

DISTRIBUTION OF HARP SEALS, *Phoca
groenlandica*, OFF NEWFOUNDLAND AND
LABRADOR IN RELATION TO ABIOTIC
AND BIOTIC CONDITIONS

CENTRE FOR NEWFOUNDLAND STUDIES

**TOTAL OF 10 PAGES ONLY
MAY BE XEROXED**

(Without Author's Permission)

KARINE LACOSTE



INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps. Each original is also photographed in one exposure and is included in reduced form at the back of the book.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

UMI

A Bell & Howell Information Company
300 North Zeeb Road, Ann Arbor MI 48106-1346 USA
313/761-4700 800/521-0600

**Distribution of Harp Seals,
Phoca groenlandica,
off Newfoundland and Labrador in Relation
to Abiotic and Biotic Conditions**

by

©Karine Lacoste, B.Sc.

A thesis submitted to the
School of Graduate Studies
in partial fulfillment of the
requirements for the degree of
Master of Science

Biopsychology Programme
Memorial University of Newfoundland

1997

St. John's

Newfoundland



National Library
of Canada

Acquisitions and
Bibliographic Services

395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque nationale
du Canada

Acquisitions et
services bibliographiques

395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file / Votre référence

Our file / Notre référence

The author has granted a non-exclusive licence allowing the National Library of Canada to reproduce, loan, distribute or sell copies of this thesis in microform, paper or electronic formats.

The author retains ownership of the copyright in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

L'auteur a accordé une licence non exclusive permettant à la Bibliothèque nationale du Canada de reproduire, prêter, distribuer ou vendre des copies de cette thèse sous la forme de microfiche/film, de reproduction sur papier ou sur format électronique.

L'auteur conserve la propriété du droit d'auteur qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

0-612-34197-6

Canada

Abstract

This study provides the first quantitative assessment of the yearly distributions of harp seals in the northwest Atlantic, particularly during the winter. Recent abiotic and biotic changes in the northwest Atlantic concurrent with reports of seals sighted further offshore have prompted this investigation on harp seal distributions in relation to environmental factors. Seal sighting data were collected from 1991 to 1995 using line-transect techniques. Data were standardized for effort and sighting conditions and grouped by subareas of 1 degree². Numbers of seals observed were estimated using a relative group size category. Visual appraisals of data were made using a Geographical Information System. The winter distributions of harp seals were overlaid onto maps of sea ice, sea floor inclination, sea surface temperature, and several prey distributions. The influence of these variables was tested using a generalized linear model, ANOVA, and correlation, respectively. The influence of water depth at location of seal sightings was also investigated.

Offshore areas are an important habitat for harp seals. The winter distributions of harp seals showed similar patterns during 1991-1993, but shifted slightly to the southeast during 1994-1995. Water temperatures were found to be within the thermoneutral limits for this species at all locations and for all winter years. Although there was a tendency for seals to be observed along the continental slope edge and in specific ice conditions, no significant differences were found between locations of seals and sea floor inclination or ice characteristics. Seals were mainly seen in waters of depths ranging from 300 to 500 m, values known to be within their diving range. Sea floor topography and water depth were the only environmental variables that remained constant throughout the 1991-1995 winter distributions. The spatial distribution of prey investigated concurred with the documented

diet of harp seals. Further investigations will be needed to quantify the relationship existing between them.

Acknowledgments

The completion of this project would not have been possible without the help and support of many people. First and foremost, I wish to acknowledge the financial support of the Biopsychology Programme of Memorial University as well as the great logistical support offered by the Department of Fisheries and Ocean. DFO not only provided me with an excellent supervisor but also permitted me to use their facilities on land and at sea. In this regards, I would like to thank D. McKinnon, W. Penney, and D. Wakeham who travelled many sea miles to collect the seal data. I would also like to thank the crew members of the Teleost and the Templeman who made me feel at home although miles away at sea. Thanks to J. Helbig and D. Reddin who dug out data sets of Bathymetry and Sea Surface Temperatures. J. Anderson and E. Dalley were also kind enough to provide me with the complete data sets for prey distribution. C. Pennell and N. Ollerhead also need to be thanked for being my SPANS/Explorer mentors and for gracefully explaining to me the works of digitizing and creating maps.

I am immensely grateful for the excellent advice and great commitment that my supervisor, G.B. Stenson, and two committee members, J.W. Lawson and W.A. Montevicchi, provided me. It is important for me to acknowledge how valuable they were in the improvement of not only my scientific skills but also my writing skills.

Finally, I wish to thank Dimitri and all my friends from biopsychology who, one way or another, stood by me and helped me maintain my sanity through it all!

Many thanks to all of you.

*J'aimerais dédier ce manuscrit à mon grand-papa Tonton et ma maman Michou.
Vous m'avez démontré et appris ce qu'était l'amour de vivre, le courage et la persévérance.
Sans vous je ne me serais pas rendu si loin. Un simple merci ne suffira jamais...*

Table of Contents

	Page
Abstract.....	ii
Acknowledgments.....	iv
Table of Contents.....	vi
List of Tables.....	viii
List of Figures.....	ix

Chapter 1: General Introduction

1.1 Populations of Harp Seals in the North Atlantic.....	1
1.2 Historic Distribution and Migration Pattern.....	3
1.3 Outline of Present Study	6

Chapter 2: Spatial and Temporal Distributions of Harp Seals off Eastern Newfoundland and Labrador

2.1 Introduction.....	11
2.2 Materials and Methods.....	12
2.3 Results.....	15
2.3.1 Winter Distribution.....	16
2.3.2 Spring Distribution.....	17
2.3.3 Summer Distribution.....	18
2.4 Discussion.....	19

Table of Contents, Cont'd

Chapter 3: Winter Spatial Distribution of Harp Seals Relative to Abiotic and Biotic Features of the Northwest Atlantic	
3.1 Introduction.....	38
3.2 Materials and Methods.....	40
3.3 Results	
3.3.1 Distribution in Relation to Ice Conditions and Thermal Habitat.....	44
3.3.2 Distribution in Relation to Bathymetry.....	46
3.3.3 Distribution in Relation to Prey.....	48
3.4 Discussion.....	50
Literature Cited.....	83
Appendix 1.....	97
Appendix 2.....	98
Appendix 3.....	99
Appendix 4.....	100
Appendix 5.....	102
Appendix 6.....	104

List of Tables

Table 2.1.	Research vessel trips between 1991 and 1995.....	26
Table 2.2.	Detectability index for observation of harp seals.....	27
Table 2.3.	Standardized and unstandardized sampling effort and sightings by period.....	28
Table 2.4.	Abundance peaks of winters 1991-1995.....	29
Table 3.1.	January-February distribution of harp seals according to ice thickness.....	61
Table 3.2.	Results of GLM analyses of winter seal distribution relative to ice conditions.....	62
Table 3.3.	Yearly sampling effort and number of seals $\cdot \text{km}^{-1}$ according to CI class and model.....	63
Table 3.4.	Results of GLM analyses of winter seal distribution relative to bathymetry.....	64
Table 3.5.	Numbers of seals sighted (n) according to year and depth class (100 m range).....	65
Table 3.6.	Winter sampling effort according to maximum depth.....	66
Table 3.7.	Areal overlap of the distributions of Newfoundland harp seals (HS) and their major prey species.....	67

List of Figures

Figure 1.1.	Historically documented distribution and migration patterns of harp seals in the north Atlantic.....	9
Figure 1.2.	Bathymetric features of the study area.....	10
Figure 2.1.	Annual sampling effort in surveys of the January-February period.....	30
Figure 2.2.	Annual relative sighting rates for harp seals standardized to 1 km effort in surveys of the January-February period	32
Figure 2.3.	Annual sampling effort in surveys of the April-May period.....	34
Figure 2.4.	Annual relative sighting rates for harp seals standardized to 1 km effort in surveys of the April-May period.....	35
Figure 2.5.	Annual sampling effort in surveys for the June-August period.....	36
Figure 2.6.	Annual relative sighting rates for harp seals standardized to 1 km effort in surveys of the June-August period.....	37
Figure 3.1.	Winter 1991: Distribution of seals in relation to ice conditions.....	68
Figure 3.2.	Winter 1992: Distribution of seals in relation to ice conditions.....	69
Figure 3.3.	Winter 1993: Distribution of seals in relation to ice conditions.....	71
Figure 3.4.	Winter 1994: Distribution of seals in relation to ice conditions.....	72
Figure 3.5.	Winter 1995: Distribution of seals in relation to ice conditions.....	73
Figure 3.6.	Harp seal winter thermal habitat.....	74
Figure 3.7.	Models of the percentage of change in depth (CI value) for areas of 1 degree ²	75

List of Figures, Cont'd

Figure 3.8.	Annual mean catch of Arctic cod per 30 min tow for the December-January period.....	76
Figure 3.9.	Annual mean catch of capelin per 30 min tow for the December-January period.....	77
Figure 3.10.	Annual mean catch of Atlantic herring per 30 min tow for the December-January period.....	78
Figure 3.11.	Annual mean catch of 1 yr old Atlantic cod per 30 min tow for the December-January period.....	79
Figure 3.12.	Annual mean catch of 2 yr old Atlantic cod per 30 min tow for the December-January period.....	80
Figure 3.13.	Annual mean catch of 3 yr old Atlantic cod per 30 min tow for the December-January period.....	81
Figure 3.14.	Correlation coefficient Pearson product-moment of numbers of major prey species and harp seal.....	82

Chapter 1: General Introduction

1.1 Populations of Harp Seals in the North Atlantic

Based on a general knowledge of the location of whelping concentrations, skull morphometrics (Yablokov and Sergeant 1963) and tagging experiments (e.g., Rasmussen and Øritsland 1964; Sergeant 1965), three populations of harp seal, *Phoca groenlandica*, have been identified in the north Atlantic: White Sea, Greenland Sea (Jan Mayen) and northwest Atlantic (Figure 1.1). The northwest Atlantic population is usually subdivided into two components: the Newfoundland component which breeds off northeast Newfoundland and southern Labrador, and the Gulf component which breeds in the southern, and occasionally northern Gulf of St. Lawrence (Sergeant 1965). Electrophoresis revealed significant differences among blood transferrins collected in the Newfoundland area and the two northeast Atlantic whelping areas (Nævdal 1966; Møller *et al.* 1966). Furthermore, reproductive isolation of the Greenland Sea and the Gulf of St. Lawrence populations was implied by interherd differences in underwater vocalizations (Terhune 1994). Therefore, harp seals from opposite sides of the northern Atlantic ocean have distinct genotypes and are thought not to interbreed (Sergeant 1991). However, recaptures of tagged seals revealed that all three populations share common summer feeding grounds (Larsen 1981; Kapel 1995; Øien and Øritsland 1995).

Electrophoresis and isoelectric focusing methods revealed no significant differences in blood transferrins or polymorphic esterase systems of muscle and liver enzymes between White Sea and the Greenland Sea populations (Nævdal 1966; Møller *et al.* 1966; Meisjord *et al.* 1991). In contrast, a fatty acid study by Grahl-Nielsen *et al.* (1993) detected a small but significant difference in jaw bone samples between these two

populations suggesting that the degree of interbreeding between these populations is still questionable.

Electrophoresis revealed no significant differences between serum transferrins or tissue samples from the Gulf and Newfoundland (Nævdal 1969; Lavigne *et al.* 1978). Historically, the two components of the northwest Atlantic population were thought to mix only during summer (Sergeant 1965), but based on annual variations in the proportion of pups born in each area, Sergeant (1971, 1991), Winters (1978), and Stenson *et al.* (1995) postulated movements of seals between the two areas, although the extent of intermixing remains unknown.

In the northwest Atlantic, the harp seal is the most abundant species of seal. Prior to 1990, various methods were used to estimate the annual pup production of harp seals. For example, aerial censuses conducted in 1975 and 1977 by Lavigne *et al.* (1980, 1982) gave estimates ranging from approximately 126 000 - 200 000 pups, while mark-recapture experiments conducted from 1978 to 1983 by Bowen and Sergeant (1983, 1985) gave estimates ranging from 489 000 - 534 000 pups. Reconciling these conflicting results, the Royal Commission on Seals and Sealing in Canada concluded that pup production was in the order of 300 000 - 350 000 pups for the years 1975 to 1983 (Anonymous 1986). In March of 1994, aerial censuses were conducted and pup production was estimated to be 446 700 (SE = 57 200) for the Newfoundland area, 57 600 (SE = 13 700) in the northern Gulf, and 198 600 (SE = 24 200) in the southern Gulf (Stenson *et al.* 1995). The northwest Atlantic harp seal population has therefore reached estimated levels of 4.8 million and is demonstrating signs of growth of approximately 5% per year (Shelton *et al.* 1995).

1.2 Historic Distribution and Migration Pattern

Most of the historical information available on the distribution of Newfoundland harp seals is anecdotal. Allen (1880, cited in Sergeant 1965) and Fisher (1955) gave very brief accounts of the movements of harp seals in the northwest Atlantic. Robinson (1897), Chafe (1923) and Nansen (1925) also documented observations by Newfoundland and Scottish sealing captains during the late 19th, and early 20th centuries. These reports resulted in a general description of the spatial range of the populations in the north Atlantic, migrational routes and breeding areas (Figure 1.1). Thus, the historical range of the Newfoundland harp seal was described as being roughly from the 45° to the 70° N and from the 40° to the 90° W.

Sergeant (1965) summarized the seasonal distribution of harp seals based on results of extensive tagging of young pups as well as sightings collected during aerial and vessel surveys. However, the coverage was biased towards certain areas and time periods - only fishing or sealing grounds, coastal areas and previously-identified moulting/whelping areas were investigated and offshore observations were made only during the whelping and moulting period (March and April). Furthermore, the distribution was based on imprecise coastal landmarks rather than actual sea location (latitude/longitude coordinates). The descriptive nature of Sergeant's study also did not allow the calculation of sighting effort necessary to determine distributional trends. In addition, little attention was given to weather conditions which affect the detectability of the seals during surveys. Nonetheless, the distributions of the Newfoundland and Gulf populations described by Sergeant (1965, 1991) is, to date, the most comprehensive information available.

Harp seals undertake an annual migration from the east coast of Newfoundland and the Gulf of St. Lawrence to the western coast of Greenland and eastern Canadian Arctic.

Most harp seals spend their summer in western Greenland and in the Canadian Arctic before returning southwards in late autumn. As the population reaches the Strait of Belle Isle in late November or December, it splits into two groups, one which moves into the Gulf of St. Lawrence while the other remains off the coast of Newfoundland and Labrador. Wintering grounds are occupied during January and February. Very little is known about this time period except perhaps that harp seals tend to stay in open waters, and that it is a time of heavy feeding (Sergeant 1991). Large whelping concentrations are formed a few weeks before the birth of the pups in late February-early March in the Gulf and about a week later off Newfoundland. Whelping patches were found in offshore areas of northeastern Newfoundland and southern Labrador for the Newfoundland population, and close to the Magdalen Islands and in the northern Gulf for the Gulf population (Sergeant 1965; Lavigne *et al.* 1980; Bowen and Sergeant 1985; Stenson *et al.* 1995). Following mating (late March), the seals disperse until mid-April-mid-May when they haul-out on ice pans in large concentrations to moult. Once the moult is completed, a northern migration is undertaken. Young seals are believed to migrate northwards later than adults, therefore resulting in a greater dispersion of the population during this period (Sergeant 1965).

Occasional shifts in the distribution of harp seals have been reported in both the eastern and western populations. Fisher (1955) indicated that the timing of the southern migration of Newfoundland harp seals changed between early 1920s and the 1950s. He hypothesized that a warming trend that occurred in the Canadian Arctic waters in the early 1950s extended the open water area further north which permitted the seals to enlarge their summer range towards higher latitudes. The population moved from southwest Greenland to areas of northwest Greenland during summers thereby delaying the return of the seals to Newfoundland waters in the fall. There have been additional reports of delayed migration

in mid-Labrador during the 1950s which may have been the result of a decrease in the population's size (H.A. Williamson, unpublished data, cited in Sergeant 1965), or changes in environmental conditions (Williamson 1973, cited in Boles 1979). Similar changes in distribution have been reported in the eastern Atlantic. Haug *et al.* (1990) described the southern movements of an unusually large number of harp seals in coastal regions of Norway in 1987-1988 which coincided with a period of low temperatures, salinity and extensive ice cover in the Barents Sea. Alternately, it was suggested that the collapse of the Barents Sea capelin stock in 1985-1986 could have been a contributing factor in the distributional changes observed in the eastern harp seal population.

In recent years, significant oceanographic and biological changes have occurred in Newfoundland waters. From the mid-1980s through the mid-1990s, conditions colder than normal were observed in the waters off northern and eastern Newfoundland (Drinkwater 1994, 1996; Drinkwater *et al.* 1992; Colbourne *et al.* 1994) and declines of abundances and southeastern distributional shifts have been documented in many prey species (Baird *et al.* 1992; Lilly *et al.* 1994; Miller 1994; Gomes *et al.* 1995; Montevicchi and Myers 1996). During this same period, harp seals were reported in areas where this species was not thought to occur previously. For example, the offshore waters of Newfoundland were documented as being important wintering grounds for harp seals (Stenson and Kavanaugh 1993). Although these findings confirmed historical reports by Robinson (1897) and Chafe (1923), they were in contrast with Sergeant (1991) who considered the harp seal as a nearshore species seldom seen in offshore waters. Anecdotal reports have also suggested that harp seals were arriving sooner and staying longer in Newfoundland waters (Stenson and Kavanaugh 1993), suggesting that changes in their residency might also be occurring. It is unclear how intensively offshore areas are utilized, and if recent observations reflect true distributional changes or simply changes in survey

effort. It is apparent, though, that the annual range of the northwest Atlantic harp seal needs to be reexamined, and that environmental influences need to be included in the investigation.

1.3 Outline of the Present Study

The first objective of this study is to determine the spatial and temporal variability in the distribution of Newfoundland harp seals from 1991 through 1995, during non-whelping periods, using a spatial data analysis and correcting for observation effort and sighting conditions (Chapter 2). Geographical Information System (GIS) provides an easily accessible means for this type of analysis. It can store and manipulate a wide range of data types whose results can then be displayed graphically. Furthermore, an overlaying of various physical and biological parameters can easily be done using different scales or time frames. GIS has proven to be of great use in many studies of terrestrial migrating species. For example, information on the migrational movements of a caribou herd was given by using a GIS to map monthly patterns of distribution of caribou via radio collar data (Simms and Ollerhead 1995). GIS has also been useful in habitat suitability studies. For example, areas suitable for salmonid culture were determined by overlaying physical and oceanographical characteristics of adjacent small areas and selecting areas that contained combinations of physical and oceanographical characteristics most suitable for salmon (Ross *et al.* 1993). However, applying GIS technology to marine mammal distributional research is preliminary and has been limited to modelling studies. French and Reed (1989) used a GIS to predict the seasonal migration of the northern fur seal (*Callorhinus ursinus*) in the Bering Sea, while Moses (1995) used a GIS to determine the summer habitat of the north Atlantic right whale (*Eubalaena glacialis*) and to predict other potential summering grounds. This study does not intend to model or predict the

distribution of the harp seal in the northwest Atlantic. Rather, it has used a GIS to illustrate seal distributional patterns that have emerged from the data.

The second objective of this study is to examine the harp seal distribution in relation to the physical and biological features of the northwest Atlantic (Chapter 3). Ice conditions are known to influence harp seal migration (Timoshenko 1986), as well as their distribution on the ice fields (Dorofeev 1939; Nazarenko 1981; Sergeant 1991; Haug *et al.* 1994). While the influence of bathymetric conditions on the distribution of harp seals is still understood poorly, it is becoming more commonly studied in other pinnipeds species. Bengtson and Boveng (1995) found that although preferring the edge of the ice, crabeater seals (*Lobodon carcinophagus*) did not advance further than the continental slope edge, even when the ice edge extended beyond. Harp seals are wide ranging and highly mobile animals. Information on the influence of physical and biological characteristics such as ice conditions and bathymetry, as well as characteristics such as water temperature and prey distribution, on the harp seal distribution would allow areas of higher seal habitat utilization to be identified, increasing our understanding of the seasonal distribution of seals and how they utilize their environment. This information is important in planning future research as well as when attempting to determine the degree of potential interaction with prey species such as commercial fish stocks.

The study area consists of the continental shelf/slope of the northwest Atlantic ocean between 46° and 56° N and 46° and 57° W, covering the southern Labrador Shelf, the northeast Newfoundland Shelf, the northern Grand Banks and the adjacent continental slope to a maximum depth of approximately 3640 m (Figure 1.2). The continental shelf is a broad and relatively flat area of approximately 400 m, which extends from the coast to depths of 500 m. Currents over the continental shelf are slow and are not unidirectional over the entire area (Petrie and Anderson 1983). On the other hand, the continental slope is

an area where depth changes from 500 to 2000 m over less than 100 km in distance. The Labrador Current is a strong current that passes over and seaward of the shelf break (Tang 1992). Sea ice forms in mid-January in northern Newfoundland and extends southwards until the end of March, covering the northeast Newfoundland Shelf and the northern Grand Banks throughout most of the winter and spring (Cote 1989). The position and velocity of the Labrador Current are not affected by the presence of sea ice (Tang 1992).

Figure 1.1. Historically documented distribution and migration patterns of harp seals in the north Atlantic (taken from Nansen 1925).

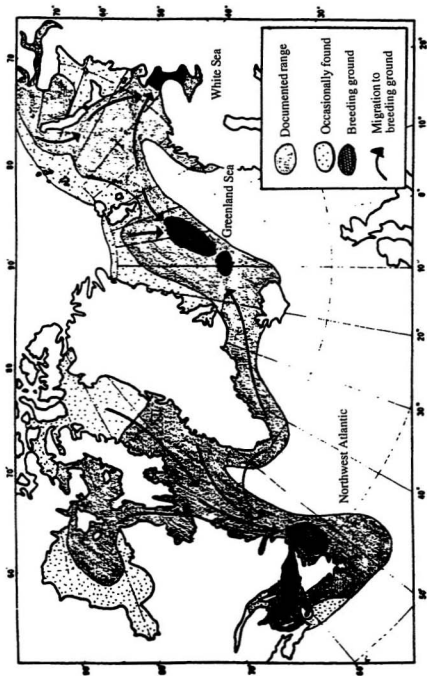




Figure 1.2. Bathymetric features of the study area (taken from Lilly *et al.* 1994).

Chapter 2: Spatial and Temporal Distributions of Harp Seals off Eastern Newfoundland and Labrador

2.1 Introduction

Our knowledge of the distribution of seals is usually based on information obtained from anecdotal sightings, tagging surveys, by-catch reports, or sightings of hauled-out animals. Usually the data are limited in terms of periods or areas covered, and cannot be quantified because of the lack of information on sampling effort. Therefore, a comprehensive assessment of the year-round distribution of these animals is not available.

Relatively few details are known about the distribution of harp seals in the Newfoundland area. It was considered to be primarily a nearshore species (Sergeant 1991), although, at the turn of the century there were reports of seals offshore on the Grand Banks (Robinson 1897; Chafe 1923). There have also been indications, since the late 1980s, that harp seals arrive in Newfoundland waters earlier in the fall, stay later in the spring, and are seen in offshore areas more commonly than in previous years (Stenson and Kavanaugh 1993). Providing preliminary data on offshore distribution, these recent findings are viewed as the first attempt to quantify harp seal distribution while controlling for sampling effort. Because of the absence of knowledge on distribution of sampling effort in time and space in previous studies, it is unclear if the recent increase in harp seal sightings in offshore areas is due to variations in sampling effort or shifts in distribution related to recent environmental conditions. It was therefore clear that further studies should control for survey variables, such as sampling effort, to permit further knowledge to be gained.

Weather conditions such as visibility, sea state, and wind force have also been acknowledged as potential biases in studies that involve observation of marine mammals at sea (e.g., Holt 1987). Nonetheless, previous studies on harp seals have not corrected for sighting conditions (e.g., Stenson and Kavanaugh 1993). An index of sighting conditions has been constructed by Clarke (1982) for cetaceans, but an index for sighting pinnipeds still needs to be devised.

The objective of this chapter is to examine seasonal and inter-annual changes in the distribution of harp seals from 1991 through 1995, using sighting rates and a Geographical Information System. Data were standardized for differences in sampling effort and sighting conditions based upon a newly-developed detectability classification index that I designed for the purpose of this study.

2.2 Materials and Methods

Information on the presence of seals in the northwest Atlantic was collected using line-transect methodology aboard research vessels from 1991 to 1995 (Table 2.1). The majority of the surveys were carried out from platforms of opportunity during cruises directed towards surveys of groundfish. Transects were conducted while the vessel proceeded at a constant speed and lasted for 2 h, or until there was a change in heading. Ship speed during transects ranged from 0 to 26 km/h, though modal speed was approximately 18.5 km/h. One or two observers, located on the bridge or crows nest at a height of 8 to 17 m above sea level, scanned to the horizon the area within a 180° swath in front of the vessel. The majority of observers (71%) were trained in sighting marine mammals with 46% classified as 'Expert' (because of their extensive experience in sighting seals) and 25% classified as 'Reliable'. The remaining observers were either

untrained (8%) or of unknown experience (21%). Data provided by untrained or unknown observers was not used in the analysis with the exception of the survey done in July and August of 1991 as it was the only survey providing information on summer distribution.

The start and finish locations (latitude and longitude), date, weather conditions, position and number of harp seals sighted were recorded for each transect. The actual number of seals was recorded when 10 seals or fewer were sighted. Because of the difficulty estimating group size of seals, a relative group size category (11-50 seals; 51-100 seals; ≤ 101 seals) was recorded for larger groups. The lowest number in each category was used to calculate total sightings of seals. Whenever possible, seals were classified according to species, often with the use of binoculars (7 X 30). If the species could not be identified, it was coded 'unknown'. Since hooded seals (the other common pinniped in these waters) have been known to be easily identified by observers and that other seal species have not been observed in the area, the majority of unknown sightings were assumed to be of harp seals. Therefore, all unknown seals, accounting for only 4.6% of the total sightings, were combined with harp seals in the analysis.

The year was blocked into five periods representing the different ecological phases of the harp seal migration; data from January and February were grouped to indicate the wintering period; March portrayed the distribution of the seals during the whelping period; April and May constitute the moulting period referred to as the spring period; June to August, the harp seal's northern migration and summering period; and September to December, the southern migration period. Since the distribution of harp seals during the whelping period has been the subject of a number of publications (e.g., Sergeant 1982; Stenson *et al.* 1995), the whelping period was not investigated. Furthermore, due to the lack of data, the southern migration period was also not investigated.

The study area was divided into subareas of 1° latitude and longitude. Sampling effort was estimated as the linear distance, in km, between the start and finish of a transect line. Occasional changes in the heading of the vessels were not always noted and therefore, the calculated effort represents the minimum possible. In some cases, transect lines overlapped more than one block of analysis. For these, the segment travelled in each block was calculated and the corresponding distance travelled were added to the total sampling effort of the blocks encountered. Total sampling effort for each area was considered to be the total km travelled in that area. For descriptive purposes, nearshore areas were defined as being all areas that abutted land.

I created a detectability index using estimates of visibility, Beaufort sea state, wind speed and ice cover information (Table 2.2). This multi-variate index was created in order to exclude from the data set transects that were travelled under conditions which would reduce the probability of sighting seals. *A priori*, visibility conditions had to allow for sightings of at least 4 km ahead of the vessel in order for a transect to be used. When Beaufort sea state information was available and ice cover was less than 70%, only transects collected in Beaufort of less than 5 (winds of less than 46 km/h, waves of less than 1.8 m, etc.) were accepted for further analyses. When Beaufort sea state information was unavailable (55% of the transects) wind conditions were used. Only transects in which winds were less than 46 km/h (25 knots) were used. All transects through areas of >70% ice cover were used because Beaufort sea state and wind conditions are considered irrelevant when there is high ice coverage. Statistical differences between the data discarded in each period was investigated using an ANOVA with a type two error rate of $\alpha = 0.05$.

The high variability in sampling effort among years and areas, as well as the absence of replication which precludes evaluating the standard error and mean sighting rate,

prevented me from statistically quantifying the variation in the harp seals distribution among years compared. Because of the limits of the analysis, the present study should be considered as more of a description of distributional trends throughout time than of a statistical demonstration of differences in distributional patterns. Nonetheless, visual appraisals of the distribution of sampling effort and sightings were made using a GIS. Each area was coded using the latitude and longitude of the southeast corner. For example, area 4950 would represent the area north of the 49° N and west of 50° W. The sampling effort (km travelled) and the sighting rate of seals (number of seals \cdot km⁻¹) were determined for each area. The intensity of sampling effort was grouped into six classes (<0-9.9 km; 10-19.9 km; 20-29.9 km; 30-39.9 km; 40-69.9 km; \geq 70 km), while the sighting rates of seals were classified into 6 groups (<0-0.1 seals \cdot km⁻¹; 0.11-0.5 seals \cdot km⁻¹; 0.51-1.0 seals \cdot km⁻¹; 1.01-2.0 seals \cdot km⁻¹; 2.01-5 seals \cdot km⁻¹; \geq 5.01 seals \cdot km⁻¹). For each period, areas which had the greatest number of seals \cdot km⁻¹ were defined as abundance peaks. A change in the location of peak areas from year to year would imply a change in the distribution pattern. In order to quantify the dispersion of the animals in the survey area, I defined the seal dispersion variable as the percent of areas occupied by seals divided by the total number of areas surveyed under standardized sighting conditions.

2.3 Results

Nine surveys were conducted resulting in a total of 823 transects and 12 796.7 km travelled (Table 2.3). After data standardization, 217 transects were discarded resulting in an overall reduction of 2765.3 km in the sampling effort and 735 seal sightings. Surveys conducted by untrained or unknown observers (1991 spring period and 2 transects of the 1992 spring period) accounted for 10% of the discarded sampling effort. Among the

discarded data, 64.4% of the sampling effort and 90.3 % of the seal sightings came from the winter period. A significant difference was found among periods in the % sampling effort ($n = 9$, $F = 235.6$, $p < 0.05$) and % seal sightings ($n = 8$, $F = 104.76$, $p < 0.05$) which were removed.

2.3.1 Winter Distribution

The greatest sampling effort occurred during the winter period (January-February) with surveys conducted in all years from 1991 to 1995 (Figure 2.1). Most surveys were done in February, although 1994 surveys began slightly earlier (25 January; Table 2.1). The range of sampling effort was less than 1 km to 727.7 km travelled per area (Appendix 1). The winter of 1991 had less sampling effort compared with other years, but reasonable area coverage (Figure 2.1). The winters of 1992 and 1993 had similar area coverage (15 areas in common) and similar sampling effort (Figure 2.1). The winters of 1994 and 1995 were also both similar in sampling effort but surveyed exclusively the northern Grand Banks (Figure 2.1).

The 1991 dispersion of seals was impossible to assess due to low sampling effort and sighting rate (Figure 2.2). However, the few sightings did provide general information on the range of the harp seals, not being observed south of 49° N or north of 53° N. 1992 had sightings in only 38% of all areas covered, ranging from 48° to 53° N. In the winter of 1993, 73% of all areas covered had seal sightings, ranging from 46° to 52° N, indicating a wider dispersion of seals than the previous year. Seals were sighted in 88% and 100% of all areas covered in 1994 and 1995 respectively (Figure 2.2). Total range was impossible to assess for these two years because of small latitudinal coverage. When viewed as a whole, harp seals appear to be dispersed widely during the winter period, being observed from 46° to 53° N.

Due to low sampling effort and sighting rate (only 5 seals were sighted), no abundance peak was determined for 1991. Nonetheless, most of these seals were observed in area 4950 which is consistent with the abundance peak obtained in 1992 (Figure 2.2). A large number of seals $\cdot\text{km}^{-1}$ also occurred in area 4849 in 1992. In 1993, harp seals were observed predominantly in area 4951. They also appeared in high number in area 4950. These results suggest that during the winters 1991 to 1993, harp seals were observed primarily in the area of the northern Grand Banks around the 49° parallel N and 50°, 51° meridian W (areas 4950 and 4951; Table 2.4).

The winters of 1994 and 1995 showed a different distributional pattern (Figure 2.2) than the winters of 1991-1993. Sighting peaks were located for both years in the northern area of the Grand Banks but this time in area 4849. Winter 1994 appears to exhibit an intermediate distribution between patterns revealed in the 1991-1993 period and in the 1995 period. The two highest number of seals $\cdot\text{km}^{-1}$ were located in area 4849 (1.50 seals $\cdot\text{km}^{-1}$) and in area 4952 (1.37 seals $\cdot\text{km}^{-1}$). In contrast, the 1995 winter showed a predominant aggregation in area 4849. In 1994, numbers of seals $\cdot\text{km}^{-1}$ were similar among survey areas, while in 1995 numbers of seals $\cdot\text{km}^{-1}$ were dissimilar among survey areas such that there was a greater concentration in area 4849. These results indicate that during the winters 1994 and 1995 harp seals were mostly seen along the 48° parallel N in more offshore areas (along the 49° meridian W) than what had been observed in the 3 previous years (Table 2.4).

2.3.2 Spring Distribution

Surveys were conducted during the spring period (April-May) of 1992 and 1993 (Figure 2.3). 1992 surveys were done during April, while 1993 was surveyed throughout

May (Table 2.1). The range of sampling effort was approximately 0.3 to 239.8 km travelled per area (Appendix 2). 1992 was a very broad (38 areas) and intense (average of 80.8 km travelled) survey year, covering a number of near- and offshore areas of eastern Newfoundland and Labrador while the 1993 period covered areas within the 48° and 51° N and the 48° and 53° W.

Harp seals were present in 51% of areas surveyed in 1992 (Figure 2.4). Due to the small survey coverage, dispersion was not assessed for 1993. Peak abundance occurred in area 5052 for 1992, although there was low sampling effort (18.7 km travelled; Figure 2.4). Areas 4950 and 5051 also had high concentrations of seals but had a higher sampling effort. Due to higher sampling effort, areas 4950 and 5051 should be regarded as “alternative peak” areas, area 5051 having the greatest number of seals $\cdot \text{km}^{-1}$ of the two areas. In 1993, the peak was in area 4952. Results from 1992 are therefore the most informative and suggest that harp seals are widely dispersed during the spring period, being observed from 47° to 54° N, although harp seals were observed predominantly along the 50° N.

2.3.3 Summer Distribution

1991 was the only year during which summer surveys (June to August) were conducted under fair to excellent sighting conditions (Figure 2.5). There was low sampling effort in most areas travelled, the range being between 2.6 and 114.4 km for each area (Appendix 3), although there was very wide coverage (32 areas).

Seals occupied only 22% of the total number of areas covered, sightings being limited to nearshore areas of northeastern Newfoundland and Labrador between 49° and 54° N (Figure 2.6). The sighting peak was in area 5456 (0.37 seals $\cdot \text{km}^{-1}$) with slightly

smaller numbers of seals $\cdot \text{km}^{-1}$ in areas 5154 and 5356. Hence, the relatively small number of harp seals in the study area were aggregated along the coastline of eastern Labrador for the 1991 summer period.

2.4 Discussion

This study is the first to quantify harp seal distribution in the northwest Atlantic while controlling for changes in weather conditions by using a detectability index. Furthermore, data from the winter period proved to be the most informative due to the consistency in dates surveyed, the higher levels of sampling effort and also due to its 5 year span therefore providing information on seal distribution during a period not well known to this point. The use of a sighting rate proved to be an efficient way to allow for interareal comparisons of relative abundance of seals using data standardized for effort. Surveys were conducted on platforms of opportunity, which meant that sampling effort was designed for other purposes and areas surveyed were not under my control. However, this allowed for a better coverage of the northwest Atlantic which in return increased our knowledge of harp seal distribution in areas that had not been previously investigated. It also resulted in geographical variation in sampling from year to year as well as from period to period. Statistical analyses of interannual variations was therefore not possible due to inconsistency in areas surveyed.

The detectability index that was created in this study was based on criteria that are considered mandatory in studies that have standardized for sighting conditions. I chose to discard data beyond certain limits of visibility, Beaufort sea state, wind speed and ice conditions. Those limits were based on suggestions made by the expert observers and

were selected in a conservative manner due to the problems associated with sighting a species like the harp seal. The guidelines used in my detectability index are similar to those used in other small marine mammal studies. For instance, the use of index 5 in Beaufort state as a cut-off is consistent with other surveys of small marine mammals (e.g., Holt 1987; Reilly and Fiedler 1994; Northridge *et al.* 1995). Although behavioural differences prevent us from making direct comparisons of the sightability of the two species, the minimum sighting conditions are similar to those proposed for harbour porpoises (*Phocoena phocoena*; Clarke 1982) which is regarded as having similar sightability characteristics as the harp seal. In this study, visibility was the prime factor in the detectability index. Usually, transects that are travelled in visibility conditions of more than 1 km are considered acceptable (e.g., Northridge *et al.* 1995). However, since most seals were rarely sighted within 1 km distance of the survey vessel in this study, I chose to increase the limits of visibility conditions and accept transects only greater than 4 km of visibility. This limit was viewed by experienced observers as being a minimum under which there was a higher probability of missing seals. Since Beaufort sea state was often absent from the data, wind speed was also included in the detectability index. The high level of correlation of wind velocity and Beaufort sea state allowed me to approximate Beaufort state data when it was not recorded. Weather variables used in the detectability index represent the average condition for a complete transect and were constant throughout the transect. Although meteorological conditions may have varied during a single transect, they were unlikely to have varied significantly without being recorded and the transect stopped. Therefore, I believe that this method, although not perfect, ensures reliable comparisons among data sets.

When assessing relative abundance of harp seals, the lowest value of each group size category was used. Surveys were originally designed so that sightings of more than

11 seals were classified according to a group size category. Thus, it was impossible to reassess seal numbers once surveys were completed. Since the last category (>100 seals) did not have an upper limit, it was judged best to use the lower values rather than the higher or median values for each category. The use of the lower value of the categories were unlikely to bias the resulting trends since 92% of the sighting events ($n = 514$ events) were of groups smaller than 10 seals. Sightings of groups of 50 - 100 seals occurred only on 4 occasions, while 9 groups of >100 seals were sighted (winter period). Therefore, using the lower value of each category for groups of more than 50 seals was rarely done and any bias present would underestimate sightings of groups of >100 seals which were representative of much larger aggregations.

The number of seals sighted can be influenced by a variety of factors such as avoidance response to the sighting platform, location of seal in water or on ice, group size and the experience of the observer. In this study, the extensive temporal and spatial scope meant that numerous observers of various experience levels were used. However, observer experience was accounted for in the analysis by discarding data collected by untrained or unknown observers. An exception to this was the summer data which were collected by an observer of unknown experience. Although not conforming to the previously stated standards, I chose to make use of these data since only one observer was used throughout the summer survey. Furthermore, since this was the only year surveyed during the summer, no interseasonal comparisons were made which eliminated any bias caused by the difference in the observer's level of experience among years compared.

Detectability of seals is likely to decrease if seals are solitary or if seals are in water rather than on ice. Most of the sighting events were of seals in small groups. Therefore, some seals might not have been detected. However, since sightings of small groups were predominant in all periods, even in the spring period when seals tend to aggregate in large

patches, underestimations were assumed to be constant throughout the survey period. Seals were sighted mainly in water during the winters of 1991 to 1994 (70%, n = 1410 seals) while in 1995 seals were sighted more frequently in water (99%, n = 482) than on ice. Nonetheless, seals were predominantly in water in all winters. As for the spring period, the percentage of seals sighted on ice was dissimilar between 1992 and 1993 (85% and 19% respectively). However, 1992 and 1993 were not compared due to dissimilarities in sampling effort. Thus, interannual comparisons were made only among winters when group size and location of seal (in water or on the ice) were relatively consistent such that although underestimations of sightings is surely present it is likely constant among winters compared.

The behavioural response of harp seals to an approaching vessel is unpredictable (Pemberton *et al.* 1994). In other studies, dolphins were found to alter the direction and the speed of their movement when approached by surveying vessels (Au and Perryman 1982; Hewitt 1985). Since the reactions of harp seals were assumed to have cause similar bias throughout the study, the potential influence of differences in behavioural responses was not considered further.

GIS was the primary tool for analyzing and presenting the results in this study. This visual aid allowed for a rapid evaluation of the extent of the survey coverage as well as the identification of the peak seal areas in relation to physical features. One degree blocks were used in the analysis since this area size was considered to be the smallest area with sufficient sampling effort. Previously, several authors have used this block size when analyzing distribution of marine mammals over large survey areas (e.g., Bigg 1990; Reilly and Thayer 1990; Buckland *et al.* 1991; Northridge *et al.* 1995). There was some concern that comparisons among near- and offshore areas could be biased; the areal coverage available is equal among offshore areas while nearshore areas have less actual

water surface resulting in greater coverage for a given level of effort. Nonetheless, this did not effect the results of this study since sightings per area were standardized for effort.

Due to logistical constraints, knowledge of Newfoundland harp seal distribution has mainly focused on periods when seals aggregate i.e., whelping and moulting periods. Thus, knowledge of the distribution of seals in winter has been preliminary until now (Stenson and Kavanaugh 1993). This study provides the first quantitative assessment of the yearly distribution of harp seals in the northwest Atlantic, therefore allowing a better understanding of the distribution of harp seals, particularly in winter.

Harp seals were found to occupy over 8° of latitude of the northwest Atlantic during the winter and covering the upper 6° of latitude of the survey area during the summer period. This broad dispersion of harp seals in the northwest Atlantic confirms results from Sergeant (1965) who thought that the difference in timing of migration of young and adult seals, young seals migrating later than adult seals, explained the spread of the seal population over 1400 km during their migration. Harp seals were also dispersed over 8° of latitude during the spring period. This broad dispersion was unexpected since the moulting period was considered to be a period where seals aggregated in large patches north of 50° N at the eastern edge of the sea ice, east of Belle Isle (Sergeant 1965), as was also found in this study. Seals were therefore solely found within the moulting patch boundaries during moult. But as pointed out by Sergeant (1965) it is possible that the aerial surveys conducted during his study had not extended far enough south from the Strait of Belle Isle to cover the entire range of the seal population. Furthermore, the location of moulting patches can vary greatly among years (G.B. Stenson, pers. comm.) so the distribution of seals is highly variable, and greatly influenced by ice conditions (Sergeant 1991). This study therefore provides new insight on harp seal distribution

during the spring period by identifying areas that are not within the traditional moulting patches.

Overall, the distribution of harp seals does not conform to the traditional belief that this species is predominantly a nearshore resident (Sergeant 1965, 1991). Within the survey area, larger numbers of harp seals were located in areas covering the most eastern part of the Newfoundland Shelf during the spring and winter periods. Some sightings did occur in nearshore areas although areas abutting land were not well covered. Nearshore areas were found to be occupied by most seals only during the summer. This accords with Huntsman *et al.* (1954) and Boles (1979) who stated that harp seals continue their northern migration along the coastline after they reach the Strait of Belle Isle. This study therefore confirms, over an extended time frame while controlling for detectability differences, previous reports (Robinson 1897; Chafe 1923; Boles 1979; Stenson and Kavanaugh 1993) that offshore waters are utilized by harp seals. Due to dissimilarities between previous studies and the present one as well as reduced coverage of nearshore areas during winter, I am not able to infer that the distribution of the seals in nearshore areas has decreased due to shifts from nearshore areas to more offshore areas. It is clear though from these results, that offshore areas are used by harp seals during most of the year with the possible exception of the summer northern migration.

Indications of changes in distribution and migration patterns in the late 1980s (Stenson and Kavanaugh 1993; Solcum 1995) are confirmed by the results of the winter and summer periods of this study. During the winter, Sergeant (1991) observed seals mainly near 50° N, whereas in this study they were seen further south near 48° and 49° N. It is uncertain that a southern shift has occurred between the study periods of Sergeant (1991; 1950 to the 1970's) and the 1990s, however, a southern expansion was observed between 1991-1993 and 1994-1995. Furthermore, harp seals have been reported during

the early 1990s as far south as New-Jersey (Slocum 1995) which is well beyond their known range. As for the summer, Fisher (1955) and Sergeant (1965) mentioned that by the end of May, Newfoundland seals were all seen north of Belle Isle (52° N). Due to changes in the winter distribution, the summer distribution may have also been modified. If true, this could explain the greater number of seals reported in southern nearshore areas of Labrador compared with previous findings. If not, it may indicate that for some unknown reason seals might have delayed their northern migration. Alternatively, these recent observations could simply be due to difference in sampling effort. However, it is most likely that the presence of seals in coastal southern Labrador and northern Newfoundland as late as August is indicative of changes in the migration pattern in recent years.

Harp seal distributional changes have been previously attributed to variation in oceanographic and biological conditions (Fisher 1955; Haug *et al.* 1990). In the next chapter, I investigate the physical and biological factors that might directly or indirectly influence distributional patterns harp seals in the northwest Atlantic.

Table 2.1. Research vessel trips between 1991 and 1995 during which marine mammal surveys were conducted.

Year	Dates	Weather data	Name of vessel	Purpose of Survey
Winter Period				
1991	3-25 Feb.	Available	Gadus Atlantica	Groundfish
1992	5-29 Feb.	Available	Gadus Atlantica	Groundfish
1993	4-28 Feb.	Available	Gadus Atlantica	Groundfish
1993	10-25 Feb.	Available	Brandal	Seal
1994	25 Jan.-7 Feb.	Available	Polar Explorer	Seal
1995	2-15 Feb.	Available	Wilfred Templeman	Seal
Spring Period				
1991	5-8 May	N/A	Alfred Needler	Groundfish
1991	11 May	N/A	NFLD. Lynx	Groundfish
1992	7-27 April	Available	NFLD. Lynx	Groundfish
1992	7-27 April	Available	Northern Kingfisher	Groundfish
1992	15-30 April	Available	Beothic Endeavor	Seal
1993	12-21 May	Available	Polar Explorer	Seal
Summer Period				
1991	23 July-5 Aug.	N/A	NFLD. Lynx	Oceanography

Note: N/A means non-available.

Table 2.2. Detectability index based on criteria having an adverse effect on the ability to observe harp seals at sea.

Ice coverage	Beaufort sea state index	Wind speed	Visibility conditions	
			< 4km	>4km
<70%	<5		discarded	accepted
	>5		discarded	discarded
	N/A	< 46km/h	discarded	accepted
		>46km/h	discarded	discarded
>70%			discarded	accepted

Table 2.3. Standardized and unstandardized sampling effort and number of sightings by period.

Year	Sampling effort				Number of sightings					
	# transect		Km travelled		Harp seals		Unknown seal sp.		Total	
	Stand.	Unstand.	Stand.	Unstand.	Stand.	Unstand.	Stand.	Unstand.	Stand.	Unstand.
Winter Period										
1991	19	28	210.9	280.9	4	5	1	2	5	7
1992	91	120	2082	2549	308	335	16	17	324	352
1993	115	162	1652	2007	550	971	57	74	607	1045
1994	49	61	752.9	1171.3	467	479	7	8	474	487
1995	81	127	772.2	1243.9	297	480	2	2	299	482
Spring Period										
1991	0	10	0	240.8	0	0	0	0	0	0
1992	135	158	3035	3333	341	341	22	23	363	364
1993	28	64	524.4	923.8	51	118	1	2	52	120
Summer Period										
1991	88	93	1002	1047	3	3	28	30	31	33

Table 2.4. Abundance peaks (number of seals km⁻¹) of winters 1991-1995.

Area	Number of seals · km ⁻¹				
	1991	1992	1993	1994	1995
4849	0	2.20	0.69	1.50	1.63
4850			0.14	0.26	0.01
4851			0	0	0.04
4852			0.08	0.06	0.01
4949	0	0.02	0.26	0.06	
4950	0.22	3.05	1.77	0.18	
4951		0	7.94	0.68	0.05
4952		0		1.37	0.30
5050	0	0.10	0.13		
5150	0.15	0.32	0.05		
5151	0	0.07	0.14		
5251	0	0.02	0.02		
5352	0.02	0.01	0		
5353	0	0	0		
5453	0	0	0		

Figure 2.1. Annual sampling effort in surveys conducted under fair to excellent sighting conditions for the January-February period.

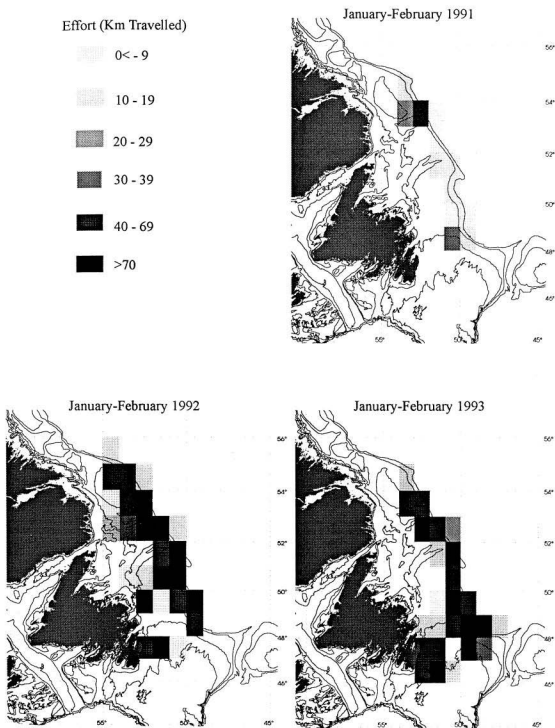


Figure 2.1. Continued

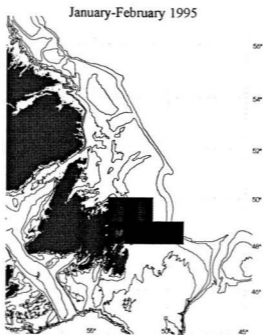
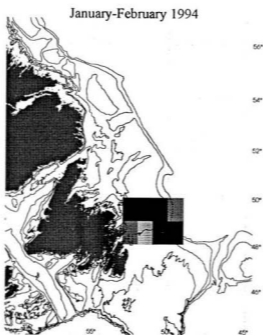
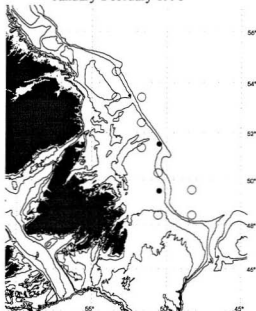


Figure 2.2. Annual relative sighting rates for harp seals standardized to 1 km effort in surveys conducted under fair to excellent sighting conditions for the January-February period.

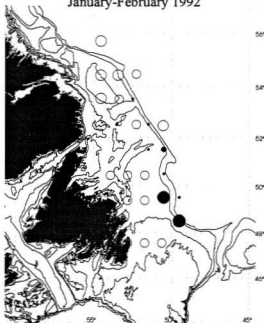
Number of Seals Sighted per Km Travelled

- 0.00
- <0.00 - 0.10
- 0.11 - 0.50
- 0.51 - 1.00
- 1.01 - 2.00
- 2.01 - 5.00
- > 5.01

January-February 1991



January-February 1992



January-February 1993

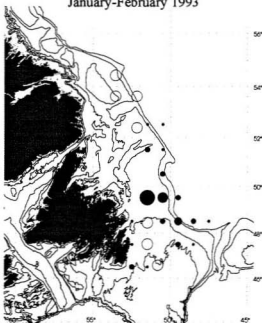
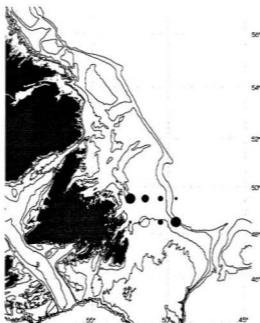


Figure 2.2. Continued

January-February 1994



January-February 1995

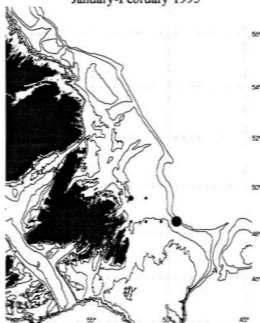


Figure 2.3. Annual sampling effort in surveys conducted under fair to excellent sighting conditions for the April-May period.

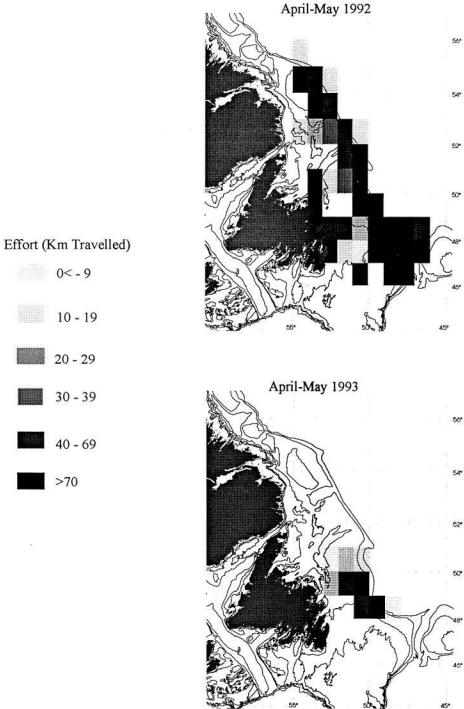


Figure 2.4. Annual relative sighting rates for harp seals standardized to 1 km effort in surveys conducted under fair to excellent sighting conditions for the April-May period.

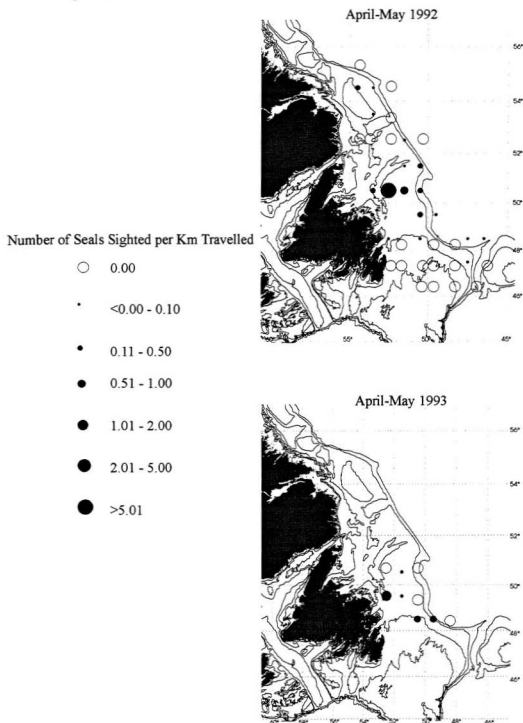


Figure 2.5. Annual sampling effort in surveys conducted under fair to excellent sighting conditions for the June-August period.

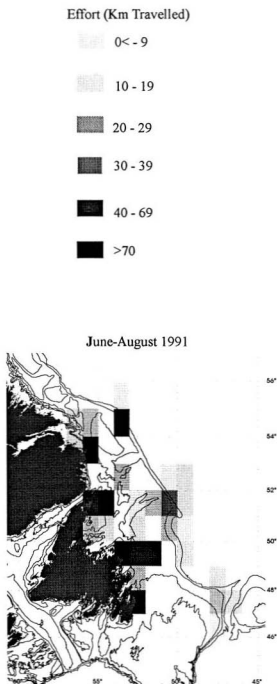
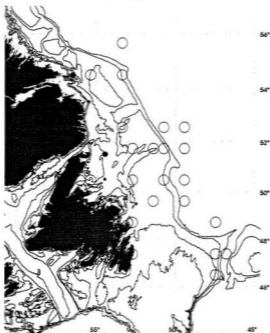


Figure 2.6. Annual relative sighting rates for harp seals standardized to 1 km effort in surveys conducted under fair to excellent sighting conditions for the June-August period.

Number of Seals Sighted per Km Travelled

- 0.00
- <0.00 - 0.10
- 0.11 - 0.50
- 0.51 - 1.00
- 1.01 - 2.00
- 2.01 - 5.00
- >5.01

June-August 1991



Chapter 3: Winter Spatial Distribution of Harp Seals Relative to the Biotic and Abiotic Features of the Northwest Atlantic

3.1 Introduction

In chapter 2, the northern part of the Grand Banks was defined as the main area occupied by Newfoundland harp seals during January and February. A change in their winter distribution was also observed, being similar from 1991 to 1993 while shifting slightly southward in 1994 and 1995. During that same period, significant changes in the northwest Atlantic environment occurred; 1991 through 1993 was characterized by strong northwesterly winds, cold sea temperatures, low salinities, early ice formation and greater than normal areal extent of ice in the waters off northern and eastern Newfoundland (Drinkwater 1994, 1996; Drinkwater *et al.* 1992; Colbourne *et al.* 1994) while environmental conditions became more temperate during the winter months of 1994 and 1995 (Colbourne 1995, 1996). Furthermore, many prey species declined in abundance, and southeastward distribution shifts have been documented (Baird *et al.* 1992; Lilly *et al.* 1994; Miller 1994; Gomes *et al.* 1995; Montevecchi and Myers 1996). Changes in the distribution of harp seals populations have been linked previously to changes in oceanographic and biological conditions (Fisher 1955; Haug *et al.* 1990). The concurrence of recent changes in the winter distribution of Newfoundland harp seals with abnormal environmental conditions suggests that physical and biological factors may influence the distribution of this population.

Little research has directly addressed the effects that environmental factors have on the distribution of harp seals. Sergeant (1991) suggested that ice thickness influenced the location of whelping sites but this was not measured directly. In contrast, severe ice conditions have been correlated with whelping patches being further offshore in the northwest Atlantic population (Sergeant 1982), and with changes in the migration routes of the White Sea population (Timoshenko 1986). In addition, the edges of ice fields have been documented as been occupied by harp seals (Dorofeev 1939; Koski 1980; Haug *et al.* 1994), particularly during severe winter years (Nazarenko 1981). Perhaps this is due to the large concentrations of prey species that have been reported at or close to the edge of the ice edge (Templeman and May 1965; Fréchet 1990; Chumakov and Savvatimsky 1990). Unfortunately, surveys dealing specifically with the northwest Atlantic population were conducted only during haul-out periods (i.e., whelping and moulting; Sergeant 1965) or during the summer (Koski 1980) which precludes any information on the winter period.

The influence of physical factors such as bathymetry on harp seal distribution has also not been examined. A preliminary study that used satellite link time depth recorder on individual seals found that harp seals are capable of dives greater than 400 m (Stenson and Sjare 1997) however dives have not been examined in details in relation to bottom topography or feeding behaviour. In contrast, several cetacean studies have investigated the influence of bathymetry on distribution. Controlling for effort and using a percent change in depth per area as an objective measure to quantify the degree of inclination of the sea bottom, dolphins (genus *Delphinus*) and pilot whales (*Globicephala macrorhynchus*) were found to be sighted more frequently in areas of high percent change in depth (Hui 1979, 1985; Selzer and Payne 1988). Water depth has also been reported to influence the distribution of small cetaceans (Hui 1979; Watts and Gaskin 1985;

Polacheck 1987) and marine birds (Stone *et al.* 1995; Schneider 1997; W. A. Montevecchi, pers. comm.), but does not appear to be as strong an influence as the percent change in depth.

The topography of the ocean floor has major influences on the oceanographic characteristics of a given area which ultimately determines prey composition and distribution. Pepin and Paranjape (1996) reported that the higher concentrations of nitrate and phytoplankton along the Newfoundland continental slope allow the area to be more productive than that upon the Newfoundland Shelf. Upwelling and water temperatures are also likely to be different between shelf and slope areas. This broad continental shelf, bordered by a steep continental slope, characterize the bathymetric environment of northwest Atlantic harp seals. Hence, comparisons of bathymetry, ice conditions, water temperature and the distribution of major prey species with harp seal distribution could help identify some of the critical elements of the harp seal's environment.

The objective of this chapter is to determine the harp seal's winter habitat by using a Geographical Information System (GIS) to describe the distribution of seals in relation to ice conditions, water temperature, degree of inclination of the sea bottom, water depth, and prey distribution within the northwest Atlantic from 1991 through 1995.

3.2 Materials and Methods

Seal sightings from January-February of 1991-1995 (as described in Chapter 2) were plotted on ice charts closest, in time (range 0 - 6 days), to the sightings. The ice charts were provided by the Atmospheric Environmental Services (AES) of Environment Canada. For descriptive purposes, seal location was described as either in water or on ice relative to the ice charts. Seal location on the ice chart was made even more specific by the

identification of ice thickness and size of ice floes. First year white ice (30-70 cm thick) and grey-white ice (15-30 cm thick) were investigated particularly since they have been reported to be the minimum ice thickness required by whelping seals (Sergeant 1965; G.B. Stenson pers. comm.). In this analysis, data consisted of actual locations of seal sightings unweighted for effort.

A generalized linear model (GLM) was used to test the locations of seals in water or on ice. Other GLM analysis' were performed using variables such as total concentration of ice, ice thickness and size of ice floes to investigate the influence of ice characteristics on the location of animals. Two separate analyses were performed; one using data pertaining to the thickest ice present and the second using data pertaining to the greatest partial concentration of ice in the area. Due to the non-normality of the residuals, randomization tests (1000 iterations) were performed using a Monte Carlo method (Crowley 1992). A SAS program (T. Bult, Department of Biology, Memorial University of Newfoundland) was used to randomly reassign values of the number of seals to the various combinations of ice characteristics found, without replacement. *P*-values were based on the distribution of *F* statistic values generated through these randomization procedures. These *p*-values were calculated as being the probability of obtaining an *F* statistic greater than that obtained in the original analysis.

Sea surface temperature (SST) was investigated in order to quantify the thermal habitat of harp seals regardless of ice conditions. Based on data from Reynolds and Smith (1994), SST data extended from 1991 to 1995 and consisted of monthly SST values on a 1 degree grid. Only February SST values were used in the analysis because most surveys were conducted during that period. The SST data are meant to be a rough estimate of the prevailing water temperature for each 1 degree² area during the winter surveys. A GLM was used to test the areal location of seals relative to general thermal conditions of the area

using SST values and number of seals $\cdot \text{km}^{-1}$ for each area. Since residuals were viewed as normal, no randomization test was necessary.

To examine the possible relationship between bathymetry and distribution of harp seals, winter sighting data (Chapter 2) were compared to topographical data from the Marine Environmental Data Service (MEDS, Ottawa). The MEDS topographical data are measures of distance (m) to sea floor, collected aboard vessels every 1/12 degree. From the MEDS data, bathymetry maps were generated using SPANS Explorer and isobaths created for each 10 m interval.

The influence of degree of inclination of the sea bottom was examined to determine if changes in bottom profile (slope effect) are an important factor in the distribution of harp seals. The study area was divided in subareas of 1 degree blocks (see Chapter 2) and the continental slope areas were defined as being any block that abutted isobaths of 500 or 1000 m. I used a Contour Index (CI), defined by Evans (1975), that incorporates changes in depth and maximum depth for a given area. The CI is a dimensionless number that ranges from 0.01 to 99.99 indicating the percent change in depth in the sample area and is defined as:

$$CI = 100 \times [(Maxdepth - mindepth) / Maxdepth]$$

Previous studies (Hui 1979, 1985; Selzer and Payne 1988) used 1 or 1.83 m as a minimum depth in Evans' formula for areas that abutted land. Due to the rapid change in depth of water along the Newfoundland coastline, the appropriateness of these minimums for this study was questioned. I therefore chose to test three different CI models to ensure that at least one of these models would correspond to the actual topography of the northwest Atlantic. A minimum depth of 1 m was used in model I. In model II and model III, minimum depths of 100 and 200 m, respectively, were used for areas in which the actual

minimum value sampled was smaller than the minimum value proposed by the model. The range of CI values were then grouped into five equal classes (0 - 19.99%; 20 - 39.99%; 40 - 59.99%; 60 - 79.99%; 80 - 99.99%) which were, along with number of seals $\cdot \text{km}^{-1}$, assigned to each block of analysis. Peaks were defined as areas of highest number of seals $\cdot \text{km}^{-1}$. A GLM was used to test the distribution of seals relative to the degree of inclination of the sea bottom. Due to the non-normality of the residuals, randomization tests were performed, as described previously, using number of seals $\cdot \text{km}^{-1}$ and CI values. Since no significant differences were found among years, data for all years were grouped in the analysis.

The importance of water depth was investigated using both actual water depth at each seal sighting point, which was estimated using the value of the closest isobath, and maximum depth of areas of 1 degree². This allowed me to determine, using two different spatial scales, if harp seals occupied areas where sea bed was within their diving scope (i.e., 100 - 400 m). No statistical analysis could be carried out using the actual water depth due to the absence of standardized effort. However, a GLM was used to test the relationship between maximum water depth of 1 degree² areas and distribution of harp seals. For each area, I determined the number of seals $\cdot \text{km}^{-1}$ and maximum water depth value. As the residuals were not normally distributed, randomization, as described previously, was carried out. Data from all years were grouped since no significant differences were found among years.

Distributions of prey such as Arctic cod (*Boreogadus saida*), capelin (*Mallotus villosus*), Atlantic herring (*Clupea harengus*), juvenile Atlantic cod (*Gadus Morhua*; individuals < 391 mm), and squid (Teuthoidea), were investigated by using data provided by the Department of Fisheries and Oceans, St. John's, NF. A complete description of the

methodology employed to gather this data may be found in Dalley *et al.* (1995). Demersal trawl surveys were conducted in December 1992, December 1993 to January 1994, and December 1994 to January 1995. These surveys are among the first to allow for catches of not only fish of commercial size but also of smaller fish which are also known to be preyed upon by harp seals (Lawson *et al.* 1995; Lawson and Stenson 1997). Numbers of fish caught for each species were grouped according to 1 degree² areas and were expressed as number of fish caught · 30 min tow⁻¹ · area⁻¹. Visual appraisals of the distribution of fish species were made using a GIS. A Pearson product-moment test was employed to determine the correlation between distribution densities of seals and various prey. Due to small sample size ($n < 42$), a corrected formula for r was used (Kendall and Stuart 1961).

3.3 Results

3.3.1 Distribution in Relation to Ice Conditions and Thermal Habitat

A total of 16 charts were examined; the maximum interval between date of ice chart and date of sighting being 6 days. In general, grey-white ice was located between limits of ice edge and first year white ice. The seaward edge of the ice field corresponded in most cases to the limits of the two types of ice thickness investigated. Between 1991 and 1994, all sampled areas had partial to complete ice coverage (Figures 3.1 to 3.4). In contrast, only 62% ($n = 772$ km) of the sampling effort in 1995 was conducted in areas with partial to complete ice coverage, and the remaining 38% was conducted in areas with no ice (Figure 3.5). Nonetheless, surveys of all years were conducted in both ice covered areas and water areas and the southern edge of the ice field was surveyed in all years.

From 1991 to 1993, the majority of harp seals (98%, $n = 936$) were located seaward of the ice cover (Figures 3.1 to 3.3). The remaining 2% were on the coastal side

of the ice cover. With the exception of 18 February 1991 and 8 February 1993, seals appeared to be located within the ice pack, their distances varying from roughly 50 to 200 km from the edge. In 1994, seals were located over most of the southeastern area of the ice cover, dispersed from the edge towards the inside of the ice field (Figure 3.4). In 1995, seals were either close to the ice edge off the southeastern coast of Newfoundland or in the open water at distances greater than 100 km away from the seaward edge (Figure 3.5).

The 1995 distribution of harp seals, on ice versus in water, was distinct from previous years (Table 3.1). From 1991 to 1994, only 0.6% ($n = 1410$) of harp seals were located in areas with no ice (i.e., water or bergy water). In contrast, most seals (80%, $n = 299$) were located in bergy areas in 1995. This may reflect the greater sampling effort in water areas than in ice areas during 1995 to some extent. However, numbers of seals in the water were much higher than those expected even accounting for the greater sampling effort.

No significant relationship was found between the distribution of seals and all ice conditions investigated (Table 3.2, $p > 0.05$). Nonetheless, 87% ($n = 1709$) of all seals were located in areas where ice concentration was greater than 70%. Generally seals were located in areas of both first year white ice and grey-white ice (Table 3.1). However, in 1993 and 1994, seals were located also on thinner ice such as new (<10 cm thick) and grey ice (10 - 15 cm thick, Table 3.1). During 1991 to 1995, harp seals ($n = 1709$) were distributed mainly on small (56%, 20 -100 m wide) or medium floes of ice (23%, 100 - 500 m wide). The remaining 7% were located either on larger floes of ice (500 m - 5 km wide), or on strips of ice.

Sea surface temperatures of areas surveyed ranged from -1.8 to 1.2° C. Seals were found to be distributed in water surface temperatures ranging from -1.8 and 0.3° C (Figure 3.6). No significant difference was found in the distribution of seals relative to sea

surface temperature ($n = 44$, $F = 1.05$, $p > 0.05$). The year effect was also non significant ($n = 44$, $F = 1.14$, $p > 0.05$).

3.3.2 Distribution in Relation to Bathymetry

Three models of sea floor relief were created during the investigation of the influence of bathymetry on seal distribution (Appendix 4). With the exception of two regions, similar patterns of sea floor relief were observed in all 3 models (Figure 3.7). As expected, CI classes changed in coastal and Grand Bank areas as the models used higher minimum values. Surprisingly though, areas east of the Funk Island Bank (i.e., areas 5050 and 4949) failed to exhibit the high CI values characteristic of continental edge areas. In general, all models indicated that the continental shelf is a rather flat area while the continental edge has a abrupt change in depth. Nonetheless, model II was viewed as being the most realistic of all three models created because it resembled the actual topography of the continental shelf. In contrast, models I and III were considered not to be very good models since areas that abutted land had dissimilar values of percent change in depth in comparison to the rest of the continental shelf.

From 1991 to 1993, winter survey effort was greater along the continental edge in areas of high CI classes (i.e., $\geq 60\%$), than in areas of low CI classes for all three models created (Table 3.3). In 1994 and 1995, survey effort was more evenly distributed between shelf and slope areas although areas of high CI class remained more traveled during surveys. Nonetheless, with the exception of some classes in 1991 and 1993, all classes of the contour index were sampled. Seals were distributed mainly along the margin of the continental slope edge in winters 1991 and 1992 (Figure 2.2). In 1993, seals were observed mainly on the continental shelf though still occupying areas along the continental slope (Figure 2.2). In 1994 and 1995, seal distribution was spread out on the continental

slope and shelf, most seals being observed on the slope (Figure 2.2). With the exception of 1993 and 1994, all abundance peaks occurred in areas of high CI classes. In 1993, the abundance peak of sightings was on the continental shelf in a block area having a CI value of 18.9%. In 1994, the abundance peak was in an area of high CI value, but a second area with a similar magnitude of seals $\cdot \text{km}^{-1}$ to the first, was in an area having a CI value of 36%. No significant difference was found between CI class and winter distribution of seals regardless of model tested (Table 3.4).

When investigating actual water depth at the location of seal sighting, 94% ($n = 1709$) of all harp seals were observed in waters of depths ranging from 200 to 599 m, all classes of depths having been surveyed (Table 3.5). In the winter of 1991, 4 of the 5 seals sighted were observed in waters of 500 to 599 m of depth. In the winter of 1992, seals were distributed mainly (78%, $n = 324$) in the 300 to 499 m depth range. Harp seals were predominantly concentrated in waters of 300 to 399 m deep in the winter of 1993 to 1995. Seals were rarely observed beyond the 1000 m isobath (less than 5%, $n = 1405$) for winters of 1992 to 1994. No seals were sighted in waters deeper than 1000 m in 1991 and 1995.

Sampling effort among classes of maximum depth of an area was uneven within and among years (Table 3.6). The 1992 and 1993 winter surveys concentrated mostly within areas of 100 - 699 m and beyond the 1800 m maximum depth range. 1991 was similar though fewer shallow areas were surveyed and most sampling effort occurred in areas of maximum depth greater than 2000 m. 1994 and 1995 sampled areas of maximum depths of 300 - 599 m and 1800 - 1999 m; most effort being within the more shallow depths. Areas of common sampling therefore within the ranges of 300 - 599 m and 1800 - 1999 m. No pattern emerged from the maximum depth analysis. Furthermore, no

significant differences were found between maximum depth of area and the winter distribution of seals (Table 3.4).

3.3.3 Distribution in Relation to Prey

Prey surveys had excellent yearly areal coverage, covering 30 (winters 1992 and 1993/94) and 32 areas (winter 1994/95) consistently for all species investigated. Although seal surveys had a lower coverage (26 areas in the winter of 1992 and 8 areas in the winters 1993/94 and 1994/95), most areas surveyed during the seal surveys were also surveyed during the prey surveys (14, 7 and 8 areas in common for winters 1992, 1993/94 and 1994/95 respectively).

Abundance and distribution varied among prey species and years. Arctic cod and capelin were the two most abundant species, with Atlantic herring, squid, and Atlantic cod of 1 to 3 yr old being less abundant. Numbers of fish caught in the winters of 1993-1994 were lower than in other years surveyed for species such as Arctic cod, capelin, 2 yr old Atlantic cod, and herring. Arctic cod were distributed from the continental shelf edge to the nearshore areas, their numbers roughly increasing from the edge to the coast (Figure 3.8). The distribution patterns show a general increase in numbers of Arctic cod in the northern part of the study area as well as a decrease in numbers of Arctic cod in the northern Grand Banks area between 1992 and 1995. In contrast, capelin were in high numbers on the continental shelf in areas close to its edge and across the shelf along the 50° N in the winters of 1992 and 1994-1995, numbers of capelin caught along the 50° N increasing in the winter of 1994-1995 (Figure 3.9). No particular pattern was observed in the distribution of capelin in the winter of 1993-1994. Herring were caught only in nearshore areas or areas abutting nearshore areas (Figure 3.10). No squid were caught in the winters of 1992 and 1993-1994, while in 1994-1995 the few catches were distributed across the

shelf north of the 49°N (Appendix 5). One and 2 yr old Atlantic cod were dispersed across the continental shelf although most were caught in nearshore areas of the southeastern shore and in the Fogo Island area (only for 1 yr old Atlantic cod in the winter of 1993-1994; Figures 3.11 and 3.12). Numbers of 1 and 2 yr old Atlantic cod caught in the eastern section of the northern Grand Bank increased in the winter of 1994-1995 when compared to previous years, particularly for 2 yr old Atlantic cod. One yr old Atlantic cod were more abundant in 1993-1994 and 1994-1995, while 2 yr old cod were more common in 1992. Three yr old Atlantic cod were dispersed on the continental shelf in all winters (Figure 3.13). The abundance of 3 yr old Atlantic cod was lower than 1 and 2 yr old cod in all years with the lowest being in the winter of 1994-1995. In the winter of 1992, most 3 yr old Atlantic cod were caught in the mid-shelf areas along the 49° N and the Avalon Peninsula. During the winters of 1993-1994 and 1994-1995 however, most 3 yr old Atlantic cod were caught in areas on the continental shelf edge.

When investigating overlap between prey and harp seal distribution, it was found that seals were observed mostly in areas where prey species such as capelin, Arctic cod and 1 to 3 yr Atlantic old cod had been caught (Table 3.7). Two exceptions to this trend were seen. In the winter of 1994-1995, seals were seen predominantly in areas where 3 yr old Atlantic cod had not been caught and in the winter of 1992, seals were seen predominantly in areas where 1 yr old Atlantic cod had not been caught. Most seals were distributed in areas where herring and squid were not present. Pearson product-moment coefficients of correlation (r values) ranged from -0.55 to 0.43 (Figure 3.14). The distribution of harp seals was found to be negatively correlated with distributions of Arctic cod ($n = 29$, $r = -0.40$, $t = 2.27$, $p < 0.05$) and herring ($n = 29$, $r = -0.55$, $t = 3.42$, $p < 0.05$), and positively correlated with 3 yr old Atlantic cod ($n = 29$, $r = 0.43$, $t = 2.47$, $p < 0.05$). Correlations between the distribution of harp seals and other prey were not significant.

However, the distribution of harp seals had a negative relationship with capelin ($n = 29$, $r = -0.30$, $p > 0.05$) and 1 yr old Atlantic cod ($n = 29$, $r = -0.27$, $p > 0.05$) and a positive relationship with 2 yr old Atlantic cod ($n = 29$, $r = 0.29$, $t = 1.57$, $p > 0.05$).

3.4 Discussion

This study is the first to attempt to describe physical and biological factors that might influence the winter distribution of harp seals in the northwest Atlantic. The environmental variables chosen had been documented previously to effect the distribution of harp seals or other marine mammals. It is important to note that due to the absence of comparable data prior to 1991, the short time span of this study, and difficulties encountered with spatial scale, results on the winter habitat of the Newfoundland harp seal remain preliminary. Further studies will have to be undertaken to create an improved better data set which would permit a fuller assessment of the factors involved in this system.

The choice of the spatial scale (areas of 1 degree², 111 km²) in this study was dictated by the spread of harp seal data. Previous studies found that the spatial scale employed influenced the results obtained. For instance, capelin distribution was found not to be associated with water temperatures at a small scale (~2000 km²), but was on a larger spatial scale (~90 000 km²; Shackell *et al.* 1994). Studies that dealt with seabirds (e.g., Schneider and Piatt 1986), prey (e.g., Horne and Schneider 1994), and cetaceans (e.g., Marques 1996; Jaquet and Whitehead 1996) have found that aggregative responses of predators with their prey occur only at specific spatial scales, smaller scales often demonstrating a weaker relationship than larger spatial scales. The use of the 1 degree block was considered at first to have been adequate to distinguish the relationship between seal distribution and its physical (bathymetry and SST) and biological (prey distribution) environment. In terms of assessing thermal habitat and CI patterns, the use of the 1 degree

blocks gave results that appeared to reflect the general state of sea temperatures and sea bottom profiles of the study area. In contrast, grouping data by such areas was inappropriate for ice condition analyses and was therefore not employed. Distribution of prey species relative to seal distribution was problematic when this spatial scale was used; in many instances, the actual relationship between the two distributions was obscured by its use. For example, in some cases an area with a high abundance of prey and a low abundance of seals was adjacent to an area with the converse. If the high abundances of both groups were along the opposite sides of common areal limits, then a negative correlation between the two would exist. However, if the high abundances of both groups occurred next to each other, but separated by the limits of the two blocks, then our view of the proximity of the two groups would be skewed. Unfortunately, prey data and seal data were not collected simultaneously or on similar transect lines. Thus, tows of fish were not always located spatially in areas where seal transects crossed. Smaller areal partitioning was therefore not possible due to spatial incoherence at a smaller scale. The prey/seal distributional results presented in this study are therefore meant as general measures of the relationship between harp seals and their major prey. Nonetheless, it should be noted that results obtained for the capelin distribution are similar to results obtained in a more detailed analysis by Dalley *et al.* (1995), despite the different type of analysis used. Thus, my choice of 1 degree blocks does not appear to have modified the representation of prey distributional patterns.

Ice conditions change daily. Increasing time between the date of ice chart and date of seal sighting therefore would increase the potential error in the estimations of ice conditions at the seal location. Comparisons between the ice conditions represented on the AES ice charts and those that would be recorded during seal surveys would have allowed me to identify such errors. Unfortunately, this could not be done because only the

percent ice coverage was recorded during transects and this was done inconsistently during seal surveys. Therefore, the use of ice charts was viewed as the only means to assess ice conditions. Since 93% of all sightings were made within a two day period of the ice chart date, conditions are considered to be relatively similar to those that could have been observed at the time of the sighting.

Little is known about the habitat of wintering harp seals except perhaps that they were not thought to be in contact with ice during this period (Sergeant 1965). Due to the variability in the sampling of ice and water areas throughout the survey period, it is impossible to determine which of the two habitats was more utilised. However, results from all winters suggest that seals can be found both on the ice and in the water during the winter. The increased ice extent present during the early 1990s might explain why seals were observed predominantly on the ice rather than on its edge or in the water. In contrast, in the later years of the survey, seals were observed predominantly in water or near it, possibly due to reduced ice extent. Distribution of seals in 1991 through 1993 could therefore be thought of as reflecting distribution patterns resulting from colder winter conditions. It is impossible to determine if the present results confirm those of Sergeant (1965) due to the difference in climatic conditions in the two studies. Nonetheless, the location of wintering harp seals does not appear to vary in response to changing ice conditions, as was reported during the 1970s when whelping patches of harp seals were seen further offshore because of harsher ice conditions (Sergeant 1982). Ice conditions are therefore not viewed as being the sole factor contributing to the winter distribution of harp seals in the northwest Atlantic.

Although there are no previous studies to which I could compare, comparisons with other periods of the year has provided information on differences existing among the harp seal's habitats relative to ice conditions. Wintering seals are mainly located where ice

concentration is greater than 70%, roughly 50 to 200 km away from the ice edge, seaward (1991-1993) or landward (1994-1995) of the ice cover. They are also found mainly in areas where ice thickness is 15 to 70 cm thick and ice floes are 20 to 100 m wide. The ice concentration and size of ice floes defined in the winter habitat of northwest Atlantic harp seals was similar to those reported in a preliminary study on whelping seals in the Greenland Sea (Estep *et al.* 1994). The size of ice floes appears to be smaller than those used by harp seals during the whelping period, ice floes being reported previously to be of more than 2 km wide (Sergeant 1965), although floe size can vary greatly during the whelping period in the northwest Atlantic (G.B. Stenson, pers. comm.). In contrast, the position of wintering seals relative to ice edge is much more within the ice pack than for moulting seals. Moulting harp seals of the northwest Atlantic population were previously reported to be close to the ice edge, or laying 8 km or more inside the ice edge during adverse weather conditions (Sergeant 1965). The results of this study showed that wintering harp seals make use of a wider range of ice thickness, including thinner ice, than during the whelping period. Whelping harp seals of the northwest population were observed primarily on ice of 50 cm thick (Sergeant 1965) while in the White Sea, whelping seals were observed on thinner ice although, whelping on ice thinner than 25 cm considered to be an exception (Dorofeev 1939). Therefore, wintering seals appear to be less discriminant towards thickness of ice than whelping seals and moulting seals. January and February are known to be months where harp seals are very active i.e., feeding heavily (Sergeant 1991; Chabot *et al.* 1995). In contrast, during the whelping and moulting months, seals are much less mobile, tend to refrain from feeding (Sergeant 1991; Chabot *et al.* 1995), and aggregate on ice pans located in areas northeast of Newfoundland (Sergeant 1971, 1991). Therefore, larger ice floes and thicker ice would seem to be important habitat characteristics in whelping and moulting periods, when substrate stability is essential. In contrast, wintering seals do not need ice conditions of specific

characteristics except perhaps to sustain their weight during resting periods and to allow for easy access to water and prey, which might explain the presence of seals in areas of smaller ice floes and of thinner ice.

Harp seals summering in the Canadian Arctic also seem to occupy a different ice habitat than wintering seals. Ice concentrations of areas utilized during the summer were less than 5% (Koski 1980) which is well below ice concentrations found during the winter. Furthermore, harp seals were found mostly in coastal and ice-edge areas (Koski 1980; Finley *et al.* 1990), rather than in the pack ice as was the case in winter. The winter and summer periods are both known to be times of increased feeding for harp seals (Sergeant 1991). However, the differences in the geography of the Canadian Arctic being made up of numerous islands and channels of water and the northwest Atlantic, could certainly account for the differences found between the distribution of seals relative to ice edge in the two areas.

On most ice charts of 1991 through 1993, seals were observed at a distance from the ice and shelf edges. The seaward edge of the ice overlapped with the edge of the continental shelf during that period. Due to those confounded variables, it is impossible to infer which of these two variables might have influenced the position of the seals. When ice-edge did extend further than the shelf edge (Feb. 27 1992 and Feb. 22 1993), the position of seals did not move eastwards with the ice cover but rather remained on the continental shelf. Later years of the study offered a better distinction between ice edge and shelf edge, ice cover being smaller. In 1994 and 1995, seals located at the southern tip of the ice-edge seemed to distribute themselves in relation to the position of the ice but not in relation to the shelf edge. In contrast, seals located in the water occupied areas where inclination of sea floor was high, being along the edge of the continental shelf or at the most northeastern tip of the Grand Banks. It appears that the influence of ice edge and

bathymetry on the distribution of harp seals varies according to the area occupied. Similar to findings by Bengtson and Boveng (1995) on the crabeater seals (*Lobodon carcinophagus*) in the Antarctic, harp seals distribute themselves relative to the position of the ice edge when it moves between the coastline and the edge of the shelf, but when at the far east of the continental shelf, they seem to distribute themselves relative to shelf edge regardless of ice conditions, not advancing further than the continental slope edge even when the ice edge extended beyond it. Therefore, it is possible that most harp seals distributes themselves along the continental slope possibly because it conveys a topography which facilitates greater and more reliable aggregations of prey.

Harp seals were observed mainly in waters 300 - 399 m deep. No seals were observed beyond the 1000 m isobath, except for small groups of 2 to 11 seals around the 1500 m isobath. A high degree of inclination of the sea floor was also found to be a characteristic of the winter habitat of harp seals. The combination of water depth and sea floor inclination information defined the northeastern Grand Banks and the edge of the continental shelf as being the main area where wintering seals seem to aggregate. An important oceanographical feature in that area is the Labrador Current, whose position coincides with the shelf break that occurs along the 500 m isobath (Tang 1992). The majority of the seals were found at the edge of the continental shelf, in close proximity to the Labrador Current. The small group of seals, located around the 1500 m isobath, were in proximity of another strong current, this one lying near the 2000 m isobath, to the east of the Labrador Current. The distribution of harp seals therefore appears to be closely linked to the oceanographic and bathymetric characteristics of the continental slope. Winter being an important feeding period (Sergeant 1991), harp seals could be distributing themselves according to physical cues such as the Labrador Current and the shelf edge which have been found to contain higher nitrate and phytoplankton concentrations

(Pepin and Paranjape 1996), and may likely have greater concentrations of prey (as was found in Nova Scotia waters; Sutcliffe and Brodie 1977). In addition, the continental slope could facilitate feeding by concentrating prey (e.g., Payne *et al.* 1986; Selzer and Payne 1988).

A preliminary study of Newfoundland harp seal diving behaviour found that seals regularly dive to depths between 100 and 300 m, although they are also capable of diving to over 400 m (Stenson and Sjare 1997). This means that the seals observed in this study generally occupied areas where the sea bottom was within diving reach although most of their dives would not have gone to the bottom. Unfortunately, it is presently unknown if harp seals are foraging on the sea floor, or in the water column. Dive studies of other pinniped species have shown that depth of foraging varies among species of seals and between individuals, areas, and seasons within a species. For instance, grey seals (*Halichoerus grypus*) forage close to the sea floor in depths varying from 15 to 200 m (Thompson *et al.* 1991), while crabeater (*Lobodon carcinophagus*; Nordøy *et al.* 1995) and hooded seals (*Cystophora cristata*; Stenson *et al.* 1993), which inhabit deeper waters, are more pelagic foragers. Bjørge *et al.* (1995) reported individual differences in the use of bottom topography in harbour seals (*Phoca vitulina*); some seals foraging in shallow kelp areas while others foraged in deep basins with a muddy sea bed. Hooded seals foraging depth varied depending on areas and seasons, but remained primarily pelagic feeders (Folkow and Blix 1995). Further studies will be required to determine where harp seals are foraging, and if this varies by season, area or in relation to prey distribution.

The present study was not meant to estimate the optimal thermal conditions for harp seal. Rather, it tried to determine the range of temperatures inhabited by harp seals during the wintering months. Since, in January and February, the northwest Atlantic is mostly covered with ice and experiences low air temperatures it was no surprise to find that seals

were observed in water temperatures of -1.8 to 0.3°C . No increase in metabolic rate were found in seals exposed to air temperatures between -10 and -30°C (Folkow and Blix 1989), while calculated estimations gave a thermoneutral limit of -8.7°C (Lavigne 1982). Although these behavioural studies were limited in terms of sample size (usually 3 to 5 individuals), there appears to be no evidence that harp seals would have trouble thermoregulating in the water temperatures encountered during the study period.

Capelin has been the predominant prey species of harp seals prior to 1986 (Lawson and Stenson 1995), and is the predominant prey item in the diet of offshore harp seals (Lawson and Stenson 1995; Lawson *et al.* 1995; Lawson and Stenson 1997). There is also some evidence that harp seals may select for capelin but do not appear to select for Atlantic cod, turbot, and plaice (Lawson *et al.* 1997). General distribution patterns show that harp seals and capelin often occupy common areas. Furthermore, capelin were more abundant in areas close to the shelf edge although overlapping of areas of highest abundance of capelin and harp seals did not occur in all years. Although areas of high abundance of capelin were adjacent to peak areas of seals in two of the three years investigated, statistical analysis revealed no significant relationship between capelin and harp seal distribution, but this may be due to the spatial scale used. Thus, the possibility of a relationship between capelin and harp seal distribution warrants further investigation.

Arctic cod and harp seals occupy common areas in the northwest Atlantic. However, their abundances were correlated negatively; Arctic cod were mostly in nearshore areas while seals were mostly offshore. Arctic cod were a major prey of nearshore harp seals (Lawson and Stenson 1995; Lawson *et al.* 1995) and offshore seals in northern areas (Lawson and Stenson 1997). Therefore, it appears that the distributions of these two species accord with results from diet studies.

Areas containing harp seals and Atlantic herring or Teuthoidea (squid) were observed rarely. This is mostly because harp seals were seen well offshore while herring were predominantly along the nearshore areas or abutting nearshore areas, and squid were mostly absent during the survey period. Herring are an important prey species in the diet of nearshore harp seals (Lawson and Stenson 1995; Lawson *et al.* 1995) but they were not found in any of the stomachs of offshore harp seals (Lawson and Stenson, 1997). Squid are not viewed as an important prey species in the harp seal's diet except perhaps during the summer period (Lawson and Stenson 1995). It is therefore clear from the spatial distribution of these two prey species why they are not present in stomachs of offshore wintering harp seals.

Atlantic cod have been reported to be a minor component in the diet of harp seals both near- and offshore (Lawson and Stenson 1995; Lawson *et al.* 1995; Lawson and Stenson 1997). Distribution patterns as well as statistical analysis seem to indicate that harp seals would have more distributional incentives to prey on 3 yr old Atlantic cod rather than younger cod. However, harp seals are known to consume more Atlantic cod of 10 to 20 cm in length, i.e., 1 and 2 yr old cod, than older and larger cod (Lawson *et al.* 1995). Larger Atlantic cod have been found in the stomachs of seals caught in offshore fishing nets (Lawson and Stenson 1997), but this is thought to be due to differences in feeding behaviours, seals feeding on discarded (and larger) Atlantic cod. It is possible that diet studies have underestimated the amount of 3 yr old Atlantic cod comprising the harp seal's diet because of otolith erosion (Lawson *et al.* 1995). However, because catches of 3 yr old Atlantic cod were extremely low, and harp seals have shown no selective preference for Atlantic cod (Lawson *et al.* 1997) even when this type of prey was found to be present (Lawson and Stenson 1997), the common distribution of harp seals and 3 yr old Atlantic cod may be due to a common prey such as capelin. If so, this would

agree with Lilly (1994) who found that, during the early 1990s, Atlantic cod stomachs contained a relatively high content of capelin in their stomachs and that distributions of both species highly overlapped.

Fisher (1955) and Haug *et al.* (1990) have documented historic changes in distribution of harp seals. Both hypothesized that alterations in oceanographical conditions were at the root of these changes. Harp seal distribution in the northwest Atlantic became more southeastern after the cooling water trend of the early 1990s (Chapter 2). Ice cover in 1994 and 1995 was smaller than in the 1991-1993 period. Reduction of ice cover however was not translated into a northern shift by harp seals but rather the opposite; seals being observed in water further south. The southern movement that was observed after 1993 therefore did not appear to be associated with the changes in ice coverage over those years. The levels of inclination of the sea floor and the range of water depth in which seals were observed remained similar throughout the study period. This meant that most seals maintained a constant bathymetrical habitat despite changing ice conditions. It is therefore concluded that bathymetry may be an important factor affecting the harp seal's offshore winter habitat; the distribution adopted by harp seals results in their experiencing a relatively constant bathymetrical environment regardless of changes in ice conditions. Although the general patterns (i.e., nearshore versus offshore) of prey distributions were found to be similar among years investigated, harp seal distribution was not highly correlated with any particular prey. Capelin distributions did not appear to shift or increase in southern areas (as was also found in Dalley *et al.* (1995)). This was very unexpected considering the many reports that capelin distribution had expanded to more southeast locations (i.e., the northeastern Grand Banks) during the 1990 to 1995 period (Lilly and Davis 1993; Lilly 1994; Miller 1994, 1995). Although changes in the distribution of harp seals appear to follow the reported changes in the distribution of its

most important prey species, i.e., capelin, results from this study do not clearly define this relationship. However, the influence of potential changes in capelin distribution cannot be ruled out.

Table 3.1. January - February distributions of harp seals (N) according to ice thickness.

Date of ice chart	N	Number of harp seals				
		In water	Grey-white ice	First year white ice	Both thickness	Other* ice thickness
Feb. 7, 1991	1	0	0	0	1	0
Feb. 18, 1991	4	2	0	0	2	0
Feb. 10, 1992	1	0	1	0	0	0
Feb. 13, 1992	1	0	0	0	1	0
Feb. 20, 1992	6	0	0	0	6	0
Feb. 24, 1992	32	0	0	0	32	0
Feb. 27, 1992	284	0	0	0	284	0
Feb. 8, 1993	25	3	4	0	13	5
Feb. 15, 1993	187	0	0	6	181	0
Feb. 22, 1993	395	0	0	0	395	0
Jan. 24, 1994	126	3	0	0	103	20
Jan. 31, 1994	184	0	0	0	184	0
Feb. 7, 1994	164	0	160	0	4	0
Jan. 30, 1995	132	132	0	0	0	0
Feb. 6, 1995	118	102	0	0	16	0
Feb. 13, 1995	49	4	0	0	45	0
Total	1709	246	165	6	1267	25

* Note: Other ice thickness are new ice (< 10 cm thick) and grey ice (10-15 cm thick).

Table 3.2. Results of GLM analyses on winter seal distribution relative to ice conditions on ice charts.

Analysis	Treatment	df	F value	P value
Location of seals on ice or water				
	Ice or water	1	0.08	0.69
	Year	4	0.52	0.39
	(Ice or water)*year	3	1.33	0.24
Seal location relative to ice concentration				
	Concentration	7	0.67	0.22
	Year	4	0.62	0.24
	Concentration * year	6	0.95	0.39
Seal location relative to ice characteristics from greatest partial ice concentration				
	Year	4	0.74	0.59
	Stage	3	0.86	0.50
	Form	4	2.72	0.07
	Stage * year	2	0.47	0.61
	Form * year	4	0.72	0.58
	Stage*form	1	4.4	0.06
Seal location relative to ice characteristics from thickest ice present				
	Year	4	0.44	0.74
	Stage	3	0.23	0.89
	Form	5	0.95	0.48
	Stage * year	2	0.01	0.85
	Form * year	3	0.66	0.61
	Stage*form	0	-	N/A

Table 3.3. Yearly sampling effort and number of seals·km⁻¹ according to CI class and model.

CI class	Model I			Model II			Model III		
	# areas	Effort (km)	# seals per km	# areas	Effort (km)	# seals per km	# areas	Effort (km)	# seals per km
Winter 1991									
0 - 19.99%	1	15.2	0.0	1	15.2	0.0	1	15.2	0.0
20 - 39.99%	N/S	N/S	N/S	N/S	N/S	N/S	N/S	N/S	N/S
40 - 59.99%	N/S	N/S	N/S	N/S	N/S	N/S	N/S	N/S	N/S
60 - 79.99%	6	87.9	0.2	6	87.9	0.2	6	87.9	0.2
80 - 99.99%	5	107.8	0.2	5	107.8	0.2	5	107.8	0.2
Winter 1992									
0 - 19.99%	2	43.1	0.1	2	43.1	0.1	5	174.5	0.1
20 - 39.99%	2	177.8	0.0	2	177.8	0.0	2	177.8	0.0
40 - 59.99%	7	274.4	0.0	8	325.7	0.0	5	194.4	0.0
60 - 79.99%	8	1042.0	3.2	8	1042.0	3.2	8	1042.0	3.2
80 - 99.99%	7	545.1	2.6	6	493.8	2.6	6	493.8	2.6
Winter 1993									
0 - 19.99%	2	19.2	8.1	2	19.2	8.1	9	409.6	8.6
20 - 39.99%	1	123.8	0.1	1	123.8	0.1	N/S	N/S	N/S
40 - 59.99%	3	230.3	0.0	8	436.0	0.5	4	219.6	0.1
60 - 79.99%	9	503.1	2.6	8	429.4	2.5	6	379.3	2.3
80 - 99.99%	11	776.1	1.4	7	644.0	1.0	7	644.0	1.0
Winter 1994									
0 - 19.99%	1	189.2	0.7	1	189.2	0.7	1	189.2	0.7
20 - 39.99%	1	88.1	1.4	1	88.1	1.4	1	88.1	1.4
40 - 59.99%	1	23.4	0.0	1	23.4	0.0	2	55.6	0.0
60 - 79.99%	3	316.5	0.5	4	348.7	0.6	3	316.5	0.5
80 - 99.99%	2	135.7	1.6	1	103.5	1.5	1	103.5	1.5
Winter 1995									
0 - 19.99%	1	43.9	0.1	1	43.9	0.1	1	43.9	0.1
20 - 39.99%	1	138.1	0.3	1	138.1	0.3	1	138.1	0.3
40 - 59.99%	1	73.9	0.0	1	73.9	0.0	4	297.9	0.3
60 - 79.99%	1	149.5	0.0	4	373.5	0.2	1	149.5	0.0
80 - 99.99%	4	366.8	1.9	1	142.8	1.6	1	142.8	1.6

Note: N/S means no survey.

Table 3.4. Results of GLM analyses on winter seal distribution relative to bathymetry.

Analysis	Treatment	df	F value	P value
Contour Index analysis using model I				
	CI	34	1676.22	0.30
	Year	4	2341.10	0.28
	CI*Year	36	3111.65	0.27
Contour Index analysis using model II				
	CI	34	1718.81	0.30
	Year	4	2316.02	0.27
	CI*Year	36	3030.27	0.27
Contour Index analysis using model III				
	CI	34	328.01	0.14
	Year	4	419.51	0.12
	CI*Year	36	552.61	0.09
Maximum depth				
	Max depth	36	2.92	0.62
	Year	4	9.87	0.30
	Max depth*Year	37	6.12	0.43

Table 3.5. Numbers of seals sighted (n) according to year and depth class (100 m range).

Depth class (m)	Winter 1991		Winter 1992		Winter 1993		Winter 1994		Winter 1995	
	n = 5		n = 324		n = 607		n = 474		n = 299	
	n	%	n	%	n	%	n	%	n	%
0 - 99	N/S	-	N/S	-	2	<1	N/S	-	N/S	-
100 - 199	0	0	0	0	34	6	3	1	11	4
200 - 299	0	0	1	<1	7	1	43	9	13	4
300 - 399	0	0	144	44	496	82	421	89	275	92
400 - 499	1	25	110	34	40	7	2	<1	0	0
500 - 599	4	75	45	14	1	<1	3	1	0	0
600 - 699	0	0	2	1	0	0	0	0	0	0
700 - 799	0	0	6	2	1	<1	0	0	0	0
800 - 899	0	0	5	2	4	1	0	0	0	0
900 - 999	0	0	0	0	3	<1	0	0	0	0
1000 - 1099	0	0	0	0	7	1	0	0	0	0
1100 - 1199	0	0	0	0	0	0	0	0	0	0
1200 - 1299	0	0	0	0	0	0	0	0	0	0
1300 - 1399	0	0	0	0	0	0	0	0	0	0
1400 - 1499	0	0	2	1	0	0	0	0	0	0
1500 - 1599	0	0	7	2	11	2	2	<1	0	0
>1600	0	0	2	1	1	<1	0	0	0	0

Note: N/S means no survey.

Table 3.6. Winter sampling effort according to maximum depth class of area (100 m range).

Max. depth of area (m)	Winter 1991		Winter 1992		Winter 1993		Winter 1994		Winter 1995	
	Km area	#	Km area	#	Km area	#	Km area	#	Km area	#
0 - 99										
100 - 199			52.9	2	252.7	5				
200 - 299			78.5	1	137.7	2				
300 - 399			99.8	3	65.0	4	244.8	3	341.9	5
400 - 499	15.2	1	315.4	2	173.7	2	88.1	1	138.1	1
500 - 599	56.2	2	88.4	2	85.9	2	168.9	1	149.5	1
600 - 699			55.6	1						
700 - 799										
800 - 899	9.1	1	41.0	1	164.3	1	115.6	1		
900 - 999										
1000 - 1099										
1100 - 1199										
1200 - 1299	18.4	1	92.6	1	61.2	1				
1300 - 1399										
1400 - 1499										
1500 - 1599										
1600-1699										
1700-1799										
1800-1899	2.5	1	727.7	1	41.9	1	32.1	1		
1900-1999	17.6	1	63.6	1	272.4	1	103.5	1	142.8	1
>2000	91.9	5	466.9	7	397.7	1				

Table 3.7. Areal overlap of the distributions of Newfoundland harp seals (HS) and their major prey species.

Prey species	Winter	Number of Overlapping Areas			
		HS Present Prey Present	HS Absent Prey Present	HS Present Prey Absent	HS Absent Prey Absent
Arctic Cod	1992	11	2	1	0
	1993/94	4	1	2	0
	1994/95	8	0	0	0
Capelin	1992	12	2	0	0
	1993/94	6	1	0	0
	1994/95	7	0	1	0
Herring	1992	2	0	10	2
	1993/94	2	1	4	0
	1994/95	4	0	4	0
Atlantic Cod 1 yr old	1992	5	1	7	1
	1993/94	4	0	2	1
	1994/95	7	0	1	0
2 yr old	1992	9	2	3	0
	1993/94	6	1	0	0
	1994/95	7	0	1	0
3 yr old	1992	10	2	2	0
	1993/94	5	1	1	0
	1994/95	2	0	6	0
Teuthoidea (squid)	1992	0	0	11	3
	1993/94	0	0	6	1
	1994/95	4	0	4	0

Figure 3.1. Winter 1991: Distribution of seals (black dots) in relation to ice conditions;
 n = number of seals.

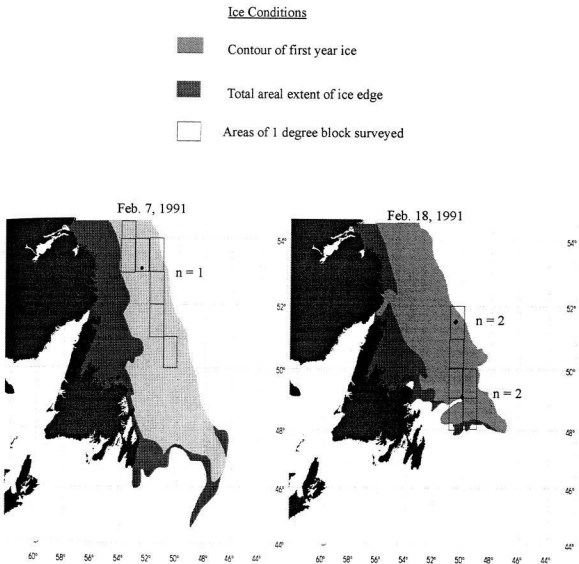


Figure 3.2. Winter 1992: Distribution of seals (black dots) in relation to ice conditions; n=number of seals.

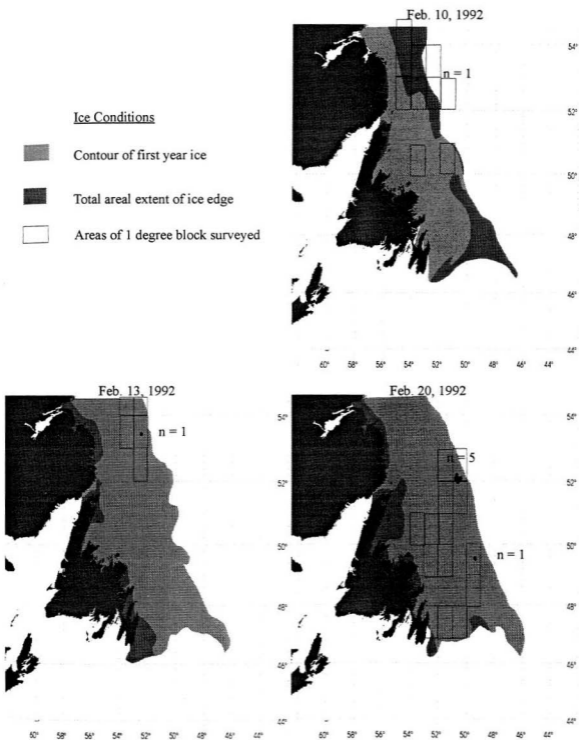


Figure 3.2. Continued

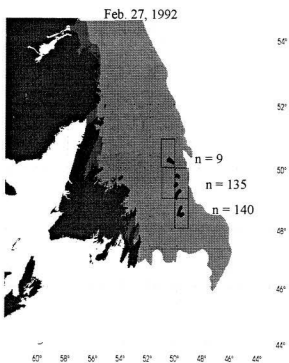
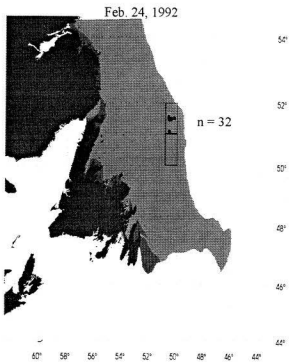


Figure 3.3. Winter 1993: Distribution of seals (black dots) in relation to ice conditions; n=number of seals.

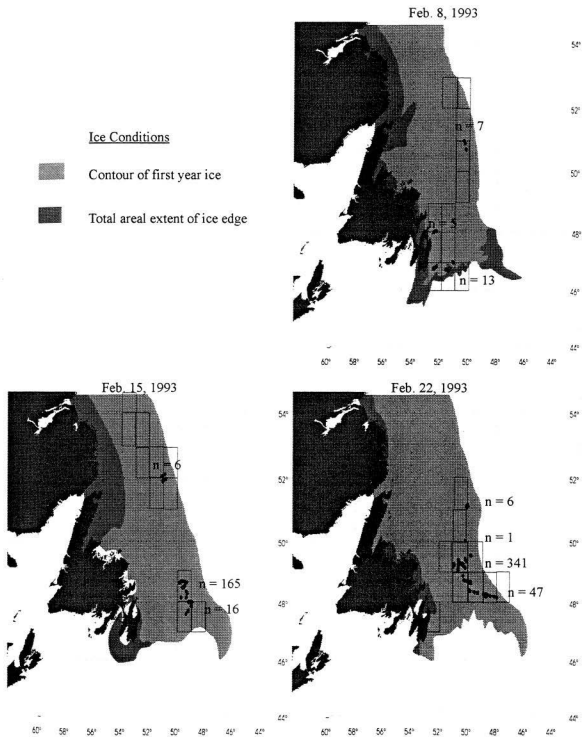


Figure 3.4. Winter 1994: Distribution of seals (black dots) in relation to ice conditions; n=number of seals.

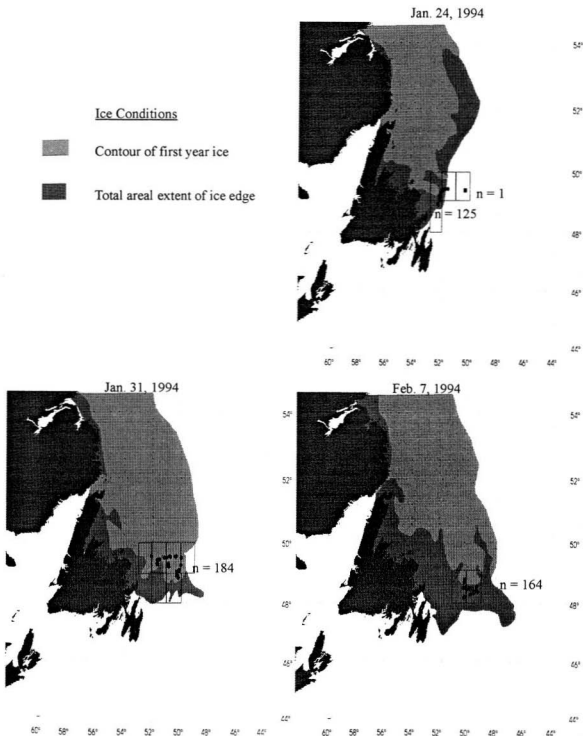


Figure 3.5. Winter 1995: Distribution of seals (black dots) in relation to ice conditions; n=number of seals.

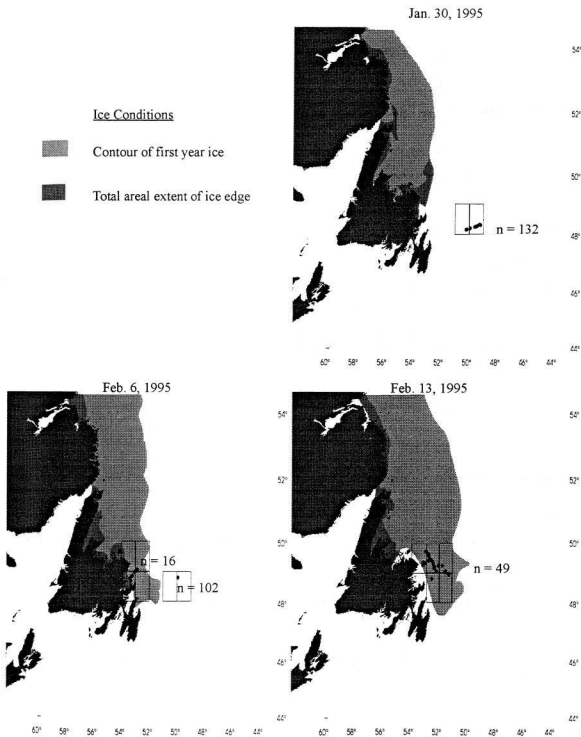


Figure 3.6. Harp seal winter thermal habitat. Top of bars indicate mean value and error bars indicate the 95% confidence interval.

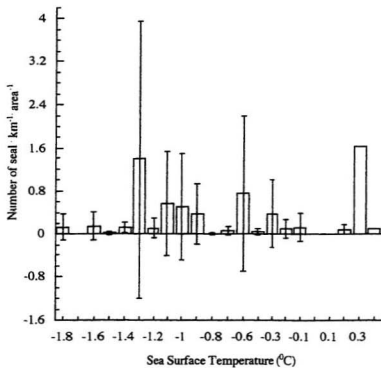


Figure 3.7. Models of the percentage of change in depth (CI value) for areas of 1 degree².

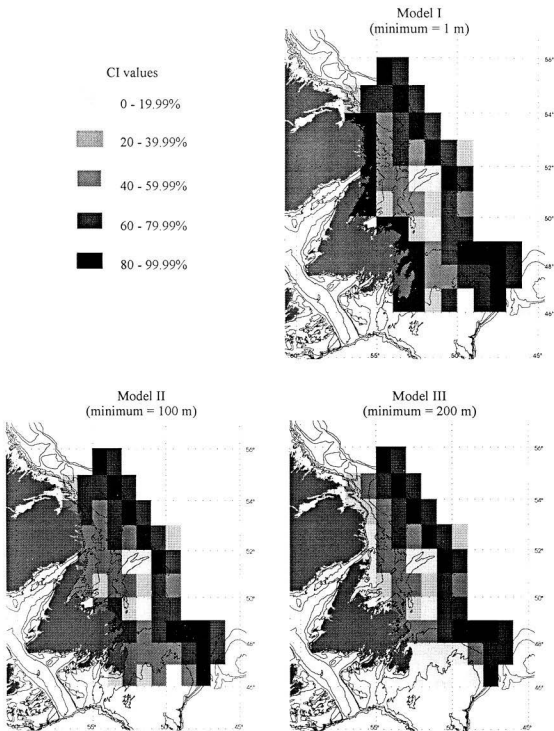
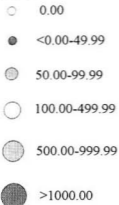
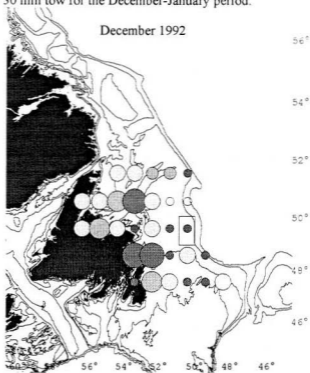


Figure 3.8. Annual mean catch of Arctic cod per 30 min tow for the December-January period.

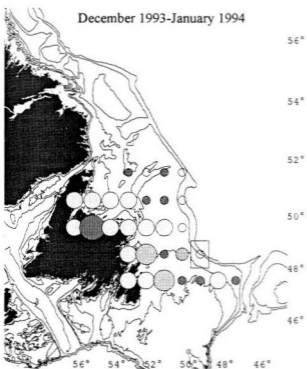
Number of Arctic Cod Caught



□ Area with highest number of seals seen



December 1993-January 1994



December 1994-January 1995

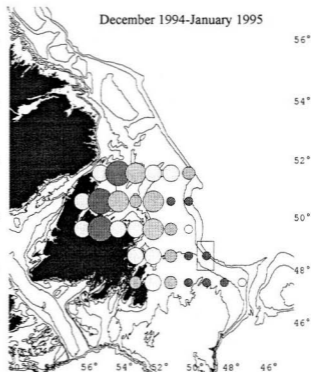
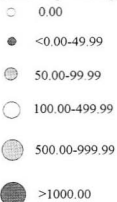


Figure 3.9. Annual mean catch of capelin per 30 min tow for the December-January period.

Number of Capelin Caught



□ Area with highest number of seals seen

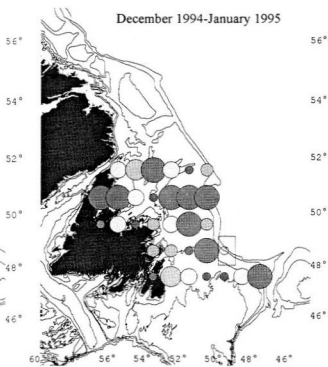
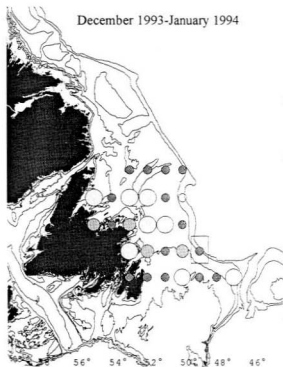
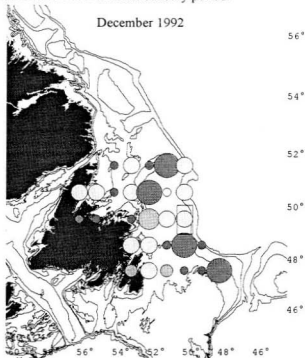


Figure 3.10. Annual mean catch of Atlantic herring per 30 min tow for the December-January period.

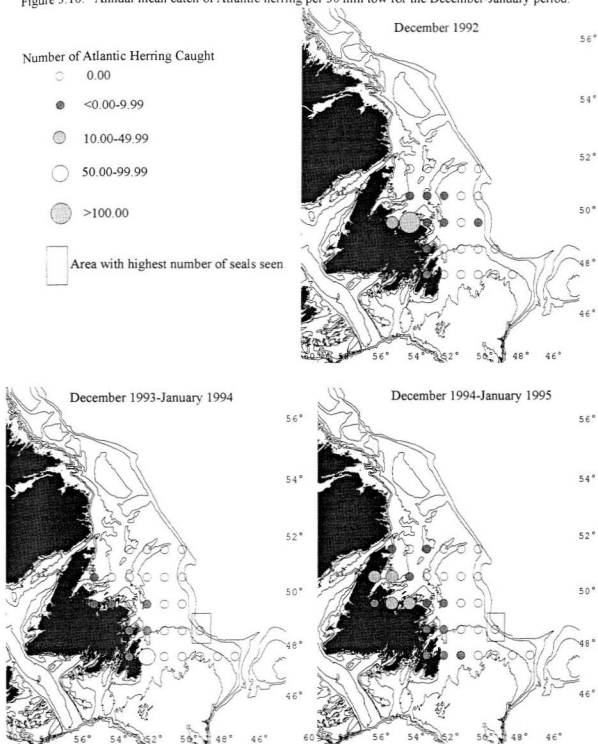


Figure 3.11. Annual mean catch of 1 yr old Atlantic cod per 30 min tow for the December-January period.

Number of 1 yr old Atlantic Cod Caught

○ 0.00

● <0.00-9.99

⊙ 10.00-49.99

○ 50.00-99.99

⊙ >100.00

□ Area with highest number of seals seen

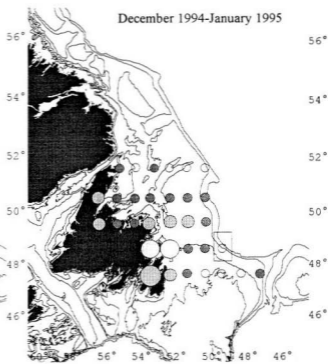
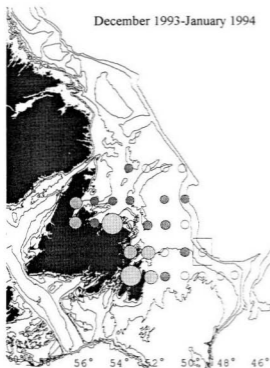
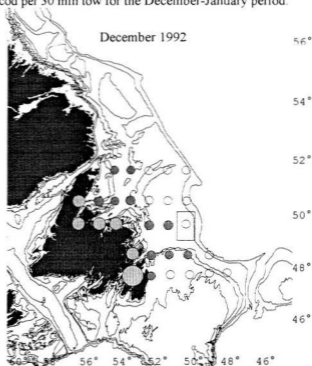


Figure 3.12. Annual mean catch of 2 yr old Atlantic cod per 30 min tow for the December-January period.

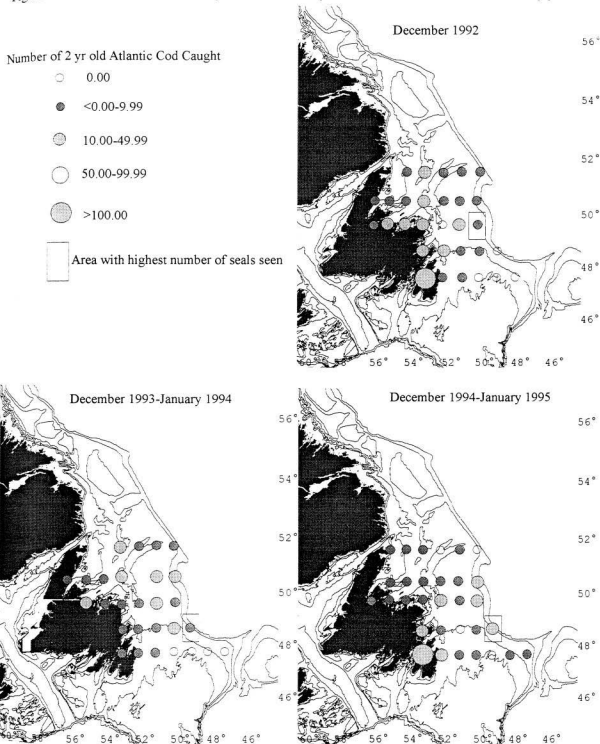


Figure 3.13. Annual mean catch of 3 yr old Atlantic cod per 30 min tow for the December-January period.

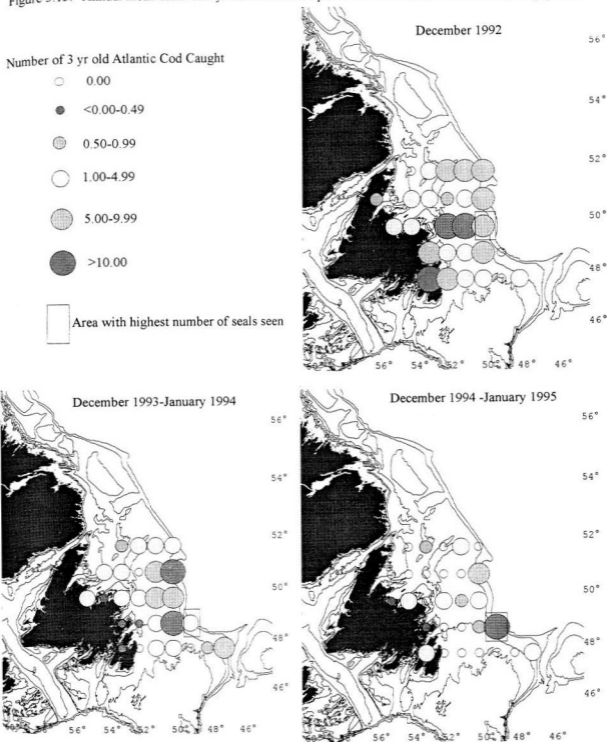
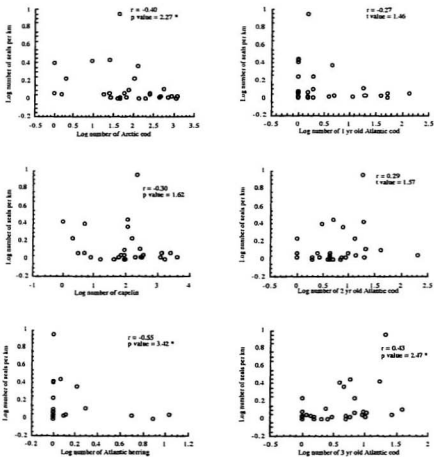


Figure 3.14. Correlation coefficient Pearson product-moment of numbers of major prey species and harp seals.



Note: * means significant correlation ($p < 0.05$).

Literature Cited

- Anonymous 1986. Seals and sealing in Canada. Report of the Royal Commission. Vol. 3. Minister of Supply and Services Canada.
- Au, D., and Perryman, W. 1982. Movement and speed of dolphins schools responding to an approaching ship. Fish. Bull. U.S. 80: 397-400.
- Baird, J.W., Stevens, C.R. and Murphy, E.F. 1992. A review of hydroacoustic surveys conducted during winter for 2J3KL cod, 1987-1992. CAFSAC Res. Doc. 92/107. CAFSAC, Dartmouth, NS.
- Bengtson, J.L., and Boveng, P.L. 1995. Seasonal movements and habitat utilization of crabeater seals. Abstract. In Proceedings of the 11th Biennial Conference on the Biology of Marine Mammals, 14 - 18 December 1995, Orlando, USA.
- Bigg, M.A. 1990. Migration of northern fur seals (*Callorhinus ursinus*) off western North America. Can. Tech. Rep. Fish. Aquat. Sci. No. 1764.
- Bjørge, A., Thompson, D., Hammond, P., Fedak, M., Bryant, E., Aarefjord, H. Roen, R., and Olsen, M. 1995. Habitat use and diving behaviour of harbour seals in a coastal archipelago in Norway. In Whales, seals, fish and man. Proceedings of International Symposium on the Biology of Marine Mammals in the Northeast Atlantic, 29 November - 1 December 1994, Tromsø, Norway. Edited by Blix, A.S., Walløe, L., and Ulltang, Ø. Developments in Marine Biology IV. Elsevier B.V., pp. 211-223.
- Boles, B.K. 1979. A study and review of the distribution and ecology of pinnipeds in Labrador. Atl. Biol. Serv. Ltd., 109p.

- Bowen, W.D., and Sergeant, D.E. 1983. Mark-recapture estimates of harp seal pup (*Phoca groenlandica*) production in the northwest Atlantic. *Can. J. Fish. Aquat. Sci.* 40: 728 - 742.
- Bowen, W.D., and Sergeant, D.E. 1985. A mark-recapture estimate of 1983 harp seal pup production in the northwest Atlantic. NAFO SRC. Doc. 85/1, Ser. No. N935, NAFO, Dartmouth, NS.
- Buckland, S.T., Cattanaach, K.L., and Anganuzzi, A.A. 1991. Estimating trends in abundance of dolphins associated with tuna in the eastern tropical Pacific Ocean, using sighting data collected on commercial tuna vessels. *Fish. Bull. U.S.* 90: 1-12.
- Chabot, D., Stenson, G.B., and Cadigan, N.B. 1995. Short- and long-term fluctuations in the size and condition of harp seals (*Phoca groenlandica*) in the northwest Atlantic. NAFO SCR Doc. 95/42, Ser. No. N2551. NAFO, Dartmouth, NS
- Chafe, L.G. 1923. Chafe's sealing book: a history of the Newfoundland seal fishery from the earliest available records down to and including the voyage of 1923. H.M. Mosdell 3rd Ed., St. John's, NF.
- Chumakov, A.K. and Savvatimsky, P.I. 1990. Distribution of Greenland halibut (*Reinhardtius hippoglossoides*) and roundnose grenadier (*Coryphaenoides rupestris*) in the northwest Atlantic in relation to hydrographic conditions in 1968-1986. NAFO Sci. Counc. Stud. 14: 51-65. NAFO, Dartmouth, NS.
- Clarke, R. 1982. An index of sighting conditions for surveys of whales and dolphins. *Rep. Int. Whal. Comm.* 32: 559-561.

- Colbourne, E. 1995. Oceanographic conditions and climate change in the Newfoundland region during 1994. Atl. Fish. Res. Doc. 95/3, Department of Fisheries and Oceans, St. John's, NF.
- Colbourne, E. 1996. Oceanographic conditions in the Newfoundland region during 1995 with comparisons to the 1961-1990 average. Atl. Fish. Res. Doc. 96/1, Department of Fisheries and Oceans, St. John's, NF.
- Colbourne, E., Narayanan, S., and Prinsenberg, S. 1994. Climatic changes and environmental conditions in the northwest Atlantic, 1970-1993. ICES Mar. Sci. Symp. 198: 311-322.
- Cote, P.W. 1989. Ice limits - East Canadian seaboard. Ice Climatol. and Applications Div., Ice Center, Environment Canada, Ottawa, ON.
- Crowley, P.H. 1992. Resampling methods for computation-intensive data analysis in ecology and evolution. Annu. Rev. Ecol. Syst. 23: 405-447.
- Dalley, E.L., Anderson, J.T., and Carscadden, J.E. 1995. Preliminary rates of capelin (*Mallotus villosus*) in inshore and offshore areas of NAFO div. 3KL during recent demersal juvenile cod surveys. In Capelin in SA2 + Div. 3KL, Atl. Fish. Res. Doc. 95/70, Department Fisheries and Oceans, St. John's, NF. pp. 133-146.
- Dorofeev, C.V. 1939. The influence of ice conditions on the behaviour of harp seals. Zool. J. URSS 18: 748-761.
- Drinkwater, K.F. 1994. Climate and oceanographical variability in the northwest Atlantic during the 1980s and early-1990s. NAFO SRC Doc. 94/71. NAFO, Dartmouth, NS.

- Drinkwater, K.F. 1996. Climate and oceanographic variability in the northwest Atlantic during the 1980s and early-1990s. NAFO Sci. Coun. Studies, 24: 7-27, NAFO, Dartmouth, NS.
- Drinkwater, K.F., Petrie, B., and Narayanan, S. 1992. Overview of environmental conditions in the northwest Atlantic in 1991. NAFO SCR. Doc. 92/73, Ser. No. N2127. NAFO, Dartmouth, NS.
- Evans, W.E. 1975. Distribution, differentiation of populations, and other aspects of the natural history of *Delphinus delphis* Linnaeus in the northeastern Pacific. Ph.D. thesis, University of California, Los Angeles, CA.
- Estep, K.W., MacIntyre, F., Noji, T.T., Stensholt, B., and Ørstrand, T. 1994. Seal sizes and habitat conditions assessed from aerial photography and video analysis. ICES J. Mar. Sci. 51: 235-261.
- Finley, K.J., Bradstreet, M.S.W., and Miller, G.W. 1990. Summer feeding ecology of harp seals (*Phoca groenlandica*) in relation to Arctic cod (*Boreogadus saida*) in the Canadian high Arctic. Polar Biol. 10: 609-618.
- Fisher, H.D. 1955. Utilization of Atlantic harp seal populations. Trans. Twentieth North Amer. Wildl. Conf.: 507-518.
- Folkow, L.P. and Blix, A.S. 1995. Distribution and diving behaviour of hooded seals. In Whales, seals, fish and man. Proceedings of International Symposium on the Biology of Marine Mammals in the Northeast Atlantic, 29 November - 1 December 1994, Tromsø, Norway. Edited by Blix, A.S., Walløe, L. and Ulltang, Ø. Developments in Marine Biology IV. Elsevier B.V. pp. 193-202.

- Folkow, L.P., and Blix, A.S. 1989. Thermoregulatory control of expired air temperature in diving harp seals. *Am. J. Physiol.* 257: R306-10.
- Fréchet, A. 1990. Catchability variations of cod in the marginal ice zone. *Can. J. Fish. Aquat. Sci.* 47: 1678-1683.
- French, D.P. and Reed, M. 1989. A simulation model of seasonal migration and daily movements of the northern fur seal. *Ecol. Model.* 48: 193-219.
- Gomes, M.C., Haedrich, R.L., and Villagarcia, M.G. 1995. Spatial and temporal changes in the groundfish assemblages on the north-east Newfoundland/Labrador Shelf, north-west Atlantic, 1978-1991. *Fish. Oceanogr.* 4: 85-101.
- Grahl-Nielsen, O., Mjåavatten, O., and Tvedt, E. 1993. Distinguishing between different populations of harp seal (*Phoca groenlandica*) by chemometry of the fatty acid profiles in the jaw bone. *Can. J. Fish. Aquat. Sci.* 50: 1400-1404.
- Haug, T., Krøyer, A.B., Nilssen, K.T., and Ugland, K.I. 1990. Harp seal (*Phoca groenlandica*) invasions in north Norwegian coastal waters: a preliminary report on age composition and feeding habits. ICES C.M. 1990/N:6. ICES, Copenhagen, Denmark.
- Haug, T., Nilssen, K.T., Øien, N., and Potelov, V. 1994. Seasonal distribution of harp seals (*Phoca groenlandica*) in the Barents Sea. *Polar Res.* 2: 163-172.
- Hewitt, R.P. 1985. Reaction of dolphins to a survey vessel: effects on census data. *Fish. Bull. U.S.* 83: 187-195.
- Holt, R.S. 1987. Estimating density of dolphin schools in the eastern tropical Pacific ocean by line transect methods. *Fish. Bull.* 85: 419-434.

- Home, J.K. and Schneider D.C. 1994. Lack of coherence of predators with prey: a bioenergetic explanation for Atlantic cod feeding on capelin. *J. Fish Biol.* 45: 191-207.
- Hui, C.A. 1979. Undersea topography and distribution of dolphins of the genus *Delphinus* in the southern California bight. *J. Mammal.* 60: 521-527.
- Hui, C.A. 1985. Undersea topography and the comparative distribution of two pelagic cetaceans. *Fish. Bull.* 83: 472-475.
- Huntsman, A.G., Bailey, W.B., and Hachey, H.B. 1954. The general oceanography of the Strait of Belle Isle. *J. Fish. Res. Brd. Can.* 11: 198-260.
- Jaquet, N. and Whitehead, H. 1996. Scale-dependant correlation of sperm whale distribution with environmental features and productivity in the South Pacific. *Mar. Ecol. Prog. Ser.* 135: 1-9.
- Kapel, F.O. 1995. Recoveries in Greenland, 1949-1994, of tagged or branded harp and hooded seals. NAFO SCR. Doc. 95/35, Ser. No. N2544, NAFO, Dartmouth, NS.
- Kendall, M.G., and Stuart, A. 1961. *The Advanced Theory of Statistics*. Vol. 2, Hafner, New York.
- Koski, W.R. 1980. Distribution and migration of marine mammals in Baffin Bay and eastern Lancaster Sound, May-July 1979. Petro-Canada Explorations, Calgary, AB.
- Larsen, F. 1981. Report on harp seal recoveries in Greenland, 1980-1981. NAFO SCR. Doc. 81/149, Ser. No. N454, NAFO, Dartmouth, NS.
- Lavigne, D.M. 1982. Pinniped thermoregulation: comments on the "effects of cold on the evolution of pinniped breeding systems". *Evol.* 36:409-414.

- Lavigne, D.M., Bogart, J.P., Danzman, R., Barchard, W.W., Earle, M., and Downer, R.G.H. 1978. Genetic variability in Northwest Atlantic harp seals, *Pagophilus groenlandicus*. ICNAF Res. Doc. 78/90, Ser. No. 5306, ICNAF, Dartmouth, NS.
- Lavigne, D.M., Innes, S., Barchard, W., and Doubleday, W.G. 1980. The 1977 census of northwest Atlantic harp seals, *Phoca groenlandica*. ICNAF Sel. Papers No. 6: 55-70. ICNAF, Dartmouth, NS.
- Lavigne, D.M., Innes, S., Kalpakis, K., and Ronald, K. 1982. An aerial census of western Atlantic harp seals, *Phoca groenlandica*, using ultraviolet photography. ICNAF Res. Doc. 75/144, Ser. No. 3717, ICNAF, Dartmouth, NS.
- Lawson, J.W. and Stenson, G.B. 1995. Historic variation in the diet of harp seals (*Phoca groenlandica*) in the northwest Atlantic. In Whales, seals, fish and man. Proceedings of International Symposium on the Biology of Marine Mammals in the Northeast Atlantic, 29 November - 1 December 1994, Tromsø, Norway. Edited by Blix, A.S., Walløe, L. and Ulltang, Ø. Developments in Marine Biology IV. Elsevier B.V. pp. 261-269.
- Lawson, J.W., and Stenson, G.B. 1997. The diet of northwest Atlantic harp seals (*Phoca groenlandica*) in offshore areas, and a comparison with synoptic hooded seals (*Cystophora cristata*). Can. J. Zool., Submitted.
- Lawson, J.W., Stenson, G.B. and McKinnon, D.G. 1995. Diet of harp seals (*Phoca groenlandica*) in nearshore waters of the northwest Atlantic during 1990-1993. Can. J. Zool. 73: 1805-1818.
- Lawson, J.W., Anderson, J.T., Dalley, E.L., and Stenson, G.B. 1997. Selective foraging by harp seals (*Phoca groenlandica*) in Newfoundland waters. In Harp seal - fishery interactions in the northwest Atlantic: toward research & management actions,

- Edited by Harwood, J., Lavigne, D.M., and Bowen, W.D. Canadian Centre for Fisheries Innovation, St. John's, NF. Working Paper 11.*
- Lilly, G.R. 1994. Predation by Atlantic cod on capelin on the southern Labrador and northeast Newfoundland shelves during a period of changing spatial distributions. ICES Mar. Sci. Symp. 198: 600-611.
- Lilly, G.R., and Davis, D.J. 1993. Changes in the distribution of capelin in divisions 2J, 3K, and 3L in the autumns of recent years, as inferred from bottom-trawl by-catches and cod stomachs examinations. NAFO SCR Doc. 93/54, Ser. No. N2237, NAFO, Dartmouth, NS.
- Lilly, G.R., Hop, H., Stansbury, D.E., and Bishop, C.A. 1994. Distribution and abundance of polar cod (*Boreogadus saida*) off southern Labrador and eastern Newfoundland. ICES C.M. 1994/0:6. ICES, Copenhagen, Denmark.
- Marques, F.F.C. 1996. Baleen whale distributional patterns and the potential influence of biological and physical processes. M.Sc. thesis, Memorial University of St. John's, NF.
- Meisfjord, J., Fyllingen, I., and Nævdal, G. 1991. A study of genetic variability in Northeast Atlantic harp seals, *Pagophilus groenlandicus*. ICES C.M. 1991/N: 5. ICES, Copenhagen, Denmark.
- Mikhnevich, O.Ch. and Potelov, V.A. 1967. Data on seal distributions in the Greenland Sea depending on the position of ice edge. Mater. Rybokhoz. Issled. Sev. Bass. 9: 67-72.
- Miller, D.S. 1994. Results from an acoustic survey for capelin (*Mallotus villosus*) in NAFO divisions 2J3KL in the autumn of 1993. In Capelin in SA2 + Div. 3KL.

- Edited by* J. Carscadden, Atl. Fish. Res. Doc. 94/18, Department Fisheries and Oceans, St. John's, NF. pp. 91-98.
- Miller, D.S. 1995. Results from an acoustic survey for capelin (*Mallotus villosus*) in NAFO divisions 2J3KL in the autumn of 1994. *In* Capelin SA2 + Div. 3KL., Atl. Fish. Res. Doc. 95/70, Department Fisheries and Oceans, St. John's, NF. pp. 63-71.
- Montevocchi, W.A., and Myers, R.A 1996. Dietary changes of seabirds indicate shifts in pelagic food webs. *Sarsia* 80: 313-322.
- Moses, E. 1995. Distribution of north Atlantic right whales (*Eubalaena glacialis*) in relation to oceanographical features of the Scotian Shelf. M.Sc. thesis, University of Massachusetts, Amherst.
- Møller, D., Nævdal, G., and Valen, A. 1966. Report on serological work in population studies. *Fiskin og Havet* 2: 1-17. (Translated Summary).
- Nævdal, G. 1966. Protein polymorphism used for identification of harp seal population. *Årbok Univ. Bergen*. 1965. Mat.-Naturv. Serie 9: 1-20.
- Nævdal, G. 1969. Blood protein polymorphism in harp seals off eastern Canada. *J. Fish. Res. Board Can.* 26: 1397-1399.
- Nansen, F. 1925. *Hunting and adventure in the Arctic*. Duffield & Co., New York.
- Nazarenko, Y.I. 1981. The influence of extreme ice and weather conditions on the ecology of the Greenland seal. *Ekologiya* 5: 101-103. (Translated from Russian by Department of Fisheries and Ocean, St. John's, NF. UDC 591.524)

- Nørdoy, E.S., Folkow, L and Blix, A.S. 1995. Distribution and diving behaviour of crabeater seals (*Lobodon carcinophagus*) off Queen Maud Land. *Polar Biol.* 15: 261-268.
- Northridge, S.P., Tasker, M.L., Webb, A., and Williams, J.M. 1995. Distribution and relative abundance of harbour porpoises (*Phocoena phocoena* L.), white-beaked dolphins (*Lagenorhynchus albirostris* Gray), and minke whales (*Balaenoptera acutorostrata* Lacepède) around the British isles. *ICES J. Mar.Sci.*, 52: 55-66.
- Øien, N., and Øritsland, T. 1995. Use of mark-recapture experiments to monitor seal populations subject to catching. *In* Whales, Seals, Fish and Man. Proceedings of International Symposium on the Biology of Marine Mammals in the Northeast Atlantic, 29 November - 1 December 1994, Tromsø, Norway. *Edited by* Blix, A.S., Walløe, L., and Ultang, Ø. *Developments in Marine Biology IV.* Elsevier B.V. pp. 35-45.
- Payne, P.M., Nicolas, J.R., O'Brien, L., and Powers, K.D. 1986. The distribution of the humpback whale, *Megaptera novaeangliae*, on Georges Bank and in the Gulf of Maine in relation to densities of the sand eel, *Ammodytes americanus*. *Fish. Bull.* 84: 271-277.
- Pemberton, D., Merdsoy, B., Gales, R., and Renouf, D. 1994. The interaction between offshore cod trawlers and harp *Phoca groenlandica* and hooded *Cystophora cristata* seals off Newfoundland, Canada. *Biol. Cons.* 68: 123-127.
- Pepin, P. and Paranjape, M.A. 1996. Summary of biological oceanographic variables in the Newfoundland region. *Atl. Fish. Res. Doc.* 96/2, Department Fisheries and Ocean, St. John's, NF.
- Petrie, B., and Anderson, C. 1983. Circulation on the Newfoundland continental shelf. *Atmos.-Ocean* 21: 207-226.

- Polacheck, T. 1987. Relative abundance, distribution and inter-specific relationship of cetacean schools in the eastern tropical Pacific. *Mar. Mamm. Sci.* 3: 54-77.
- Rasmussen, B., and Øritsland, T. 1964. Norwegian tagging of harp seals and hooded seals in north Atlantic waters. *Fiskeridir. Skr.* 13: 43-55.
- Reilly, S.B., and Thayer, V.G. 1990. Blue whale (*Balaenoptera musculus*) distribution in the eastern tropical Pacific. *Mar. Mamm. Sci.* 6: 265-377.
- Reilly, S.B., and Fiedler, P.C. 1994. Interannual variability of dolphin habitats in the eastern tropical Pacific I: Research vessel surveys, 1986-1990. *Fish. Bull. U.S.* 92: 434-450.
- Reynolds, R. W., and Smith, T. M. 1994. Improved global sea surface temperature analyses using optimum interpolation. *J. Climate* 7: 929-948.
- Robinson, CDR. G. 1897. Ice-riding pinnipeds. J.D. Potter, London.
- Ross, L.G., Mendoza, Q.M., and Beveridge, M.C.M. 1993. The application of geographical information systems to site selection for coastal aquaculture: an example based on salmonid cage culture. *Aquaculture* 112: 165-178.
- Schneider, D.C. 1997. Habitat selection by marine birds in relation to water depth. *Ibis* 139: 175-178.
- Schneider, D.C. and Piatt, J.F. 1986. Scale-dependant correlation of seabirds with schooling fish in a coastal ecosystem. *Mar. Ecol. Prog. Ser.* 32: 237-246.
- Selzer, L.A. and Payne, P.M. 1988. The distribution of white-sided (*Lagenorhynchus acutus*) and common dolphins (*Delphinus delphis*) vs. environmental features of the continental shelf of the northeastern United States. *Mar. Mamm. Sci.* 4: 141-153.

- Sergeant, D.E. 1965. Migration of harp seals, *Pagophilus groenlandicus* Erleben, in the northwest Atlantic. *J. Fish. Res. Bd. Can.* 22: 433-464.
- Sergeant, D.E. 1971. Calculation of production of harp seals in the western north Atlantic. ICNAF Res. Doc. 71/7, Ser. No. 2476. ICNAF, Dartmouth, NS.
- Sergeant, D.E. 1982. Some biological correlates of environmental conditions around Newfoundland during 1970-79: harp seals, blue whales and fulmar petrels. NAFO Sci. Coun. Studies 5: 107-110, NAFO, Dartmouth, NS.
- Sergeant, D.E. 1991. Harp seals, man and ice. *Can. Spec. Publ. Fish. Aquat. Sci.* No. 114.
- Shackell, N.L., Carscadden, J.E., and Miller, D.S. 1994. Migration of pre-spawning capelin (*Mallotus villosus*) as related to temperature on the northern Grand Banks, Newfoundland. *ICES J. Mar. Sci.* 51: 107-114.
- Shelton, P.A., Stenson, G.B., Sjare, B., and Warren, W.G. 1995. Model estimates of harp seal numbers at age for the northwest Atlantic. *Atl. Fish. Res. Doc.* 95/21, Department of Fisheries and Ocean, St. John's, NF.
- Simms, A.E., and Ollerhead, N. 1995. The development of a methodology for the visualisation of caribou radio collar database in a GIS. *In* Report: Labrador Institute for Northern Studies, Memorial University of Newfoundland, St. John's. pp. 4-23.
- Slocum, C.J., Schoelkopf, R., and Tulevech, S. 1995. Population changes in seals overwintering in New Jersey: a pilot study. Abstract. *In* Proceedings of the 11th Biennial Conference on the Biology of Marine Mammals, 14 - 18 December 1995, Orlando, USA.

- Stenson, G.B. and Sjare, B. 1997. The seasonal migrations and diving behavior of harp seals in the northwest Atlantic based on satellite telemetry. *In* Harp seal - fishery interactions in the northwest Atlantic: toward research & management actions. Edited by Harwood, J., Lavigne, D.M., and Bowen, W.D. Canadian Centre for Fisheries Innovation, St. John's, NF. Working Paper 16.
- Stenson, G.B., and Kavanagh, D.J. 1993. Distribution of harp and hooded seals in offshore waters of Newfoundland. NAFO SRC. Doc. 93/45, Ser. No. N2226. NAFO, Dartmouth, NS.
- Stenson, G.B., Hammill, M.O. Kingsley, M.C.S., Sjare, B., Warren, W.G., and Myers, R.A. 1995. Pup production of harp seals, *Phoca groenlandica*, in the northwest Atlantic during 1994. Atl. Fish. Res. Doc. 95/20, Department of Fisheries and Oceans, St. John's, NF.
- Stenson, G.B., Hammill, M.O., Fedak, M.A. and McConnell, B.J. 1993. The diving behaviour and seasonal migration of adult hooded seals. Abstract. *In* Proceedings of the 10th Biennial Conference on the Biology of Marine Mammals, Galveston, TX.
- Stone, C.J., Webb, A., and Tasker, M.L. 1995. The distribution of auks and Procellariiformes in the north-west European waters in relation to depth of sea. Bird Study 42: 50-56.
- Sutcliffe, W.H. and Brodie, P.F. 1977. Whale distribution in Nova Scotia Waters. Fish. Mar. Serv. Tech. Rep. 722, 83p. Fisheries and Marine Service, Bedford Institute of Oceanography, Dartmouth, NS.
- Tang, C.L. 1992. Oceanographic features in the Newfoundland marginal ice zone, March-April 1990. Atmos.-Ocean 30: 151-172.

- Terhune, J.M. 1994. Geographical variation of harp seal underwater vocalizations. *Can. J. Zool.* 72: 892-897.
- Templeman, W. and May, A.W. 1965. Research vessel catches of cod in Hamilton Inlet Bank area in relation to depth and temperature. ICNAF Spec. Publ. 6: 149-166. ICNAF, Dartmouth, NS.
- Thompson, D., Hammond, P.S., Nicholas, K.S., and Fedak, M.A. 1991. Movements, diving and foraging behaviour of grey seals (*Halichoerus grypus*). *J. Zool. (London)* 224: 223-232.
- Timoshenko, Y.K. 1986. Effects of ice and meteorological conditions on several representatives of true seals. *Ekologiya* 3: 72-78. (Translated from Russian, UDC 591.52: 599+745)
- Watts, P. and Gaskin, D.E. 1985. Habitat index analysis of the harbour porpoise (*Phocoena phocoena*) in the southern coastal Bay of Fundy, Canada. *J. Mamm.* 66: 733-744.
- Winters, G.H. 1978. Production, mortality, and sustainable yield of northwest Atlantic harp seals (*Pagophilus groenlandicus*). *J. Fish. Res. Bd. Can.* 35: 1249-1261.
- Yablokov, A.V., and Sergeant, D.E. 1963. Cranial variation in the harp seal (*Pagophilus groenlandicus*, Erxleben 1777). *Zool. Zh* 42: 1857-1865. (Transl. from Russian by Fish. Res. Bd. Can. Transl. Ser. No. 485).

Appendix 1. Sampling effort (km travelled) and number of seals km⁻¹ of areas in 1991-1995 during the winter period.

Area	Number of km travelled					Number of seals km ⁻¹				
	1991	1992	1993	1994	1995	1991	1992	1993	1994	1995
4650			10.0							0
4651			123.8							0.05
4652			49.8							0.14
4748			36.8							0.05
4749			76.9							0.18
4750		1.6					0			
4751		78.5	60.9				0	0		
4752		51.3	50.4				0	0.04		
4753			18.6							0.11
4847			10.4							0.10
4848			92.3							0.18
4849	17.6	63.6	272.4	103.5	142.8	0	2.22	0.69	1.50	1.63
4850	36.3		41.5	168.9	149.5	0		0.14	0.26	0.01
4851			9.9	23.4	73.9			0	0	0.04
4852			13.3	32.2	70.8			0.08	0.06	0.01
4853					89.2					0.13
4949	2.5	727.7	41.9	32.0		0	0.02	0.26	0.06	
4950	9.1	41.0	164.3	115.6		0.22	3.05	1.77	0.18	
4951		< 0.01	5.0	189.2	43.9		0	7.94	0.68	0.05
4952		83.6		88.1	138.1		0		1.37	0.30
4953					64.0					0.08
5050	18.4	92.6	61.2			0	0.10	0.13		
5051		94.2					0			
5052		17.0					0			
5053		2.5					0			
5150	13.7	98.6	166.7			0.15	0.32	0.05		
5151	15.2	43.1	14.1			0	0.07	0.14		
5250		17.8	26.1				0	0.04		
5251	9.0	116.4	40.8			0	0.02	0.02		
5252		148.5	159.6				0	0		
5253		31.4					0.06			
5254		20.7					0			
5351	1.7					0				
5352	52.8	144.2	46.5			0.02	0.01	0		
5353	19.9	57.0	44.3			0	0	0		
5354		5.6					0			
5452		18.8					0			
5453	14.6	55.9	15.0			0	0	0		
5454		55.6					0			
5554		15.1					0			

Appendix 2. Sampling effort (km travelled) and number of seals km^{-1} of areas in 1992 and 1993 during the spring period.

Area	Number of km travelled		Number of seals km^{-1}	
	1992	1993	1992	1993
4647	101.0		0	
4648	102.0		0	
4650	104.9		0	
4746	102.1		0	
4747	217.2		< 0.01	
4748	175.6		0	
4749	132.0		0	
4750	0.3		0	
4751	9.8		0	
4752	165.0		0	
4846	45.5		0.02	
4847	75.1		0.03	
4848	77.8	0.7	0	0
4849	239.8	113.9	0	0.18
4850	24.4	65.3	0.04	0.17
4851	42.9		0	
4852	48.3		0.08	
4853	43.7		0.02	
4949	94.4		0.01	
4950	132.3	217.1	0.49	0
4951		56.5		0.02
4952		24.2		0.74
4953	75.9		0.09	
5050	184.0	14.0	0.11	0
5051	36.6	28.6	0.68	0.07
5052	18.7	4.3	9.19	0
5053	71.1		0.11	
5150	86.4		0.16	
5151	65.9		0.05	
5250	11.4		0	
5251	62.1		0.02	
5252	35.6		0	
5253	24.6		0	
5254	12.5		0	
5352	47.0		0	
5353	190.5		0.01	
5452	11.4		0	
5453	62.0		0.02	
5454	88.1		0.39	
5554	16.6		0	

Appendix 3. Sampling effort (km travelled) and number of seals \cdot km⁻¹ of areas for the summer of 1991.

Area	Number of km travelled	Number of seals \cdot km ⁻¹
4647	2.6	0
4746	18.5	0
4747	28.0	0
4752	91.0	0
4847	17.6	0
4852	20.5	0
4949	13.5	0
4951	42.3	0
4952	64.1	0.02
4953	72.8	0
4954	5.1	0
5049	4.7	0
5050	22.8	0
5052	11.8	0
5054	18.2	0.06
5055	20.9	0
5056	56.4	0
5149	11.5	0
5150	31.0	0
5151	22.6	0
5152	7.1	0
5154	70.6	0.16
5155	42.9	0.05
5249	19.3	0
5250	9.2	0
5253	24.2	0
5355	114.4	0.08
5356	16.8	0.12
5453	78.5	0
5455	24.9	0
5456	13.6	0.37
5553	4.2	0

Appendix 4. Contour index (CI) of areas of 1 degree block according to model used.

Area	Number of samples per area	CI values		
		Model I	Model II	Model III
		Min = 1 m	Min = 100 m	Min = 200 m
4553	132	50.77	23.08	-53.85
4554	143	73.33	55.56	11.11
4555	132	85.33	55.56	11.11
4647	143	93.88	92.45	84.89
4648	156	71.28	46.81	-6.38
4650	156	64.29	48.98	-2.04
4651	169	39.69	23.66	-52.67
4652	141	99.48	48.45	-3.09
4653	120	99.23	23.08	-53.85
4655	138	99.50	49.75	-0.50
4746	143	71.60	71.60	71.60
4747	121	83.14	83.14	79.06
4748	132	74.53	72.90	45.80
4749	143	65.67	57.08	14.16
4750	132	54.59	48.98	-2.04
4751	143	51.21	51.21	3.38
4752	102	99.49	49.50	-1.01
4753	36	99.48	48.45	-3.09
4754	75	99.49	48.98	-2.04
4846	169	68.18	68.18	68.18
4847	143	84.58	84.58	84.58
4848	156	87.24	87.24	87.24
4849	169	91.13	91.13	89.86
4850	156	70.08	70.08	62.12
4851	169	44.78	44.78	40.30
4852	142	99.71	71.35	42.69
4853	91	99.72	71.67	43.34
4949	169	71.27	71.27	71.27
4950	156	63.75	63.75	63.75
4951	169	18.85	18.85	18.85
4952	143	35.92	35.92	35.92
4953	137	99.74	74.49	48.98
4954	106	99.54	53.92	7.83
5049	156	59.57	59.57	59.57
5050	144	70.35	70.35	70.35
5051	156	25.65	25.65	25.65
5052	132	51.58	51.58	51.34

Appendix 4. Continued

Area	Number of samples per area	CI values		
		Model I	Model II	Model III
		Min = 1 m	Min = 100 m	Min = 200 m
5053	144	52.43	52.43	51.46
5054	156	36.24	36.24	32.89
5055	137	99.53	53.05	6.10
5056	9	99.51	51.22	2.44
5149	156	76.37	76.37	76.37
5150	144	86.91	86.91	86.91
5151	156	16.67	16.67	16.67
5152	132	15.35	15.35	15.35
5153	144	53.51	53.51	51.57
5154	156	51.90	51.90	41.69
5155	121	99.50	49.75	-0.50
5249	156	29.23	29.23	29.23
5250	144	78.18	78.18	78.18
5251	156	89.68	89.68	89.68
5252	132	54.45	54.45	54.45
5253	144	60.88	60.88	60.08
5254	156	55.77	55.77	50.86
5255	124	99.51	51.46	2.91
5351	156	70.95	70.95	70.95
5352	132	86.21	86.21	86.21
5353	144	67.06	67.06	61.01
5354	156	58.51	58.51	48.45
5355	134	99.66	65.64	31.27
5356	7	99.52	51.69	3.38
5452	143	76.88	76.88	76.88
5453	156	90.61	90.61	90.61
5454	169	77.37	77.37	70.80
5455	156	60.96	60.96	49.62
5456	13	36.24	36.24	36.24
5553	144	61.68	61.68	61.68
5554	156	87.82	87.82	87.82

Appendix 5. Winter period: prey catches (excluding Atlantic cod) per 30 min tow of areas surveyed.

Squid refers to Teuthoidea.

Area	Winter 1992					Winter 1993-1994					Winter 1994-1995				
	# tow	Arctic cod	Capelin	Atlantic herring	Squid	# tow	Arctic cod	Capelin	Atlantic herring	Squid	# tow	Arctic cod	Capelin	Atlantic herring	Squid
4747	N/S	N/S	N/S	N/S	N/S	1	1.0	152.0	0.0	0.0	1	0.0	2728.0	0.0	0.0
4748	2	431.0	4032.5	0.0	0.0	2	176.5	48.5	0.0	0.0	2	44.0	492.0	0.0	0.0
4749	1	24.0	4.0	0.0	0.0	1	2.0	25.0	0.0	0.0	1	18.0	9.0	0.0	0.0
4750	1	40.0	13.0	0.0	0.0	1	15.0	237.0	0.0	0.0	1	9.0	15.0	0.0	0.0
4751	2	186.5	91.5	0.0	0.0	2	507.0	36.5	0.0	0.0	2	96.5	308.5	2.0	0.0
4752	3	733.0	191.3	0.0	0.0	10	229.3	12.8	96.6	0.0	3	440.7	900.3	2.0	0.0
4753	6	17.8	83.9	0.3	0.0	6	135.3	10.8	0.7	0.0	6	73.8	17.9	2.0	0.0
4849	1	1.0	1.0	0.0	0.0	1	0.0	4.0	0.0	0.0	1	8.0	0.0	0.0	0.0
4850	4	242.8	2485.8	0.0	0.0	2	70.5	85.0	0.0	0.0	2	132.0	1627.0	0.0	0.0
4851	1	43.0	43.0	0.0	0.0	1	39.0	15.0	0.0	0.0	1	44.0	7.0	0.0	0.0
4852	3	1218.3	308.7	0.0	0.0	4	853.6	54.8	0.3	0.0	3	1100.0	87.0	7.0	0.0
4853	5	1191.8	413.8	5.0	0.0	5	435.6	247.8	3.2	0.0	5	237.0	68.9	10.0	0.0
4950	6	23.8	104.2	0.2	0.0	2	0.0	2.0	0.0	0.0	2	0.0	78.0	0.0	0.5
4951	3	40.7	192.7	0.0	0.0	2	103.0	142.0	0.0	0.0	2	64.0	1214.0	0.0	2.5
4952	3	214.7	857.0	0.3	0.0	3	127.3	106.0	0.7	0.0	3	593.0	260.0	1.0	0.7
4953	1	13.0	33.0	1.0	0.0	1	291.0	63.0	0.0	0.0	1	471.0	57.0	4.0	1.0
4954	3	192.3	0.0	132.3	0.0	3	310.3	31.0	6.3	0.0	3	455.3	24.3	12.0	1.0
4955	3	883.0	2.7	22.7	0.0	3	1203.3	84.0	1.7	0.0	3	1688.0	198.7	17.0	1.0
4956	1	243.0	11.0	0.0	0.0	1	144.0	0.0	0.0	0.0	1	318.0	10.0	7.0	0.0
5050	2	0.5	332.0	0.0	0.0	2	0.0	0.0	0.0	0.0	2	8.0	3027.0	0.0	1.5
5051	N/S	N/S	N/S	N/S	N/S	1	3.0	22.0	0.0	0.0	1	3.0	10008.0	0.0	0.0
5052	2	223.5	1367.0	0.5	0.0	2	36.0	427.0	0.0	0.0	2	813.5	1365.0	0.0	1.0
5053	1	1490.0	110.0	1.0	0.0	1	330.0	107.0	0.0	0.0	1	70.0	22.0	0.0	0.0
5054	2	541.0	28.0	1.5	0.0	2	430.0	25.5	0.0	0.0	4	696.5	203.7	1.0	1.0
5055	2	318.0	122.0	0.0	0.0	2	261.0	176.0	0.5	0.0	2	1164.0	1021.0	34.0	1.0

Note: N/S means no survey.

Appendix 5. Continued

Area	Winter 1992					Winter 1993-1994					Winter 1994-1995				
	# tow	Arctic cod	Capelin	Atlantic herring	Squid	# tow	Arctic cod	Capelin	Atlantic herring	Squid	# tow	Arctic cod	Capelin	Atlantic herring	Squid
5056	2	174.5	206.5	0.0	0.0	2	173.5	0.0	0.0	0.0	1	491.0	1554.0	18.0	0.0
5150	3	27.0	268.0	0.0	0.0	3	0.3	12.7	0.0	0.0	1	85.0	60.0	0.0	0.0
5151	2	56.0	1330.0	0.0	0.0	2	4.5	205.0	0.0	0.0	2	155.5	31.5	0.0	0.5
5152	1	90.0	20.0	0.0	0.0	1	0.0	14.0	0.0	0.0	2	223.5	140.0	0.0	7.5
5153	3	138.3	107.3	0.0	0.0	2	42.5	29.0	0.0	0.0	3	715.0	1175.0	0.0	10.7
5154	1	442.0	9.0	0.0	0.0	N/S	N/S	N/S	N/S	N/S	1	1455.0	993.0	0.0	3.0
5155	N/S	N/S	N/S	N/S	N/S	N/S	N/S	N/S	N/S	N/S	1	481.0	156.0	5.0	0.0
Total	70	9240.5	12768.8	164.8	0.0	71	5924.7	2375.4	109.9	0.0	65	11672.3	27702.8	117.0	32.9

Note: N/S means no survey.

Appendix 6. Winter period: Atlantic cod catches (1-3 yrs old) per 30 min tow of areas surveyed.

Area	Winter 1992				Winter 1993-1994				Winter 1994-1995			
	#	1	2	3	#	1	2	3	#	1	2	3
	tow	yr old	yr old	yr old	tow	yr old	yr old	yr old	tow	yr old	yr old	yr old
4747	N/S	N/S	N/S	N/S	1	0.0	0.0	5.0	1	1.0	9.0	1.0
4748	2	0.0	0.0	2.0	2	0.0	0.0	0.5	2	0.0	1.0	0.0
4749	1	0.0	0.0	0.0	1	0.0	0.0	0.0	1	0.0	0.0	0.0
4750	1	0.0	0.0	3.0	1	0.0	0.0	2.0	1	0.0	1.0	0.0
4751	2	0.0	3.5	1.5	2	1.0	4.0	2.0	2	1.5	0.5	0.0
4752	2	0.5	6.5	5.0	2	19.5	7.5	0.0	2	13.5	11.5	0.0
4753	5	130.8	202.6	25.8	5	236.8	5.2	0.4	5	581.8	175.0	3.2
4849	1	0.0	0.0	0.0	1	0.0	2.0	3.0	1	0.0	18.0	16.0
4850	2	0.5	3.5	6.0	2	1.0	40.0	37.0	2	0.5	1.0	0.5
4851	1	1.0	3.0	4.0	1	0.0	6.0	1.0	1	3.0	0.0	0.0
4852	2	4.0	19.5	4.0	3	38.3	3.3	0.3	3	51.0	4.0	0.0
4853	8	17.4	26.6	5.6	7	30.6	3.1	0.1	7	50.9	12.7	0.1
4950	2	0.0	4.0	5.0	2	0.0	9.0	8.5	2	1.0	21.5	3.0
4951	2	0.5	17.5	20.5	2	1.0	12.0	6.0	2	10.5	8.0	0.5
4952	3	3.3	31.7	10.7	3	3.7	7.0	3.7	3	17.3	20.3	1.3
4953	1	0.0	0.0	0.0	1	0.0	2.0	3.0	1	19.0	1.0	0.0
4954	3	14.0	29.0	2.3	3	215.7	9.0	0.3	3	9.3	3.3	1.0
4955	3	13.0	21.0	4.0	3	2.0	12.7	2.0	3	4.0	8.0	0.3
4956	1	13.0	6.0	0.0	1	16.0	0.0	0.0	1	11.0	3.0	0.0
5050	2	0.0	3.5	8.0	2	0.5	11.0	10.5	2	2.5	33.0	6.0
5051	1	0.0	5.0	4.0	1	1.0	16.0	6.0	1	7.0	9.0	0.0
5052	2	0.0	1.5	0.5	N/S	N/S	N/S	N/S	2	1.5	2.5	0.0
5053	1	7.0	12.0	4.0	1	1.0	17.0	2.0	1	4.0	1.0	0.0
5054	2	3.5	8.0	3.5	2	3.5	6.0	2.0	4	1.5	1.5	0.0
5055	2	1.0	1.0	0.0	2	1.5	0.5	0.0	2	3.5	0.5	0.0
5056	2	13.5	8.0	0.5	2	19.0	1.5	0.0	1	19.0	0.0	0.0
5150	3	0.0	1.7	9.3	3	0.0	3.0	1.7	1	0.0	0.0	0.0
5151	2	0.0	1.5	9.5	2	0.0	2.5	2.0	2	0.0	0.5	2.5
5152	1	0.0	5.0	6.0	1	0.0	8.0	3.0	1	0.0	0.0	0.0
5153	3	5.3	18.3	2.3	2	2.5	10.5	0.5	4	2.0	5.0	0.8
5154	1	2.0	2.0	0.0	N/S	N/S	N/S	N/S	1	0.0	3.0	0.0
5155	N/S	N/S	N/S	N/S	N/S	N/S	N/S	N/S	1	1.0	1.0	0.0
Total	64	230.3	442	147	61	594.6	199	103	66	817.3	355.9	36.25

Note: N/S means no survey.

