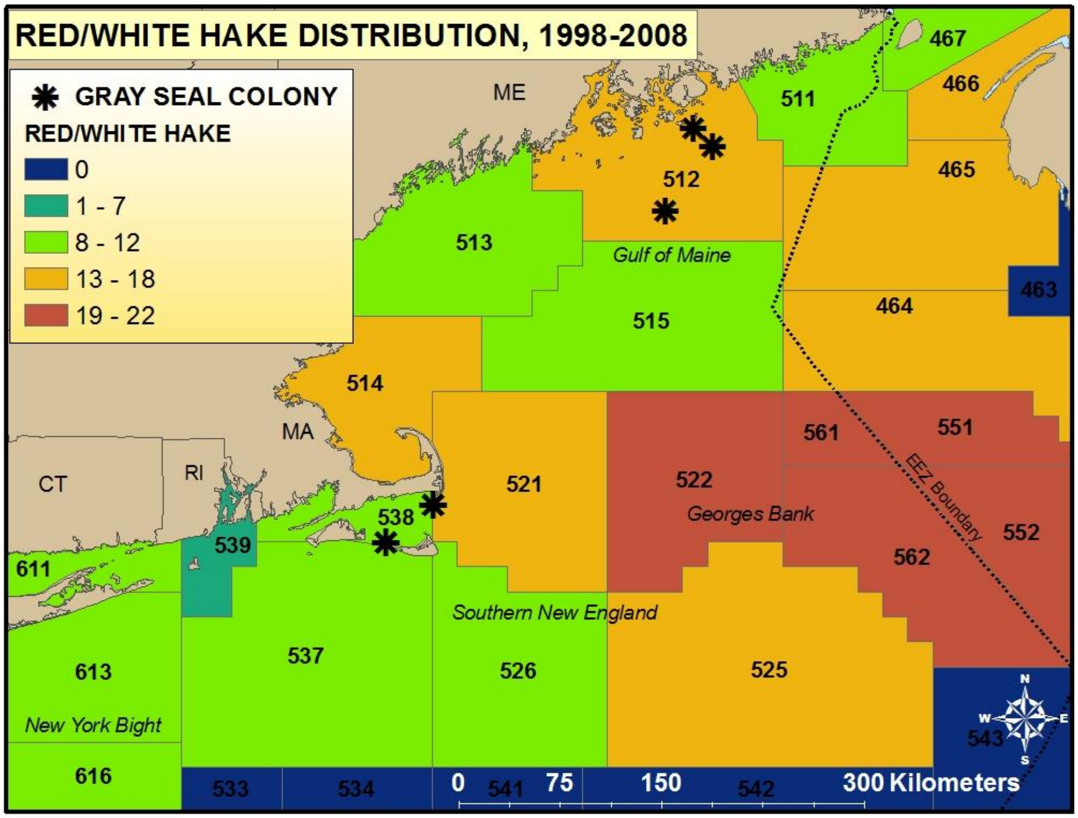

Figure 3.20: Distribution of red/white hake (*Urophycis spp*.) near U.S. seal colonies. Color block gradients indicate mean number of individuals caught per station in a given statistical area

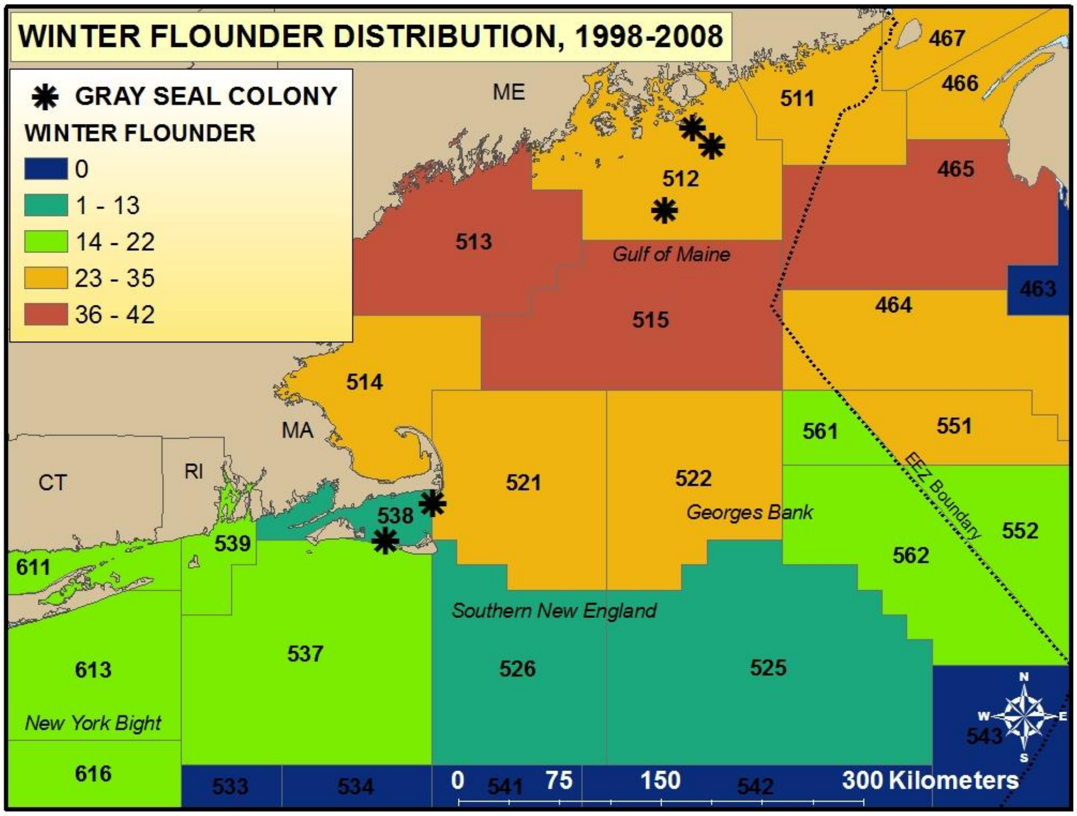

Figure 3.21: Distribution of winter flounder (*Pseudopleuronectes americanus*) near U.S. seal colonies. Color block gradients indicate mean number of individuals caught per station in a given statistical area

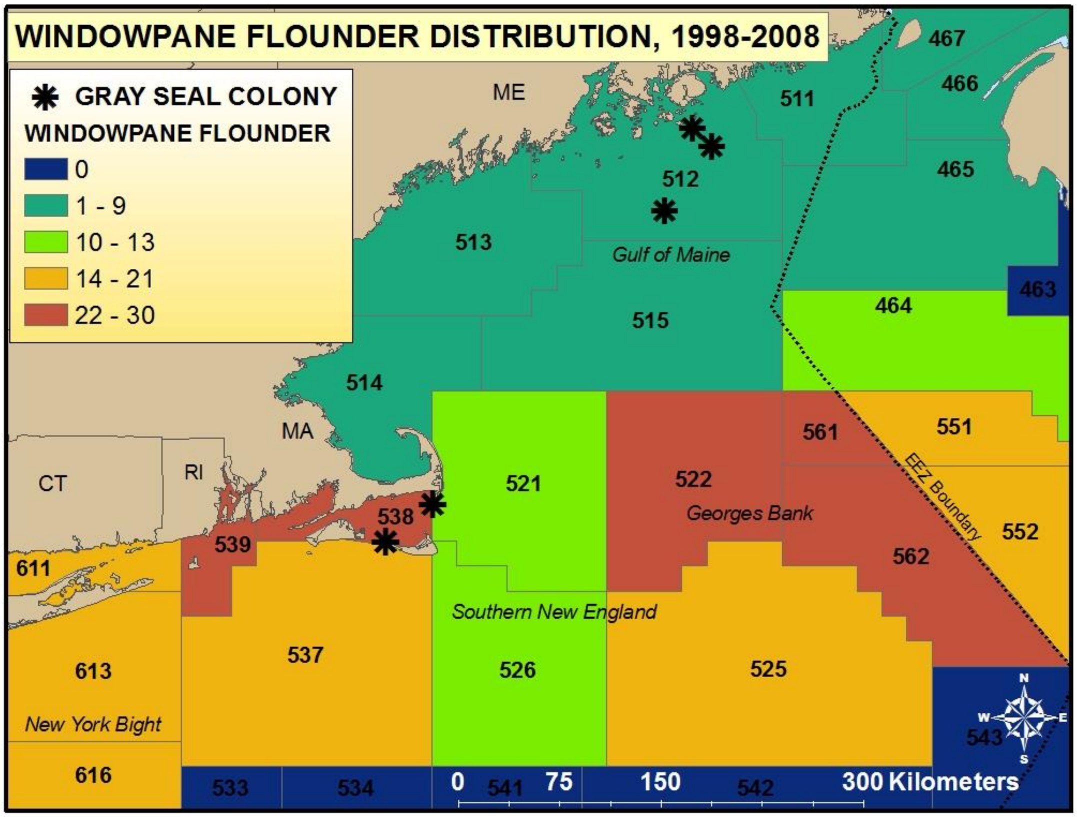

Figure 3.22: Distribution of windowpane flounder (*Scophthalmus aquosus*) near U.S. seal colonies. Color block gradients indicate mean number of individuals caught per station in a given statistical area

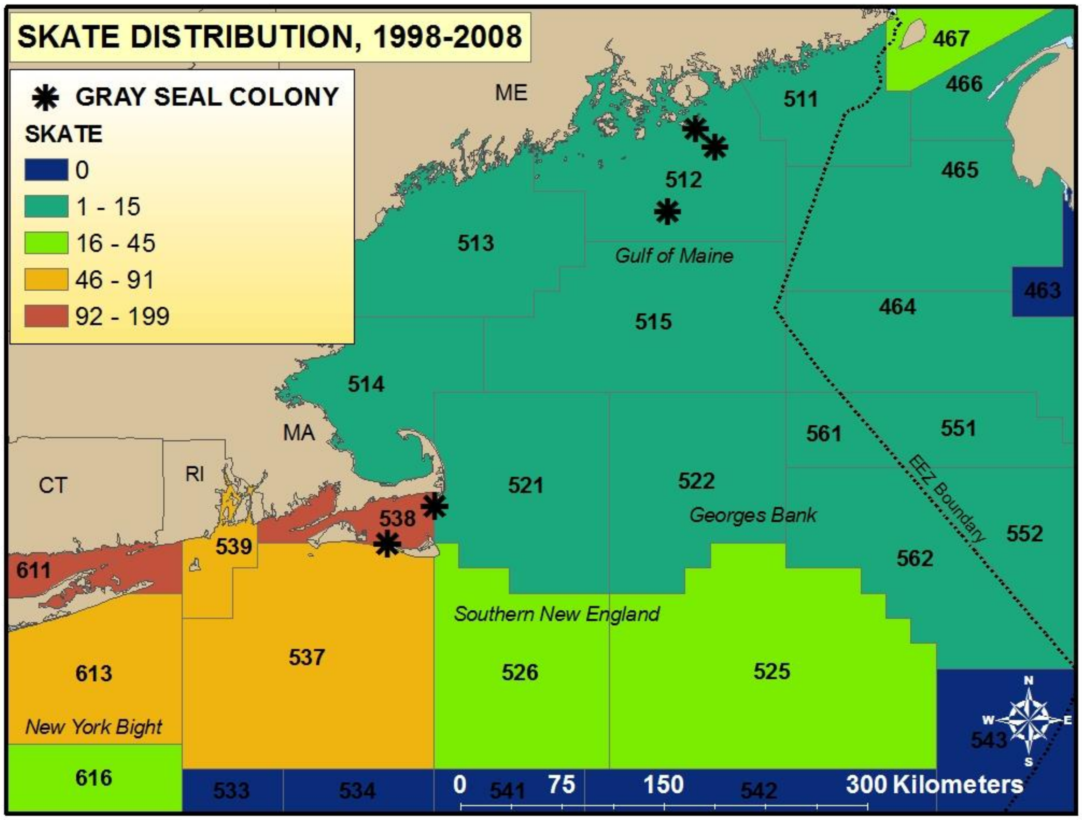

Figure 3.23: Distribution of skates (family Rajidae) near U.S. seal colonies. Color block gradients indicate mean number of individuals caught per station in a given statistical area

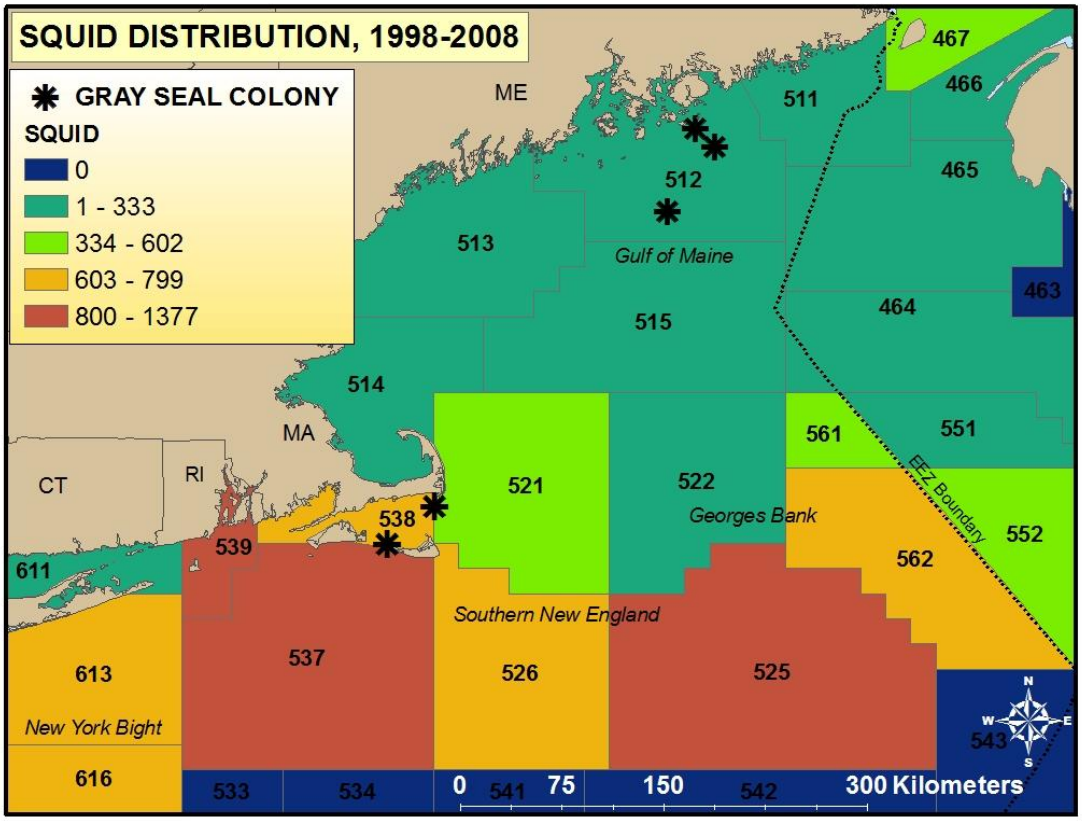

Figure 3.24: Distribution of squid (*Loligo pealeii*) near U.S. seal colonies. Color block gradients indicate mean number of individuals caught per station in a given statistical area

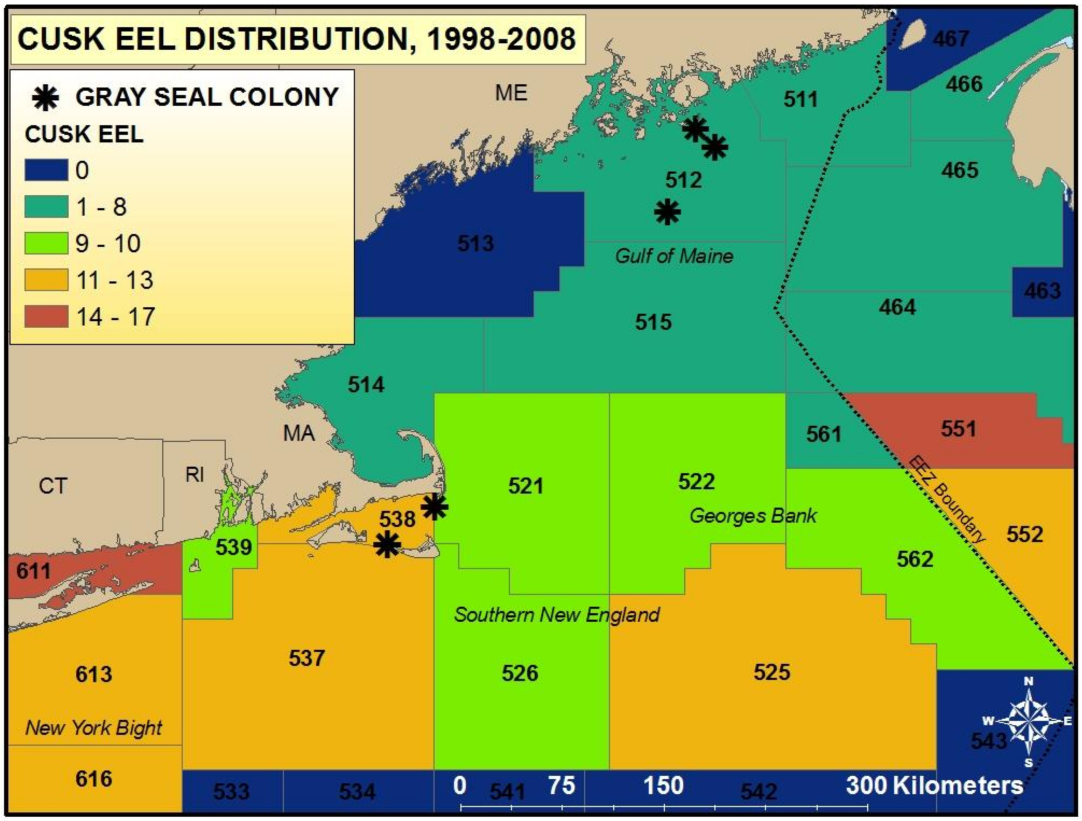

Figure 3.25: Distribution of cusk eel (*Lepophidium cervinum*) near U.S. seal colonies. Color block gradients indicate mean number of individuals caught per station in a given statistical area

Conclusions

Prey composition

In their U.S. range, the diet of gray seals was dominated by demersal species, including sand lance (*Ammodytes spp*.), gadids, and flatfish. Sand lance was the most important prey in the diet, as inferred from hard remains in scat samples. Gadids such as red/white hake (*Urophycis spp*.) and silver hake (*Merluccius bilinearis*) dominated the diet as inferred from stomach contents. The difference in results using these two methods is likely attributable to two factors: 1) scats contained prey captured mostly inshore, whereas stomach contained prey captured offshore, and 2) prey species in stomachs were similar to those targeted by commercial fisheries, since seals were foraging in and near fishing gear when they were taken.

Overall, scats likely represent a better prey picture of what most gray seals eat, since large numbers of seals, of a variety of age classes, were present at haul out sites. Six times as many scats were examined than stomachs and blubber samples. Findings from the latter two methods, however, should not be seen as an anomaly. No diet measure is representative of an entire gray seal population, since there is considerable intraspecific variation in prey choice and foraging grounds (Austen *et al.* 2004). Only by piecing together examples of diet in different regions and times, and from individuals of different age, sex, and foraging experience, can we hope to get a picture of population-wide patterns in prey consumption. Therefore, the diet of seals associated with fishing vessels represents one part of this picture, but is not representative of all seals.

Although this is the first long-term study of gray seal diet in the U.S., I found broadly similar diet patterns to those of gray seals in eastern Canada (Bowen and Harrison 1994). Sand lance dominated the diet of gray seals sampled at Sable Island, Nova Scotia, as inferred from scats, along with cod, hake, and a complex of flatfish. The most important flatfish eaten by Sable Island seals was American plaice (*Hippoglossoides platessoides*), but in the U.S, winter flounder was the dominant flatfish species in the diet. In fact, no American plaice was recovered in this study. Capelin (*Mallotus villosus*) and redfish (*Sebastes fasciatus*) appeared with some frequency in the scats of gray seals at Sable Island, and redfish was a major prey item for Sable Island gray seals when diet was estimated by Quantitative Fatty Acid Signature Analysis (Beck *et al.* 2007a). However, these species did not appear at all in scats collected at U.S. haul out sites. Redfish was abundant in the U.S. study area, and is important in the diet of harbor seals in the U.S. (Kopec 2009). It is possible that 1) redfish is not an important prey item for gray seals in the U.S., perhaps due to dietary resource partitioning with harbor seals, or 2) redfish is consumed regularly, but hard parts are not recovered. Future studies of diet estimation using QFASA would help resolve this issue.

Findings in this study were also similar to those of Rough (1995) who examined frequency of occurrence of prey species in 45 scats collected at the same haul out sites visited in this study. She found the most frequent prey items to be sand lance, skates, winter flounder, windowpane flounder, red/white hake and silver hake.

Diet variation

Significant sex differences were detected in diet using both hard parts and fatty acid analysis. This finding is of interest because all seals sampled were sexually immature, and sex differences in gray seal diet are normally attributed to size dimorphism and intraspecific resource partitioning in adults (Breed *et al.* 2006). Seasonal patterns were evident for several important prey taxa, including red/white hake, winter flounder, and skates, and sand lance consumption peaked in 2007. The temporal variation observed likely reflects changing availability of these species due to their reproductive cycles, migratory behavior, and interannual changes in abundance (Bowen *et al.* 2002, Gabriel 1992). Regional variation in diet was apparent in stomach samples, and to some extent fatty acid profiles. This suggests that seals are foraging in a variety of prey assemblages throughout the Gulf of Maine and southern New England waters, which are not uniformly distributed (Bowen and Harrison 1996, Gabriel 1992). Prey taxa and diet diversity also varied significantly between the two scat sampling sites in this study, even though the two islands are close enough for a seal to travel between the two in less than a day. This suggests that although seals can travel long distances when feeding, a significant portion of foraging is done inshore, close to haulout sites.

Seals' diets are not static, but vary with time, space, and among individual animals. Quantifying this variation is one step toward a better understanding of the foraging ecology of this species, and can improve estimates of the predation impact of gray seals on fish stocks (Hammill and Stenson 2000).

Habitat use

Important prey taxa in seal diets were also abundant in the environment, but many abundant species did not appear in seal diets at all. Although prey availability is likely a factor in prey selection (Bowen *et al.* 2002), seals in this study did not use it as their only criterion. Seals foraged close to haul out sites, and also in offshore areas such as Georges Bank. Satellite tracked seals foraged, for the most part, within an 80 km radius of haul out sites, suggesting that prey in scats are a good indicator of gray seal diet in the region.

Satellite-tracked seals consistently foraged in areas containing high abundance of sand lance and winter flounder, the two most important species in the diet by weight. There was therefore agreement between diet analysis and (albeit indirect) observations of foraging behavior. Although valuable information was provided by the small number of seals tagged in the study area, a larger number of seals, from all sex and age classes, should be included in future studies of satellite-tracked foraging behavior.

Fishery conflicts

Economically important species such as herring, mackerel, striped bass, and scup are of minor importance in the diet of gray seals in their U.S. range, and lobster was not detected by any diet measure. Gear interactions with gray seals do occur in the striped bass and lobster fisheries, but sampling in this study does not indicate that these species are important in the diet of most gray seals.

Potential conflict exists with the winter flounder fishery, since 1) this species contributed a significant portion of the diet by weight, 2) seals eat winter flounder of the same size class as that targeted by commercial and recreational fisheries, and 3) seals appear to target spawning winter flounder. Other economically important species, such as cod and hake, are important in the diet, but seals target a smaller size class than those taken in commercial fisheries. Atlantic cod comprised 6% of the diet by weight (estimated from scat samples) of gray seals in their U.S. range, although this varied seasonally. This figure is similar to that found in diet studies of gray seals at Sable Island, Canada (Beck et al. 2007a).

Literature Cited

Amos, W., Twiss, S., Pomeroy, P.P., and Anderson, S.S. 1993. Male mating success and paternity in the grey seal, *Halichoerus grypus*: A study using DNA fingerprinting. Proceedings of the Royal Society of London. Series B: Biological Sciences **252**(1335): 199-207.

Anderson, R.O., and Neumann, R.M. 1996. Length, weight, and associated structural indices. In: Fisheries Techniques, 2nd ed. B. R. Murphy and D. W. Willis, eds.: 447-482.

Anderson, S.S. 1978. Day and night activity of grey seal bulls. Mammal Review **8**(1-2): 43-46.

Andrews, J.C., and Mott, P.R. 1967. Gray seals at Nantucket, Massachusetts. Journal of Mammalogy **48**: 657-658.

Arim, M., and Naya, D.E. 2003. Pinniped diets inferred from scats: analysis of biases in prey occurrence. Canadian Journal of Zoology **81**: 67-73.

Austen, D., Bowen, W.D., and McMillan, J.I. 2004. Intraspecific variation in movement patterns: modeling individual behaviour in a large marine predator. Oikos **105**(1): 15-30.

Auster, P.J., and Stewart, L.L. 1986. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (North Atlantic)--sand lance. U.S. Fish Wildl. Serv. Biol. Rep. 82 (11.66). U.S. Army Corps of Engineers, TR EL-82-4. p. 11 pp.

Azarovitz, T.R., McGurrin, J., and Seagraves, R. 1989. Proceedings of a workshop on bottom trawl surveys. Atlantic States Mar. Fish. Comm. Spec. Rep. No. 17. 76 pp.

B.I.M. 1997. Physical interactions between grey seals and fishing gear. Irish Sea Fisheries Board. Report to the European Commission, DG XIV. Dún Laoighre, Co. Dublin, Ireland

Baker, S.R., Barrette, C., and Hammill, M.O. 1995. Mass transfer during lactation of an ice-breeding pinniped, the grey seal (*Halichoerus grypus*), in Nova Scotia, Canada. Journal of Zoology **236**(4): 531-542.

Baraff, L.S., and Loughlin, T.R. 2000. Trends and potential interactions between pinnipeds and fisheries of New England and the U.S. West Coast. Marine Fisheries Review **62**(4): 1-39.

Beck, C.A., Bowen, W.D., McMillan, J.I., and Iversona, S.J. 2003. Sex differences in the diving behaviour of a size-dimorphic capital breeder: the grey seal. Animal Behaviour **66**(4): 777-789.

Beck, C.A., Iverson, S.J., Bowen, W.D., and Blanchard, W. 2007a. Sex differences in grey seal diet reflect seasonal variation in foraging behaviour and reproductive expenditure: evidence from quantitative fatty acid signature analysis. Journal of Animal Ecology **76**(3): 490-502.

Beck, C.A., Rea, L.D., Iverson, S.J., Kennish, J.M., Pitcher, K.W., and Fadely, B.S. 2007b. Blubber fatty acid profiles reveal regional, seasonal, age-class and sex differences in the diet of young Steller sea lions in Alaska. Marine Ecology Progress Series **338**: 269-280.

Belden, D.L., Orphanides, C.D., Rossman, M.C., and Palka, D.L. 2006. Estimates of Cetacean and Seal Bycatch in the 2004 Northeast Sink Gillnet and Mid-Atlantic Coastal Gillnet Fisheries. Northeast Fisheries Science Center Reference Document 06-13: 24pp.

Bigelow, H.B., and Schroeder, W.C. 2002. Fishes of the Gulf of Maine, Online Edition. Fishery Bulletin **53**: 545pp.

Bisack, K.D. 2003. Estimates of marine mammal bycatch in the Northeast (New England) multispecies sink gillnet fishery in 1996. Northeast Fisheries Science Center, Ref. Doc. 03-18: 21 pp.

Bonner, N. 1994. Seals and Sea Lions of the World. Facts on File Books, New York, NY.

Bowen, W.D. 1997. Role of marine mammals in aquatic ecosystems. Marine Ecology Progress Series **158**: 267-274.

Bowen, W.D. 2000. Reconstruction of pinniped diets: accounting for complete digestion of otoliths and cephalopod beaks. Canadian Journal of Fisheries and Aquatic Sciences **57**(5): 898-905.

Bowen, W.D., and Harrison, G.D. 1994. Offshore diet of grey seals (*Halichoerus grypus)* near Sable Island, Canada. Marine Ecology Progress Series **112**: 1-11.

Bowen, W.D., and Harrison, G.D. 1996. Comparison of harbour seal diets in two inshore habitats of Atlantic Canada. Canadian Journal of Zoology **74**: 125-135.

Bowen, W.D., Lawson, J.W., and Beck, B. 1993. Seasonal and geographic variation in the species composition and size of prey consumed by grey seals (*Halichoerus grypus*) on the Scotian Shelf. Canadian Journal of Fisheries and Aquatic Sciences **50**(8): 1768-1778.

Bowen, W.D., McMillan, J., and Mohn, R. 2003. Sustained exponential population growth of grey seals at Sable Island, Nova Scotia. ICES Journal of Marine Science **60**(6): 1265-1274.

Bowen, W.D., Tully, D., Boness, D.J., Bulheier, B.M., and Marshall, G.J. 2002. Prey-dependent foraging tactics and prey profitability in a marine mammal. Marine Ecology Progress Series **244**: 235-245.

Bowman, R.E., Stillwell, C.E., Michaels, W.L., and Grosslein, M.D. 2000. Food of Northwest Atlantic Fishes and Two Common Species of Squid. NOAA Technical Memorandum NMFS-NE-155.

Breed, G.A., Bowen, W.D., McMillan, J.I., and Leonard, M.L. 2006. Sexual segregation of seasonal foraging habitats in a non-migratory marine mammal. Proceedings of the Royal Society B: Biological Sciences **273**(1599): 2319-2326.

Brodeur, R.D. 1979. Guide to otoliths of some northwest Atlantic fishes. NMFS/NEFSC. Laboratory Reference No. 79-36; 70 pp.

Browne, P., Laake, J.L., and DeLong, R.L. 2002. Improving pinniped diet analyses through identification of multiple skeletal structures in fecal samples-statistical data included. Fishery Bulletin **100**(3): 423-433.

Budge, S.M., Iverson, S.J., Bowen, W.D., and Ackman, R.G. 2002. Among- and within-species variability in fatty acid signatures of marine fish and invertebrates on the Scotian Shelf, Georges Bank, and southern Gulf of St. Lawrence. Canadian Journal of Fisheries and Aquatic Sciences **59**: 886-898.

Budge, S.M., Iverson, S.J., and Koopman, H.N. 2006. Studying trophic ecology in marine ecosystems using fatty acids: a primer on analysis and interpretation. Marine Mammal Science **22**(4): 759-801.

Campana, S.E. 2004. Photographic Atlas of Fish Otoliths of the Northwest Atlantic Ocean. NRC Research Press, Ottawa. 284 pp.

Casaux, R., Baroni, A., Arrighetti, F., Ramón, A., and Carlini, A. 2003. Geographical variation in the diet of the Antarctic fur seal *Arctocephalus gazella*. Polar Biology **26**(12): 753-758.

Clarke, M.R. 1986. A handbook for the identification of cephalopod beaks. Clarendon Press, Oxford. 273 pp.

Dawson, M.A. 1990. Blood chemistry of the windowpane flounder *Scophthalmus aquosus* in Long Island Sound: Geographical, seasonal, and experimental variations. . Fishery Bulletin **88**(3): 429-437.

DeLong, A.K., and Collie, J.S. 2004. Defining essential fish habitat: a model-based approach. Rhode Island Sea Grant, Narragansett, RI. 8 pp.

DeMaster, D.P., Fowler, C.W., Perry, S.L., and Richlen, M.F. 2001. Predation and competition: The impact of fisheries on marine mammal populations over the next one hundred years. Journal of Mammalogy **82**(3): 641-651

Despres, L.I., Azarovitz, T.R., and Byrne, C.J. 1988. Twenty-five years of fish surveys in the northwest Atlantic: the NMFS Northeast Fisheries Center’s bottom trawl survey program. Marine Fisheries Review **50**(4): 69-71.

Estes, J.A., and Palmisano, J.F. 1974. Sea otters: Their role in structuring nearshore communities. Science **185**(4156): 1058-1060.

Gabriel, W.L. 1992. Persistence of demersal fish assemblages between Cape Hatteras and Nova Scotia, northwest Atlantic. Journal of Northwest Atlantic Fishery Science **14**: 29-46.

Garrison, L.P., and Link, J.S. 2000. Dietary guild structure of the fish community in the northeast United States continental shelf ecosystem. Marine Ecology Progress Series **202**: 231-240.

Geddes, D., and Frank, K. 1996. Scotian Shelf sand lance. DFO Atlantic Fisheries Stock Status Report 96/77E. 2 pp.

Gilbert, J.R., Waring, G.T., Wynne, K.M., and Nikolina Guldager. 2005. Changes in abundance of harbor seals in Maine, 1981-2001. Marine Mammal Science **21**(3): 519-535.

Gravendeel, R., Neer, W.V., and Brinkhuizen, D. 2002. An identification key for dermal denticles of Rajidae from the North Sea. International Journal of Osteoarchaeology **12**(6): 420-441.

Grellier, K., and Hammond, P.S. 2005. Feeding method affects otolith digestion in captive gray seals: implications for diet composition estimation. Marine Mammal Science **21**(2): 296-306.

Grellier, K., and Hammond, P.S. 2006. Robust digestion and passage rate estimates for hard parts of grey seal (*Halichoerus grypus*) prey. Canadian Journal of Fisheries and Aquatic Sciences **63**: 1982-1998.

Hall, A.J., and McConnell, B.J. 2007. Measuring changes in juvenile gray seal body composition. Marine Mammal Science **23**(3): 650-665.

Halliday, R.G., and Pinhorn, A.T. 1990. The delimitation of fishing areas in the northwest Atlantic. Journal of Northwest Atlantic Fisheries Science **10**.

Hammill, M.O., and Stenson, G.B. 2000. Estimated prey consumption of harp seals (*Phoca groenlandica*), hooded seals (*Cystophora cristata*) grey seals (*Halichoerus grypus*) and harbor seals (*Phoca vitulina*) in Atlantic Canada. Journal of Northwest Atlantic Fisheries Science **26**: 1-23.

Hammond, P.S., Hall, A.J., and Prime, J.H. 1994. The diet of grey seals around Orkney and other island and mainland sites in north-eastern Scotland. Journal of Applied Ecology **31**: 340-350.

Härkönen, T. 1986. The Guide to the Otoliths of the North-East Atlantic. . Dainbiu, Hellerup, Denmark. 256 pp.

Holland, G.J., Greenstreet, S.P.R., Gibb, I.M., Fraser, H.M., and Robertson, M.R. 2005. Identifying sandeel *Ammodytes marinus* sediment habitat preferences in the marine environment. Marine Ecology Progress Series **303**: 269-282.

Iverson, S.J., Field, C., Don Bowen, W., and Blanchard, W. 2004. Quantitative fatty acid signature analysis: a new method of estimating predator diets. Ecological Monographs **74**(2): 211-235.

Iverson, S.J., J. E. McDonald, J., and Smith, L.K. 2001. Changes in the diet of free-ranging black bears in years of contrasting food availability revealed through milk fatty acids. Canadian Journal of Zoology **79**(12): 2268-2279.

Jobling, M., and Breiby, A. 1986. The use and abuse of fish otoliths in studies of feeding habits of marine piscivores. Sarsia **71**: 265-274.

Kopec, A.D. 2009. Prey selection in Gulf of Maine harbor seals (*Phoca vitulina*) in relation to fish abundance and fish mercury concentrations. Doctoral dissertation, University of Maine, Orono, Maine. USA. 169 pp.

Labansen, A.L., Lydersen, C., Haug, T., and Kovacs, K.M. 2007. Spring diet of ringed seals (*Phoca hispida*) from northwestern Spitsbergen, Norway. ICES Journal of Marine Science **64**(6): 1246-1256.

Lance, M.M., Orr, A.J., Riemer, S.D., Weise, M.J., and Laake, J.L. 2001a. Pinniped food habits and prey identification techniques protocol. Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA. AFSC Processed Report 2001-04.

Lance, M.M., Orr, A.J., Riemer, S.D., Weise, M.J., and Laake, J.L. 2001b. Pinniped food habits and prey identification techniques protocol. Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA. AFSC Processed Report 2001-04**.** 36 pp.

Lavigne, D. 2006. Marine mammals and fisheries: The role of science in the culling debate. Books Online **2006**(3): 31-47.

Lavigne, D.M. 1996. Ecological interactions between marine mammals, commercial fisheries, and their prey: unravelling the tangled web In: Montevecchi, W.A. (Ed.), Studies of High-Latitude Seabirds. 4. Trophic Relationships and Energetics of Endotherms in Cold Ocean Systems. **Occasional Paper 91, Canadian Wildlife Service**: 59-71.

Lea, M.-A., Cherel, Y., Guinet, C., and Nichols, P.D. 2002. Antarctic fur seals foraging in the Polar Frontal Zone: inter-annual shifts in diet as shown from fecal and fatty acid analyses. Marine Ecology Progress Series **245**: 281-297.

Lelli, B., Harris, D.E., and Aboueissa, A.-M. 2009. Seal Bounties in Maine and Massachusetts, 1888 to 1962. Northeastern Naturalist **16**(2): 239-254.

Longley, P., Goodchild, M.F., Maguire, D.J., and Rhind, D.W. 2005. Geographical information systems and science. . John Wiley and Sons, London. 517 pp.

Lundstrom, K., Hjerne, O., Alexandersson, K., and Karlsson, O. 2007. Estimation of grey seal (*Halichoerus grypus*) diet composition in the Baltic Sea. NAMMCO Science Publications **6**: 177-196.

MacArthur, R.H., and Pianka, E.R. 1966. On Optimal Use of a Patchy Environment. The American Naturalist **100**(916): 603.

Marcogliese, D.J. 1997. Fecundity of sealworm (*Pseudoterranova decipiens*) infecting grey seals (*Halichoerus grypus*) in the Gulf of St. Lawrence, Canada: Lack of density-dependent effects International Journal for Parasitology **11**: 1401-1409.

McClelland, G. 2002. The trouble with sealworms (*Pseudoterranova decipiens* species complex, Nematoda): a review. Parasitology **124**(07): 183-203.

McClelland, G., Misra, R.K., and Marcogliese, D.J. 1983. Variations in abundance of larval anisakines, sealworm *(Phocanema decipiens)* and related species in cod and flatfish from the southern Gulf of St.Lawrence (4T) and the Breton Shelf (4V). Canadian Technical Report of Fisheries and Aquatic Sciences, No. 1201.

McClelland, G., Misra, R.K., and Martell, D.J. 2000. Spatial and temporal distributions of larval sealworm (*Pseudoterranova decipiens*, Nematoda: Anisakinae), in *Hippoglossoides platessoides* (Pleuronectidae) in eastern Canada from 1980 to 1990. ICES Journal of Marine Science **57**(1): 69-88.

McConnell, B.J., Chambers, C., Nicholas, K.S., and Fedak, M.A. 1992. Satellite tracking of grey seals (*Halichoerus grypus*). Journal of Zoology **226**(2): 271-282.

McConnell, B.J., Fedak, M.A., Lovell, P., and Hammond, P.S. 1999. Movements and foraging areas of grey seals in the North Sea. Journal of Applied Ecology **36**(4): 573-590.

Middlemas, S.J., Barton, T.R., Armstrong, J.D., and Thompson, P.M. 2006. Functional and aggregative responses of harbour seals to changes in salmonid abundance. Proceedings of the Royal Society B: Biological Sciences **273**(1583): 193-198.

Murie, D.J., and Lavigne, D.M. 1985. A technique for the recovery of otoliths from stomach contents of piscivorous pinnipeds. The Journal of Wildlife Management **49**(4): 910-912.

Murie, D.J., and Lavigne, D.M. 1992. Growth and feeding habits of grey seals (*Halichoerus grypus*) in the northwestern Gulf of St. Lawrence, Canada. Canadian Journal of Zoology **70**(8): 604–1613.

NAMMCO. 2007. Grey seals in the north Atlantic and the Baltic. NAMMCO Scientific Publications **6**.

Navarrete, S.A., Menge, B.A., and Daley, B.A. 2000. Species interactions in intertidal food webs: prey or predation regulation of intermediate predators? Ecology **81**(8): 2264-2277.

Neuman, M.J., Witting, D.A., and Able, K.W. 2001. Relationships between otolith microstructure, otolith growth, somatic growth and ontogenetic transitions in two cohorts of windowpane. Journal of Fish Biology **58**(4): 967-984.

O'Brien, L. 1999. Factors influencing the rate of sexual maturity and the effect on spawning stock for Georges Bank and Gulf of Maine Atlantic cod (*Gadus morhua)* stocks. Journal of Northwest Atlantic Fisheries Science **25**: 179-203.

O'Neill, G., and Whelan, J. 2002. The occurrence of *Corynosoma strumosum* in the grey seal, *Halichoerus grypus*, caught off the Atlantic coast of Ireland. Journal of Helminthology **76**(03): 231-234.

Orians, G.H., and Pearson, N.E. 1979. On the theory of central place foraging. In: (D.F. Horn, ed.) Analysis of Ecological Systems. Ohio State University Press. pp. 155-177.

Overholtz, W.J., and Link, J.S. 2007. Consumption impacts by marine mammals, fish, and seabirds on the Gulf of Maine-Georges Bank Atlantic herring (*Clupea harengus*) complex during the years 1977-2002. ICES Journal of Marine Science **64**(1): 83-96.

Page, B., McKenzie, J., Sumner, M.D., Coyne, M., and Goldsworthy, S.D. 2006. Spatial separation of foraging habitats among New Zealand fur seals. Marine Ecology Progress Series **323**: 263-279.

Pereira, J.J., Goldberg, R., Ziskowski, J.J., Berrien, P.L., Morse, W.W., and Johnson, D.L. 1999. Essential fish habitat source document: Winter flounder, *Pseudopleuronectes americanus*, life history and habitat characteristics. NOAA Tech Memo NMFS NE 138. 39 pp.

Pierce, G.J., Thompson, P.M., Miller, A., Diack, J.S.W., Miller, D., and Boyle, P.R. 1991. Seasonal variation in the diet of common seals (*Phoca vitulina*) in the Moray Firth area of Scotland. Journal of Zoology **223**(4): 641-652.

Poland, V.F., Pomeroy, P.P., Twiss, S.D., and Graves, J.A. 2008. Fine-scale study finds limited evidence of kin clustering in a gray seal colony. Marine Mammal Science **24**(2): 371-387.

Pomeroy, P.P., Redman, P.R., Ruddell, S.J.S., Duck, C.D., and Twiss, S.D. 2005. Breeding site choice fails to explain interannual associations of female grey seals. Behavioral Ecology and Sociobiology **57**(6): 546-556.

Pomeroy, P.P., Twiss, S.D., and Redman, P. 2000. Philopatry, site fidelity and local kin associations within grey seal breeding colonies. Ethology **106**: 899-919.

Prime, J.H., and Hammond, P.S. 1990. The diet of grey seals from the south-western North Sea assessed from analyses of hard parts found in faeces. Journal of Applied Ecology **27**: 435-447.

Raclot, T., Groscolas, R., and Cherel, Y. 1998. Fatty acid evidence for the importance of myctophid fishes in the diet of king penguins, *Aptenodytes patagonicus*. Marine Biology **132**(3): 523-533.

Rahmstorf, S., Cazenave, A., Church, J.A., Hansen, J.E., Keeling, R.F., Parker, D.E., and Somerville, R.C.J. 2007. Recent Climate Observations Compared to Projections. Science **316**(5825).

Read, A.J. 2008. The looming crisis: interactions between marine mammals and fisheries. Journal of Mammalogy **89**(3): 541-548.

Reid, K., Davis, D., and Staniland, I.J. 2006. Spatial and temporal variability in the fish diet of Antarctic fur seal (*Arctocephalus gazella*) in the Atlantic sector of the Southern Ocean. Canadian Journal of Zoology **84**(7): 1025-1037.

Renner, S.C. 2005. An analysis of harbor seal (*Phoca vitulina*) and gray seal (*Halichoerus grypus*) haul-out patterns, behavior budgets, and aggressive interactions on Mount Desert Rock, Maine. M.S. Thesis, The University of Maine. 80 pp.

Retzer, M.E. 1991. Life-History Aspects of Four Species of Cusk-Eels (Ophidiidae: Ophidiiformes) from the Northern Gulf of Mexico. Copeia **1991**(3): 703-710.

Ridoux, V., Spitz, J., Vincent, C., and Walton, M.J. 2007. Grey seal diet at the southern limit of its European distribution: combining dietary analyses and fatty acid profiles. Journal of the Marine Biological Association of the UK **87**: 255-264.

Robinson, P.W., Tremblay, Y., Crocker, D.E., Kappes, M.A., Kuhn, C.E., Shaffer, S.A., Simmons, S.E., and Costa, D.P. 2007. A comparison of indirect measures of feeding behaviour based on ARGOS tracking data. Deep-Sea Research Part II **54**(3-4): 356-368.

Rough, V. 1995. Gray seals in Nantucket Sound, Massachusetts, Winter and Spring, 1994. Final Report to the Marine Mammal Commission NTIS Pub. PB95-191391.

Sjöberg, M., and Ball, J.P. 2000. Grey seal, *Halichoerus grypus*, habitat selection around haulout sites in the Baltic Sea: bathymetry or central-place foraging? . Canadian Journal of Zoology **78**: 1661-1667.

Smith, S.J., Iverson, S.J., and Bowen, W.D. 1997. Fatty acid signatures and classification trees: new tools for investigating the foraging ecology of seals. Canadian Journal of Fisheries and Aquatic Sciences **54**(6): 1377-1386.

Staniland, I.J. 2002. Investigating the biases in the use of hard prey remains to identify diet composition using Antarctic fur seals (*Arctocephalus gazella*) in captive feeding trials. Marine Mammal Science **18**(1): 223-243.

Staudinger, M.D., Juanes, F., and Carlson, S. 2009. Body size reconstruction and allometric relationships of the longfin inshore squid (*Loligo pealeii*) and northern shortfin squid (*Illex illecebrosus*) from the Northwest Atlantic Ocean. Fishery Bulletin. *In Press*(January).

Steimle, F.W., Morse, W.W., Berrien, P.L., and Johnson, D.L. 1999. Red Hake, *Urophycis chuss*, Life History and Habitat Characteristics. NOAA Technical Memorandum NMFS-NE-133. 34 pp.

Stephens, D.W., Brown, J.S., and Ydenberg, R.C. 2007. Foraging: Behavior and Ecology. University of Chicago Press, Chicago. 608 pp.

Thiemann, G.W., Iverson, S.J., and Stirling, I. 2009. Using fatty acids to study marine mammal foraging: The evidence from an extensive and growing literature. Marine Mammal Science **25**(1): 243-249.

Thompson, D., Hammond, P.S., Nicholas, K.S., and Fedak, M.A. 1991. Movements, diving, and foraging behavior of grey seals (*Halichoerus grypus)*. Journal of Zoology, London **224**: 223-232.

Thompson, D., Moss, S.E.W., and Lovell, P. 2003. Foraging behaviour of South American fur seals *Arctocephalus australis*: extracting fine scale foraging behaviour from satellite tracks. Marine Ecology Progress Series **260**: 285-296.

Thompson, P.M., McConnell, B.J., Tollit, D.J., Mackay, A., Hunter, C., and Racey, P.A. 1996. Comparative distribution, movements and diet of harbour and grey seals from the Moray Firth, N.E. Scotland. Journal of Applied Ecology **33**: 1572-1584.

Tollit, D.J., Heaslip, S.G., Barrick, R.L., and Trites, A.W. 2007. Impact of diet-index selection and the digestion of prey hard remains on determining the diet of the Steller sea lion (*Eumetopias jubatus*). Canadian Journal of Zoology **85**: 1-15.

Tollit, D.J., Heaslip, S.G., Zeppelin, T.K., Joy, R., Call, K.A., and Trites, A.W. 2004. A method to improve size estimates of walleye pollock (*Theragra chalcogramma*) and Atka mackerel (*Pleurogrammus monopterygius*) consumed by pinnipeds: digestion correction factors applied to bones and otoliths recovered in scats. Fishery Bulletin **102**: 498-508.

Tollit, D.J., Wong, M., Winship, A.J., Rosen, D.A.S., and Trites, A.W. 2003. Quantifying errors associated with using prey skeletal structures from fecal samples to determine the diet of Steller's sea lion (*Eumetopias jubatus*). Marine Mammal Science **19**(4): 724-744.

Trites, A.W., Christensen, V., and Pauly, D. 1997. Competition between fisheries and marine mammals for prey and primary production in the Pacific Ocean Journal of the Northwest Atlantic Fishery Science **22**: 173-187.

Wang, S.D.H., and Rosenberg, A.A. 1997. U.S. New England groundfish management under the Magnuson-Stevens Fishery Conservation and Management Act. Marine Resource Economics **12**: 361-366.

Waring, G.T., Josephson, E., Fairfield, C.P., and Maze-Foley, K. 2006. U.S. Atlantic and Gulf of Mexico marine mammal stock assessments--2005; Gray seal (*Halichoerus grypus*): Western North Atlantic Stock. NOAA Technical Memo 194.

Waring, G.T., Josephson, E., Fairfield, C.P., and Maze-Foley, K. 2007. Atlantic and Gulf of Mexico Marine Mammal Stock Assessments -- 2006. NOAA Tech Memo NMFS NE 201: 378 pp.

Watt, J., Pierce, G.J., and Boyle, P.R. 1997. Guide to the identification of North Sea fish using premaxillae and vertebrae. ICES Coop Res Rep 220.

Wigley, S.E., McBride, H.M., and McHugh, N.J. 2003. Length-weight relationships for 74 fish species collected during NEFSC research vessel bottom trawl surveys, 1992-9. NOAA Tech Memo NMFS NE 171; 26 pp.

Williams, A.S. 1999. Prey selection by harbor seals in relation to fish taken by the Gulf of Maine sink gillnet fishery, M.S. Thesis University of Maine, Orono, ME. 62 pp.

Wood, S., Frasier, T., McLeod, B., White, B., Bowen, W.D., Hammill, M., and Brault, S. 2005. The genetics of recolonization: an analysis of gray seal (*Halichoerus grypus*) stock structure in the northwest Atlantic. *In* The 16th Biennial Conference on the Biology of Marine Mammals, San Diego, CA.

Yodzis, P. 2001. Must top predators be culled for the sake of fisheries? Trends in Ecology & Evolution **16**(2): 78-84.

Zar, J.H. 1998. Biostatistical Analysis, 4th Edition. Prentice Hall. 929 pp.