FOOD AND FEEDING OF THE HOODED SEAL (Cystophora cristata) IN NEWFOUNDLAND

SUE-ANNE ROSS

FOOD AND FEEDING OF THE HOODED SEAL (*Cystophora cristata*) IN NEWFOUNDLAND

BY

© SUE-ANNE ROSS, B.Sc.

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

Biopsychology Program
Memorial University of Newfoundland
December 1992

St. John's Newfoundland

National Library of Canada

Acquisitions and Bibliographic Services Branch

395 Wellington Street
Ottawa, Ontario
K1A 0N4

Bibliothèque nationale du Canada

Direction des acquisitions et des services bibliographiques

395, rue Wellington
Ottawa (Ontario)
K1A 0N4

Your file Votre référence

Our file Notre référence

ISBN 0-315-82664-9

Canada

Abstract

Knowledge of diet is fundamental to studies of seal ecology and especially to any understanding of their role as predators in the northwest Atlantic marine ecosystem. Hooded seals (*Cyostophora cristata*) are one of the largest of the northern phocids and are abundant in the north Atlantic and Arctic seas, but very little quantitative data is available on their feeding behaviour and dietary preferences. The main objective of this study was to determine the diet of hooded seals in Newfoundland waters.

Otoliths of six common prey species, determined from a previous study on diet of hooded seals, were used to determine fish length / weight - otolith length / height regressions. For all species except Greenland halibut, the strongest correlations between otolith size and fish length / weight were established using maximum otolith length. For Greenland halibut, maximum otolith height gave a better correlation with fish length and weight. Least squares linear equations were used to derive fish length for Arctic cod, Atlantic herring and capelin, while second order polynomial models were used for Greenland halibut, redfish spp., and Atlantic cod. Fish weight estimates were derived using power (log - log) models for all six fish species.

Stomach contents of 67 hooded seals collected from inshore and offshore waters off Newfoundland were examined to determine the types of prey eaten by hooded seals. The majority of stomachs (73%) came from the

nearshore region along the northeast coast of Newfoundland and were taken in April. Over half of the samples collected were female (64.2%).

Fourteen prey groups were identified in stomachs (10 fish, 4 invertebrate). The relative importance of prey, expressed as the percent total wet weight of prey recovered, indicated that Greenland halibut (*Reinhardtius hippoglossoides*) was the most important species, followed in order of importance by redfish (*Sebastes spp.*), Arctic cod (*Boreogadus saida*), Atlantic herring (*Clupea harengus*), squid (*Gonatus spp.*), Atlantic cod (*Gadus morhua*) and capelin (*Mallotus villosus*).

Using otoliths from a previous study and from this study, lengths and weights of fish were estimated from a total of 72 stomachs. Hooded seals fed mainly on fish of 25 - 35 cm length for the larger species, and 15 - 25 cm for the smaller ones. Fish consumed by seals caught incidentally from offshore trawlers were larger than those taken elsewhere. The estimated lengths, and proportions (% weight) of fish found per stomach did not differ significantly between male and female hooded seals.

The proportions (percent weight) of redfish and Atlantic herring consumed by hooded seals were significantly larger in the summer months, whereas a higher proportion of Arctic cod was consumed in the winter months. No seasonal differences were found in actual lengths of fish eaten.

Total energetic values for fish eaten were calculated from estimated wet weights and energy densitites (kJ/g). Greenland halibut, Atlantic herring and Atlantic cod had the highest average energetic values (kJ), followed by redfish, Arctic cod, capelin and squid. Relative contributions of prey, expressed as the percent total energy of prey recovered, showed that Greenland halibut contributed approximately 53% of the total energy consumed, followed by redfish, Atlantic herring, Arctic cod, squid, Atlantic cod and capelin. These proportions corresponded with those obtained from percent total wet weight of prey recovered.

The relative abundance of the fish species has a strong influence on the composition of the food in the diet of seals. Hooded seals spend some time in areas that are exploited by commercial fisheries, and consume commercial fish species of commercial size. However, in order to evaluate the impact of local predation on individual fish stocks, more information on behavioural and physiological characteristics of seals and fish are needed.

Acknowledgements

I would first like to extend thanks to my supervisor, Dr. Garry Stenson, for his support, guidance (and *thorough* editing expertise!), and to Dr. Jon Lien for giving me the opportunity to work with marine mammals. I would also like to thank the members of my committee, Dr. Bill Montevecchi, Dr. Deane Renouf, and Dr. Peter Shelton for their insightful reviews of the manuscript.

At the Department of Fisheries and Oceans, thank you to D. Wakeham, W. Penney, D. McKinnon and to the sealers and fishermen for kindly providing me with my seal samples. I am also greatful to D. McKinnon for showing me the ropes and for his help throughout this study, and to W. Penney for aging teeth for me. Great appreciation is extended to G. Somerton, B. Nakashima, C. Bishop, J. Wheeler, D. Power, B. Brodie, E. Dawe, and all the technicians in the groundfish department for their expertise, and for supplying me with fish samples. Thanks to P. Pepin for use of his image analyzer, and to Dr. M. Clarke for identifying my squid samples. Special thanks to J. Lawson and D. Chabot for helpful advice and for showing me what a Mac could do!

I could never have gotten this far without the support of my Zoo - mates Rosie, Lesley, Janet and Kristina - thanks for the laughs, great zucchini bread, juggling lessons and knowing when to take a coffee break! For support from afar, Mum, Dad and Op - thanks! Finally, gotta thank the Hawk - for pushing me, for the optimism, and for everything else!

Financial support was provided by a Memorial University of Newfoundland Fellowship, and by the Department of Fisheries and Oceans Northern Cod Science Program (AFAP).

Table of Contents

List of Tables

List of Figures

CHAPTER 1:
General Introduction

1.1. Biology of hooded seals

The hooded seal (*Cystophora cristata*) is one of the largest of the northern phocids. Males reach a length of about 2.6 m and weigh between 300 - 450 kg; the females are slightly smaller at 2.2 m and 150 - 300 kg (Kovacs & Lavigne, 1986). Hooded seals grow rapidly, most females reaching sexual maturity and whelping by around six years. Males reach sexual maturity between six and ten years (Reeves & Ling, 1981). The maximum age in both sexes is approximately 35 years (Øritsland & Benjaminsen, 1975).

Hooded seals are difficult animals to study, due primarily to the environment in which they live. As pelagic deep - diving animals, they tend to remain offshore and haul out on the heavy drift ice of the north Atlantic and Arctic seas (King, 1983). They rarely frequent land or shore - fast ice and are thus isolated from much human interaction. It is believed that hooded seals are less gregarious than most other northern seals, dispersing widely while feeding, and remaining solitary or in small groups except during the breeding period when they congregate for two to four weeks (Øritsland, 1990).

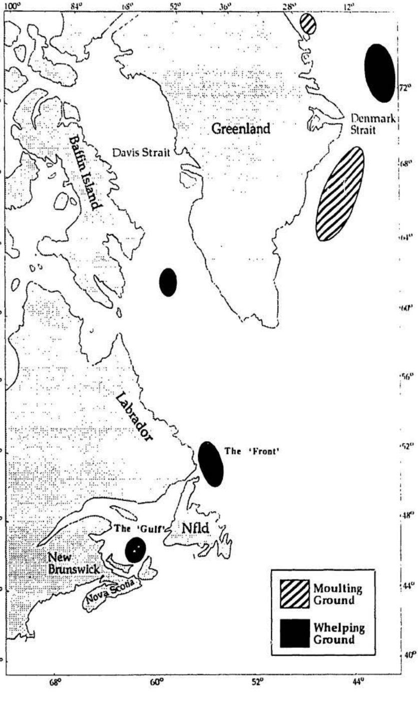
1.1.1. Distribution

Based on whelping concentrations, three populations are recognized in the north Atlantic (Figure 1.1.). The largest group whelps off the coast of southern Labrador and / or northern Newfoundland (the "Front"). A smaller group of hooded seals found in the Gulf of St. Lawrence (the "Gulf") is usually included with this population. A second major concentration of whelping hooded seals occurs in the Davis Strait, between Greenland and Canada (64° N). A third group breeds in the eastern Atlantic off Jan Mayen (71° N, 8° W) east of Greenland (Sergeant, 1974; Bowen, Bonness, & Oftedal, 1987). Although hooded seals breed in these three separate areas, stock delineations are not clear. Animals from the Davis Strait and Newfoundland / Gulf breeding areas mix at the moulting grounds, and the similar timing of whelping among all three groups suggests that the populations may not be independent (Sergeant, 1974).

The northwest Atlantic populations begin their migration to the traditional moulting area in the Denmark Strait (66° - 68° N) following breeding in late March or early April. However, recent information suggests that some hooded seals may remain in Canadian waters for a period of months before heading up to the Denmark Strait to moult (G. Stenson, Department of Fisheries and Oceans, St. John's, pers. comm.).

Fig. 1.1.

Map of the northwest Atlantic showing the whelping and moulting grounds of hooded seals (*Cystophora cristata*) surrounding Newfoundland and Greenland.



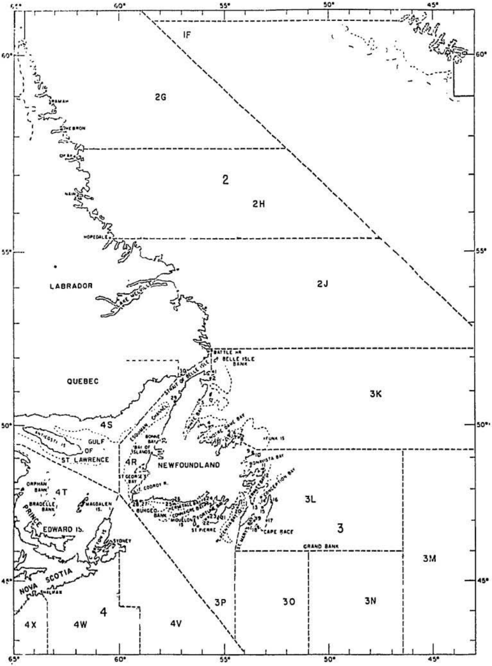
Greenland
Davis Strait
Denmark Strait
Baffin Island
Labrador
The 'Front'
The 'Gulf'
Nfld
New Brunswick
Nova Scotia
Moulting Ground
Whelping Ground

Moulting occurs in late June or July (Kapel, 1982). On completion of moulting near the end of July, the populations disperse, presumably along the coast of Greenland. Autumn and winter distribution of hooded seals in Canadian waters is poorly known, but timing of migration into Canadian waters is indicated by repeated sightings on the Grand Banks off Newfoundland in mid - winter (Rasmussen, 1960; W. Penney, Department of Fisheries and Oceans, St. John's, pers. comm.) and incidental entrapments in fishing gear off Labrador and northeastern Newfoundland in January and February (Lien, Stenson & Ni, 1988).

As a result of these patterns of distribution and the present patterns of hunting, hooded seals are most often available for sampling in Canadian waters between February and May from the deep water channels in the nearshore waters along the northeast coast of Newfoundland (Northwest Atlantic Fisheries Organization, NAFO, area 2J3KL, Fig. 1.2.), and, to a lesser extent, in waters along the south coast of Newfoundland.

Fig. 1.2.

Map of the Northwest Atlantic surrounding Newfoundland and Labrador showing divisions of areas established by the Northwest Atlantic Fisheries Organization (NAFO).


1F
2G
2
2H
2J
3K
3L
3
3M
3N
3O
3P
4
4R
4S
4T
4V
4W
4X
LABRADOR
QUEBEC
NEWFOUNDLAND
GULF
OF
ST LAWRENCE
ANTICOSTI IS.
PRINCE EDWARD IS.
NOVA SCOTIA
MAGDALEN IS.
ORPHAN BANK
BRADELLE BANK
SYDNEY
HALIFAX
HOPEDALE
NAIN
HEBRON
RAMAH
LAKE MELVILLE
BATTLE HR
BELLE ISLE BANK
STRAIT OF BELLE ISLE
ESQUIMAN CHANNEL
BONNE BAY
BAY OF ISLANDS
ST GEORGE'S BAY
WHITE BAY
NOTRE DAME BAY
FUNK IS
BONAVISTA BAY
TRINITY BAY
CONCEPTION BAY
CAPE RACE
GRAND BANK
ST PIERRE
MIQUELON
BURGEO BANK
HERMITAGE BAY
FORTUNE BAY
PLACENTIA BAY
ST MARY'S BAY
65°
60°
55°
50°
45°

1.1.2. Populations

In 1984, pup production in the whelping patches at the Front and in the Davis Strait were estimated by aerial surveys (Bowen, Myers & Hay, 1987). In the Davis Strait, pup production was estimated to be 18,600 (95% confidence interval of 14,000 - 23,000) whereas at the Front, an estimated production of 61,400 (95% C.I. 43,700 - 89,000). Roff & Bowen (1983) estimated a four to one ratio of harp seal (*Phoca groenlandica*) pups to seals aged 1 and over (1+) in order to estimate total harp seal populations. Assuming this same ratio, the total population of hooded seals at the Front would be approximately 300,000 in 1984. Estimates of pup production in the Gulf are approximately 2,000 (Hammill, Stenson & Myers, 1992).

The proportion of the total hooded seal population actually present in Canadian waters at any given time is unknown. Although hooded seals undergo regular schedules of migration and dispersal, their specific movements may vary with changes in climate and ice cover (Reeves & Ling, 1981). Immature hooded seals are not often seen in southern Canadian waters, and it is possible they remain in Greenland or the Arctic throughout the year (Kapel, 1980).

1.2. Feeding of hooded seals

A better understanding of the ecology of hooded seals can be gained through knowledge of feed..ig. For example, feeding studies can elucidate information on behaviour: whether the seals are specialist or generalist consumers, or whether gender, age or seasonal differences in feeding exists. Information on feeding is also important in the assessment of the potential interactions between hooded seals and commercial fisheries.

To understand feeding ecology several factors must be evaluated. Primarily, diet composition must be determined: information gained including type of prey consumed, size (weight, length and volumes) of various prey in the meals, and average meal size (Bonner, 1982; Beddington, Beverton & Lavigne, 1985; Bowen, 1985; Harwood & Croxall, 1988). Relative caloric contributions of various prey in the meals consumed at different locations must also be established. Energy content of the prey, as well as diet, can also vary seasonally and geographically. If such information is used in conjunction with measurements of the daily energy requirements, the quantities of different species that are consumed at different times of year throughout the seals' range can be estimated (Harwood & Croxall, 1988).

Qualitative and quantitative information on the food of seals, by examination of stomach contents, has been collected for species such as harbour seals (*Phoca vitulina*) and stellar sea lions (*Eumetopias jubatus*) in the Gulf of Alaska (Pitcher, 1981), ribbon seals (*Phoca fasciata*) in the

Bering Sea (Frost & Lowry, 1980), harp seals in the northeast Atlantic (Lydersen, Angantyr, Wiig & Øritsland, 1991), and coastal waters of west Greenland (Kapel & Angantyr, 1989), and grey seals (*Halichoerus grypus*) in eastern Canada (Benoit & Bowen, 1990) have been described in this manner. However, very little had been documented of the feeding ecology of hooded seals.

1.3. Objectives of study

The main objective of this study was to determine the diet of hooded seals in the waters off the coast of Newfoundland. This was accomplished in three phases.

In the first stage, common fish prey species of hooded seals found in waters off the coast of Newfoundland (Stenson, Ni, Ross & McKinnon, 1991) were used to derive estimates of fish length and fish weight from the measured size of otoliths into fish length / weight - otolith length / height regressions (Chapter 2). These relationships were fit with least squares regressions, using linear, polynomial and power (log - log) models. Differences in length and height between left and right otoliths of each species, as well as spatial and temporal differences in size within each fish species were also examined.

In the second stage, stomach contents of hooded seals collected from the waters off Newfoundland and Labrador were examined in order to determine the types of prey eaten (Chapter 3). The average sizes (length and weight) of prey eaten were determined from the regression equations established in the previous section. Relative importance of food items in the diet were expressed through reconstructing weights of prey species found in the stomach contents. These results were compared with frequency of occurrence results obtained from the same stomachs examined. Gender and seasonal differences in prey eaten were also examined.

In the final section, energetic importance of the six common prey species which comprised the hooded seal diet were examined (Chapter 4). Caloric values were determined by proximal composition analysis or from published values. Both winter and summer caloric values of fish were collected when possible. This information was used in conjunction with estimated wet weight values obtained from the previous section in order to determine the total energetic values for fish eaten. Seasonal and gender differences in energetic values of fish were examined. The relative importance of prey expressed as the percent total gross energy of prey recovered was determined, and compared with other methods used previously.

CHAPTER 2:
Otolith size — fish size relationships for major prey species

2.1. Introduction

Sagittal otoliths of teleost fish found in the stomachs of seals are often used in the examination and interpretation of qualitative and quantitative aspects of food habits of seals and whales (Fitch & Brownell, 1968; Frost & Lowry, 1980; Finley & Gibb, 1984). They are resistant to digestion as they are the most dense structure in fish, and situated well inside the brain cavity, otoliths are well protected from digestive juices of the stomach (Treacy & Crawford, 1981). Furthermore, otoliths possess a series of morphological features which are species - specific.

Since as early as 1903, researchers have used the presence of fish otoliths in stomachs of marine mammals to identify prey species (Fitch & Brownell, 1968). More recently, it has been demonstrated that otoliths can also be used to estimate the original lengths, weights, total numbers and ages of fish ingested (Frost & Lowry, 1981; North, Croxall & Doidge, 1983; Jobling & Breiby, 1986; Finley, Bradstreet & Miller, 1990). Fish size (length and weight) is usually derived through growth back - calculation procedures based on the ratio between fish length and some measure of otolith size (Carlander, 1981). The regression model predicts fish length from the size of the otolith using a fish length / otolith length regression equation from samples of the population. This procedure assumes no deviation of individual fish and otolith measurements from the overall regression (Campana, 1990). Recent studies have demonstrated that within a species, the otolith - fish length relationship can vary systematically with the growth rate of the fish (Reznick, Lindbeck & Bryga, 1989; Secor & Dean, 1989). For example, otoliths from slow - growing adult fish are consistently larger and heavier than those of fast - growing fish of the same size. However, since the main purpose of these correlations in marine mammal feeding studies is to attain mean back - calculated lengths and weights rather than individual values, this bias is unimportant.

A number of papers have been published in which otoliths have been described, and their measurements used to establish regression equations to determine original fish lengths and weights of prey consumed by seals. For example, published keys to otoliths exist for adult fishes in the Gulf of Alaska, Bering, and Beaufort Seas (Morrow, 1979), the Southern Ocean (Hecht, 1987), and the northeast Atlantic (Härkönen, 1986). Relationships of otolith length to fish length and weight have also been described for selective fish species of the Bering, Chukchi, and Beaufort Seas (Frost, 1980; Frost & Lowry, 1980; 1981), bays in Oregon (Brown & Mate, 1983) and California (Antonelis, Fiscus & DeLong, 1984), and off southern New England waters (Selzer, Early, Fiorelli, Payne & Prescott, 1986). However, no published data exist which estimate fish lengths or weights from otolith measurements for fishes in the northwest Atlantic.

Some studies have shown that otolith size / fish size relationships may vary both between stocks and between geographical regions (Messieh, 1972). Thus use of equations derived from one area may not be appropriate for another. Moreover, in many of the previous studies, information on sample size, sex, season, and reproductive status of the samples used were not presented. Information on whether or not both left and right otoliths were used in the analysis was often missing.

The purpose of this chapter was to formulate equations to predict body length and wet weight of fish at time of ingestion for important prey species of hooded seals found in waters off the coast of Newfoundland. The six common prey species used were determined from a previous diet study of hooded seals (Stenson et al., 1991). Regression equations were constructed by correlating otolith length and / or height with fish length and weight for undigested fish. Differences in length and height between left and right otoliths of each species were examined, as well as spatial and temporal differences in the otolith / fish size relationship within each fish species.

2.2. Materials and Methods

Common prey species of hooded seals, Greenland halibut (*Reinhardtius hippogloissoides*), redfish (*Sebastes spp* .), Atlantic herring (*Clupea harengus*), Arctic cod (*Boreogadus saida*), Atlantic cod (*Gadus morhua*), and capelin (*Mallotus villosus*) were collected off the east coast of Newfoundland by the Department of Fisheries and Oceans personnel during routine research cruises. Attempts were made to a) collect samples from areas and seasons corresponding to those from which hooded seal stomach samples were also taken, and b) collect a large size (body length) range for each fish species examined which included the size range of the prey found in the hooded seals stomachs examined. Size range of ingested fish was estimated from whole prey found in preliminary examination of stomachs.

A minimum of 30 to a maximum of 71 samples from each fish species were taken. In order to get a large enough sample size, and / or range in lengths for a particular species, in some instances, it was necessary to examine fish which had been collected from either two different areas, years and/or seasons (Table 2.1.).

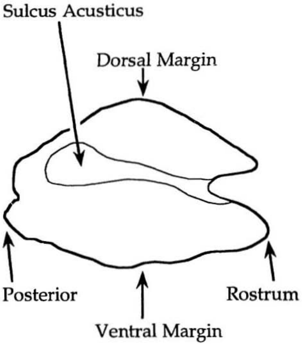
Specimens were frozen upon capture and stored at - 20° C. Samples were thawed prior to measurement. No correction was made for possible reductions in length and / or weight due to freezing. Total length of fish ($\pm$ 0.5 mm) was measured for Greenland halibut and capelin, while fork length was taken for Arctic cod, Atlantic cod, redfish spp. and Atlantic herring. Wet weight ($\pm$ 0.1 g) was also determined for each fish. Both left and right sagittal otoliths were extracted from each of these fish and stored dry until measured. Maximum length (anterior - posterior) in the sagittal plane and height (dorsal - ventral) (Fig. 2.1.), measured to the nearest 0.01 mm, was recorded for each otolith using an image analyzer.

Table 2.1. Location and date of collection of common prey species of hooded seals (*Cystophora cristata*) collected in waters off Newfoundland.

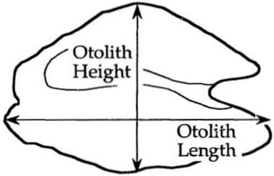
Fish Species	NAFO Area (Fig. 1.2.)	Month	Year	Number of Samples
Arctic cod (*Boreogadus saida*)	3K	November	1991	30
Atlantic cod (*Gadus morhua*)	3K	December	1991	50
Capelin (*Mallotus villosus*)	3K	July	1990	31
	3L	July	1991	40
Greenland halibut (*Reinhardtius hippoglossoides*)	3Ps	January	1991	24
	3N	November	1991	35
Atlantic herring (*Clupea harengus*)	3K	July	1990	25
	3K	July	1991	37
Redfish (*Sebastes spp*)	3N	August	1991	25
	3L	November	1991	25

Fig. 2.1.

Diagram of the inner face of a generic left sagittal otolith showing general physical characteristics of the otolith, and the maximum length and the maximum width measurements taken. In each case, length was measured first, and height taken at a perpendicular angle to the length.



Physical Features



Measurements

Differences between measurements of left and right otoliths within each species were compared using two-tailed paired t - tests. Fish length (FL) and otolith length (OL) or height (OH) comparisons were fit with least squares regressions. A linear or polynominal model was used to describe the relationship, depending upon the variance accounted for. Residuals plotted against otolith length or height were visually examined. If a pattern was found, the model was rejected.

The relationships between otolith length or height and fish weight (FW) were investigated by fitting linear least squares regressions to the log - transformed data (North et al., 1983). The power curve was determined by correlating the log of the otolith length or height with the log of fish weight. Models were rejected when patterns were found in the residuals.

Spatial differences in size correlations were examined for the Greenland halibut and redfish samples which contained fish from different areas within one year. Temporal variations of the data were examined for both Atlantic herring and capelin samples which contained fish from the same area and month, but from two years (1990 and 1991; Table 2.1.).

Regressions were developed for each subset within each of these fish species. Comparisons of slopes and intercepts of the two lines were compared using analysis of covariance. To validate the equality of the slopes, an interaction effect was introduced into the equation. The test for homogeneity of regression looked for the presence of an interaction between otolith size and either area, season, or year. If the F test failed to show a significant interaction at the 0.05 level, the slopes were considered similar (parallel) and the significance of the vertical difference between the two lines (the difference in covariance adjusted means) was tested (Hays, 1988). Generally, pooling data from different populations lowers the precision of the correlation. However, due to small sample sizes, uncertainty of existing fish stocks, and the fact that fish samples were not available from all areas, in every season, for all years needed, the samples from different years, and areas were combined in the final regression analysis.

2.3. Results

2.3.1. Relationship between left and right otoliths

Left and right otoliths were available for 28 Arctic cod, 26 Atlantic cod, 69 capelin, 52 Greenland halibut, 43 herring, and 24 redfish spp. Paired t - tests showed no significant differences between length or height measurements for left and right otoliths for each of the six fish species examined (Table 2.2.). Therefore, the measurements of the left and right otoliths were averaged for each fish, and this average was used in the subsequent regression analyses.

Table 2.2. Results of t-test analysis on the relationship between lengths (OL, in mm) and heights (OH, in mm) of right and left otoliths, from six important prey species of hooded seals (*Cystophora cristata*) in waters off Newfoundland.

Species	df	t Otolith Length	p=	t Otolith Height	p=
Arctic cod (*Boreogadus saida*)	27	0.18	0.86	-1.53	0.14
Atlantic cod (*Gadus morhua*)	25	-0.33	0.74	-1.34	0.19
Capelin (*Mallotus villosus*)	68	-0.04	0.97	-0.39	0.70
Greenland halibut (*Reinhardtius hippoglossoides*)	51	0.58	0.56	0.57	0.57
Atlantic herring (*Clupea harengus*)	42	1.45	0.15	-1.29	0.20
Redfish (*Sebastes spp*)	23	0.13	0.90	-0.57	0.57

2.3.2. Relationship between otolith size and fish size

For all fish species, with the exception of Greenland halibut, maximum otolith length provided the better correlation with fish length than did otolith height. For Greenland halibut, maximum otolith height was more highly correlated with fish length (Table 2.3.).

Both linear and quadratic regression models were applied to the data in order to determine the best relationships between otolith size and fish length for each of the six species. For Arctic cod, capelin, and herring, linear regressions provided the best predictive equations of fish length from otolith size (Figs. 2.2. and 2.3.). In each of these cases, the regression coefficients (r^2) were slightly higher using the linear model, although both regressions were highly significant (Table 2.3.). Visual examination of residuals plotted against otolith length for each of these species showed no particular pattern (see p. 635 of Hays, 1988 for a description of patterning in residuals) indicating that the assumption of homogeneous variances was not violated (Fig. 2.4. and 2.5.).

Table 2.3. Linear and quadratic regression equations of fish length (FL, in cm) on otolith length (OL, in mm) and otolith height (OH, in mm) for prey species of hooded seals (*Cystophora cristata*).

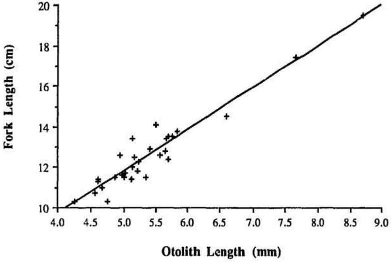
Species	Equation	p	r^2	F	n
Arctic cod	$FL = 2.05(OL) + 1.53$ *	0.0001	0.92	310.21	30
(*B. saida*)	$FL = 0.16(OL)^2 + 7.84$	0.0001	0.91	279.04	30
	$FL = 7.91(OH) - 6.19$	0.0001	0.86	174.86	30
Capelin	$FL = 5.50(OL) - 0.08$ *	0.0001	0.79	260.09	71
(*M. villosus*)	$FL = 0.90(OL)^2 + 8.21$	0.0001	0.77	231.86	71
	$FL = 7.08(OH) + 2.13$	0.0001	0.51	69.98	71
Atlantic cod	$FL = 4.85(OL) - 25.62$	0.0001	0.90	435.43	50
(*G. morhua*)	$FL = 0.17(OL)^2 + 8.47$ *	0.0001	0.92	540.78	50
	$FL = 8.85(OH) - 14.72$	0.0001	0.89	406.67	50
Greenland halibut	$FL = 5.64(OL) - 4.91$	0.0001	0.95	1172.85	59
(*R. hippoglossoides*)	$FL = 0.66(OH)^2 + 12.93$	0.0001	0.96	1567.63	59
	$FL = 7.62(OH) - 7.15$ *	0.0001	0.96	1567.63	59
Atlantic herring	$FL = 5.55(OL) + 0.04$ *	0.0001	0.97	1723.41	62
(*C. harengus*)	$FL = 0.78(OL)^2 + 8.17$	0.0001	0.96	1288.39	62
	$FL = 13.61(OH) - 4.13$	0.0001	0.94	1010.24	62
Redfish	$FL = 2.47(OL) - 1.68$	0.0001	0.95	957.92	50
(*Sebastes spp.*)	$FL = 0.12(OL)^2 + 9.82$ *	0.0001	0.96	1163.22	50
	$FL = 4.41(OH) - 5.16$	0.0001	0.93	598.72	50

* Indicates the equation used to estimate original fish lengths

Fig. 2.2.

Relationship between a) otolith length (OL) and fork length (FL) of Arctic cod (*Boreogadus saida*) ($r^2 = 0.92$, $p = 0.0001$, $n = 30$), and b) otolith length (OL) and total length (FL) of capelin (*Mallotus villosus*) ($r^2 = 0.79$, $p = 0.0001$, $n = 71$).

a) FL = 1.5 + 2.0 (OL) R^2 = 0.92



b) FL = - 0.08 + 5.50 (OL) R^2 = 0.79

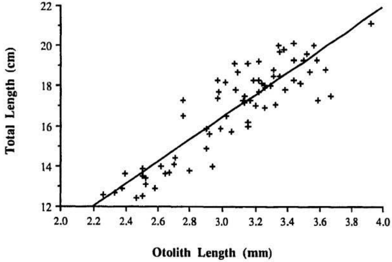


Fig. 2.3.

Relationship between otolith length (OL) and fork length (FL) of Atlantic herring (*Clupea harengus*) ($r^2 = 0.97$, $p = 0.0001$, $n = 62$).

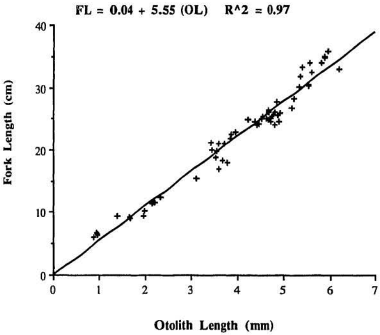
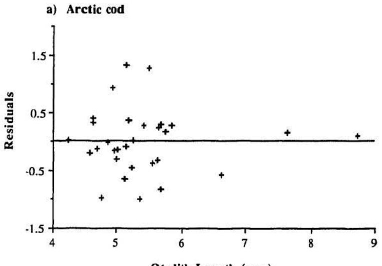

FL = 0.04 + 5.55 (OL) R^2 = 0.97
Fork Length (cm)
Otolith Length (mm)
0
10
20
30
40
0
1
2
3
4
5
6
7

Fig. 2.4.

Plots of residuals against otolith length (OL) of a) Arctic cod (*Boreogadus saida*), and b) capelin (*Mallotus villosus*) for the linear regressions shown in Fig 2.2.


a) Arctic cod
Residuals
1.5
0.5
-0.5
-1.5
4
5
6
7
8
9
Otolith Length (mm)

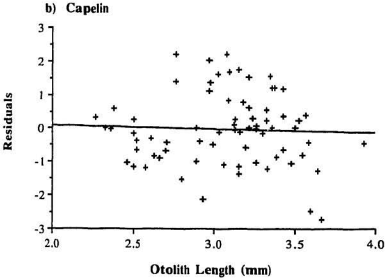
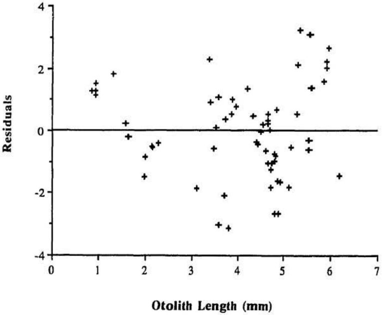

b) Capelin
Residuals
3
2
1
0
-1
-2
-3
2.0
2.5
3.0
3.5
4.0
Otolith Length (mm)

Fig. 2.5.

Plot of residuals against otolith length (OL) of Atlantic herring (*Clupea harengus*) for the linear regression shown in Fig 2.3.

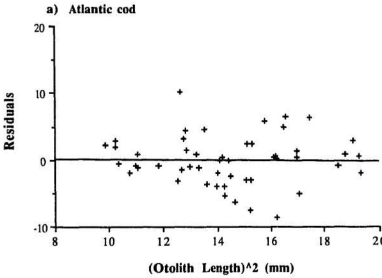

4
2
0
-2
-4
Residuals
0
1
2
3
4
5
6
7
Otolith Length (mm)

Residuals plotted against otolith length for Atlantic cod and redfish samples showed some patterning in the linear regression; all residual points fell above the zero line for both smaller and larger sized otoliths, whereas residuals for mid - sized otoliths fell equally above and below the line. This suggested that there may have been more to the relationship between otolith length and fork length than could be explained by the simple linear model, and that the assumption of homogeneity of variance had been violated. Residuals for the quadratic relationships for Atlantic cod and redfish showed no apparent abnormalities and appeared to obey all assumptions (Fig. 2.6.). Second order polynomial regressions for both species are given in Table 2.3. and are shown in Fig. 2.7.

Although the linear regression between otolith height and fork length for Greenland halibut provided a good fit to the data, visual examination of the residuals showed a slight pattern. A second order polynomial was therefore applied to the data (Fig. 2.8.). Residuals plotted against the square of otolith height showed no particular pattern (Fig. 2.9.).

Fig. 2.6.

Plots of residuals against otolith length (OL) of a) Atlantic cod (*Gadus mo*r *ua*), and of b) redfish spp. (*Sebastes spp*) for the quadratic regression.


a) Atlantic cod
20
10
0
-10
Residuals
8
10
12
14
16
18
20
(Otolith Length)^2 (mm)

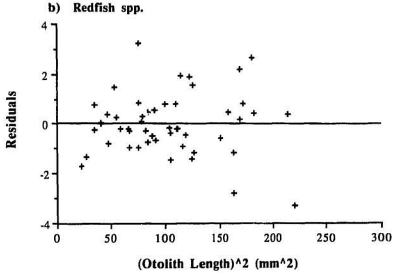
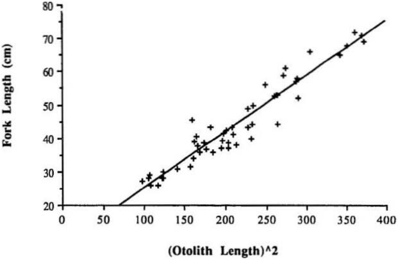

b) Redfish spp.
4
2
0
-2
-4
Residuals
0
50
100
150
200
250
300
(Otolith Length)^2 (mm^2)

Fig. 2.7.

Relationships between otolith length (OL) and fork length (FL) of a) Atlantic cod (*Gadus morhua*) ($r^2 = 0.92$, $p = 0.0001$, $n = 50$), and of b) redfish spp. (*Sebastes spp.*) ($r^2 = 0.96$, $p = 0.0001$, $n = 50$), using second order polynomial models.

a) FL = 8.47 + 0.17 (OL)^2 R^2 = 0.92



b) FL = 9.82 + 0.12 (OL)^2 R^2 = 0.96

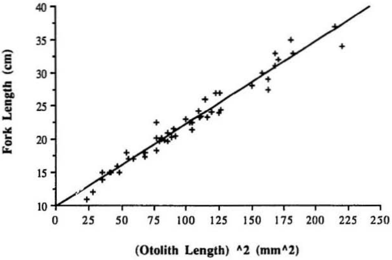


Fig. 2.8.

Relationship between otolith height (OH) and total length (FL) of Greenland halibut (*Reinhardtius hippoglossoides*) using a second order polynomial model ($r^2 = 0.96$, $p = 0.0001$, $n = 59$).

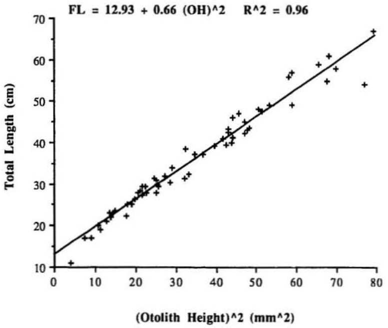
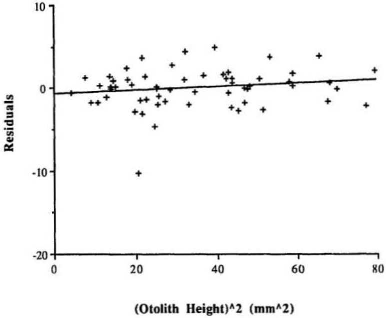

FL = 12.93 + 0.66 (OH)^2 R^2 = 0.96
Total Length (cm)
70
60
50
40
30
20
10
0
10
20
30
40
50
60
70
80
(Otolith Height)^2 (mm^2)

Fig. 2.9.

Plot of residuals against otolith height (OH) of Greenland halibut (*Reinhardtius hippoglossoides*) for the quadratic regression.


10
0
-10
-20
Residuals
0
20
40
60
80
(Otolith Height)^2 (mm^2)

For Arctic cod, capelin, Atlantic cod, and redfish spp., otolith length provided the best measurement to determine fish weight (Table 2.4.). Both otolith length and height provided equally high correlations for Atlantic herring (based on r^2 values). However, since otolith length was used in the fish length equation and it is the more commonly used measurement, this parameter was used for the reconstruction. Otolith height provided a better fit to the line than otolith length for Greenland halibut, thus, this parameter was used in the final reconstructions (Figs 2.10. to 2.13.).

2.3.3. Spatial and temporal differences between fish

For the relationship between otolith length and fish length, significant differences were found in slopes of capelin and Atlantic nerring samples between 1990 - 1991 ($p < 0.05$ for each; Table 2.5.). Redfish samples, containing subsets from two different areas, also showed significantly different slopes ($p < 0.05$). Significant differences in slopes for these fish implies that the regressions are not homogeneous, and that the linear or quadratic relationship between otolith size and fish length is dependent on year in the case of capelin and Atlantic herring, and area in the case of redfish spp. The slopes of the otolith height - fish length regression lines for Greenland halibut did not differ between the south shore and offshore groups ($p > 0.05$), and analysis of covariance using otolith height to predict fish length with area as the covariate also indicated no significant differences in the intercepts ($p > 0.05$; Table 2.5.). Plots of otolith size - fish length for

Table 2.4. Regression equations of fish weight (FW, in g) on otolith length (OL, in mm) and otolith height (OH, in mm) using log-transformed data for common prey species of hooded seals (*Cystophora cristata*).

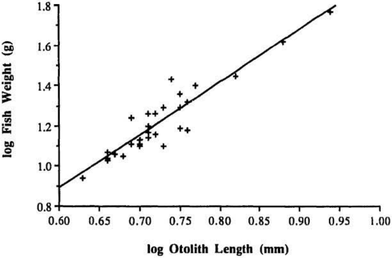
Species	Equation	p	r^2	F	n
Arctic cod	$FW = 0.20(OL)^{2.64}$ *	0.0001	0.88	205.53	30
(*B. saida*)	$FW = 0.43(OH)^{4.26}$	0.0001	0.87	186.40	30
Capelin	$FW = 0.93(OL)^{3.05}$ *	0.0001	0.79	262.58	71
(*M. villosus*)	$FW = 3.47(OH)^{2.90}$	0.0001	0.57	91.68	71
Atlantic cod	$FW = 0.0025(OL)^{4.72}$ *	0.0001	0.94	680.62	50
(*G. morhua*)	$FW = 0.37(OH)^{4.02}$	0.0001	0.92	537.68	50
Greenland halibut	$FW = 0.26(OL)^{3.64}$	0.0001	0.96	1447.36	59
(*R. hippoglossoides*)	$FW = 0.41(OH)^{3.89}$ *	0.0001	0.98	2271.91	59
Atlantic herring	$FW = 1.48(OL)^{3.08}$ *	0.0001	0.98	3156.17	62
(*C. harengus*)	$FW = 6.02(OH)^{4.22}$	0.0001	0.98	2605.35	62
Redfish	$FW = 0.13(OL)^{3.12}$ *	0.0001	0.95	882.25	50
(*Sebastes spp*)	$FW = 0.21(OH)^{3.63}$	0.0001	0.94	763.14	50

* Indicates the equation used to estimate original fish weights

Fig. 2.10.

Relationships between otolith length (OL) and fish weight (FW) of a) Arctic cod (*Boreogadus saida*) ($r^2 = 0.88$, $p = 0.0001$, $n = 30$), and of b) capelin (*Mallotus villosus*) ($r^2 = 0.79$, $p = 0.0001$, $n = 71$), using log - transformed data .

a) FW = 0.20 (OL)^2.64 R^2 = 0.88



b) FW = 0.93 (OL)^3.05 R^2 = 0.79

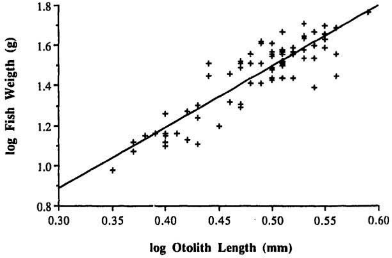
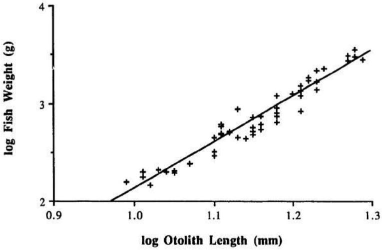


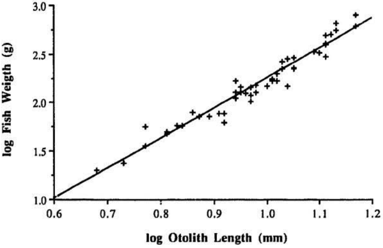
Fig. 2.11.

Relationships between otolith length (OL) and fish weight (FW) of a) Atlantic cod (*Gadus morhua*) ($r^2 = 0.94$, $p = 0.0001$, $n = 50$), and of b) redfish (*Sebastes spp.*) ($r^2 = 0.95$, $p = 0.0001$, $n = 50$), using log - transformed data.

a) FW = 0.0025 (OL)^4.72 R^2 = 0.94



b) FW = 0.13 (OL)^3.12 R^2 = 0.95



<u>Fig. 2.12.</u>

Relationship between otolith length (OL) and fish weight (FW) of Atlantic herring (*Clupea harengus*) using log - transformed data ($r^2 = 0.98$, $p = 0.0001$, $n = 62$).

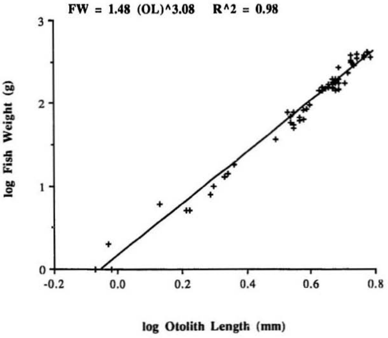

FW = 1.48 (OL)^3.08 R^2 = 0.98
log Fish Weight (g)
3
2
1
0
-0.2
0.0
0.2
0.4
0.6
0.8
log Otolith Length (mm)

Fig. 2.13.

Relationship between otolith height (OH) and fish weight (FW) of Greenland halibut (*Reinhardtius hippoglossoides*) using log - transformed data (r^2 = 0.98, p = 0.0001, n = 59).

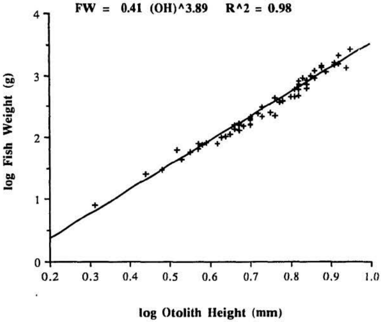

FW = 0.41 (OH)^3.89 R^2 = 0.98
log Fish Weight (g)
0
1
2
3
4
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
log Otolith Height (mm)

Table 2.5. Relationship between linear regression lines for four fish species which contained subsets of fish from different years, areas and/or seasons.

	Difference in Slope (p=)	Difference in Intercept (p=)	df
Otolith Length / Fish Length			
Capelin (*M. villosus*)	0.0034	—	67
Greenland halibut (*R. hippoglossoides*)	0.5071	0.6492	55
Atlantic herring (*C. harengus*)	0.0033	—	58
Redfish (*Sebastes spp*)	0.0129	—	46
Otolith Length / Fish Weight			
Capelin (*M. villosus*)	0.0043	—	67
Greenland halibut (*R. hippoglossoides*)	0.2836	0.0001	55
Atlantic herring (*C. harengus*)	0.1726	0.0002	58
Redfish (*Sebastes spp.*)	0.1686	0.0001	46

subsets of capelin, herring, redfish and Greenland halibut are shown in Figures 2.14. and 2.15.

For the relationship between otolith length and fish weight, significant differences in slopes for 1990 and 1991 capelin were found ($p < 0.05$; Table 2.5.). This implies that the relationship between otolith length and fish weight is dependent on the year that the samples were taken. Analyses of covariance showed that no significant differences ($p > 0.05$) occurred between slopes for subsets within Greenland halibut, Atlantic herring or within subsets of redfish spp. However, intercepts were significantly different when area or year were taken out as covariates for all of these species ($p < 0.005$). Figures 2.16. - 2.17. show the otolith size / fish weight regression lines for each subset within each of the fish species examined.

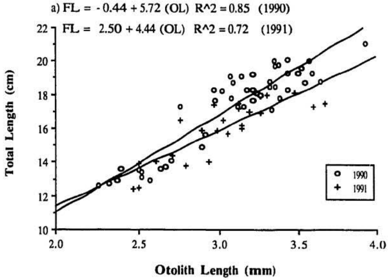
2.4. Discussion

2.4.1. Relationship between left and right otoliths

Since no differences were found between measurements from left and right otoliths, measurements of the left and right otoliths were averaged for each fish and plotted against fish length. In other studies in which otoliths were used to establish regression equations, measurements from both left and right otoliths from each fish were used separately to plot the best correlation (Frost & Lowry, 1981; G. Lilly, Department of Fisheries and Oceans, St.

Fig. 2.14.

Relationships between a) otolith length and total length for capelin (*Mallotus villosus*) ($p_{slope} = 0.0034$, $df = 67$), and between b) otolith length and fork length for Atlantic herring (*Clupea harengus*) ($p_{slope} = 0.0033$, $df = 58$), caught in 1990 and 1991.


a) FL = - 0.44 + 5.72 (OL) R^2 = 0.85 (1990)
FL = 2.50 + 4.44 (OL) R^2 = 0.72 (1991)
Total Length (cm)
Otolith Length (mm)
1990
1991
22
20
18
16
14
12
10
2.0
2.5
3.0
3.5
4.0

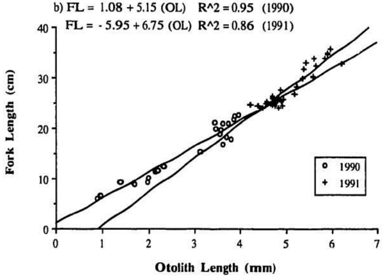
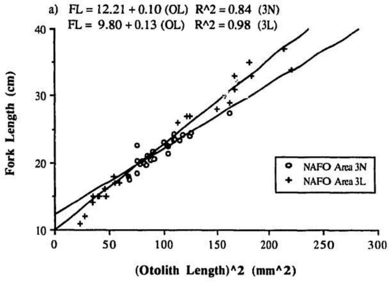

b) FL = 1.08 + 5.15 (OL) R^2 = 0.95 (1990)
FL = - 5.95 + 6.75 (OL) R^2 = 0.86 (1991)
Fork Length (cm)
Otolith Length (mm)
1990
1991
40
30
20
10
0
0
1
2
3
4
5
6
7

Fig. 2.15.

Relationship between a) otolith length and fork length for redfish spp. (*Sebastes spp.*) caught in 1991 in NAFO areas 3L and 3N ($p_{slope} = 0.0129$, df = 46), and between b) otolith height and total length for Greenland halibut (*Reinhardtius hippoglossoides*) caught in 1991 from NAFO areas 3Ps and 3N ($p_{slope} = 0.5071$, $p_{intercept} = 0.6492$, df = 55).


a) FL = 12.21 + 0.10 (OL) R^2 = 0.84 (3N)
FL = 9.80 + 0.13 (OL) R^2 = 0.98 (3L)
Fork Length (cm)
(Otolith Length)^2 (mm^2)
NAFO Area 3N
NAFO Area 3L

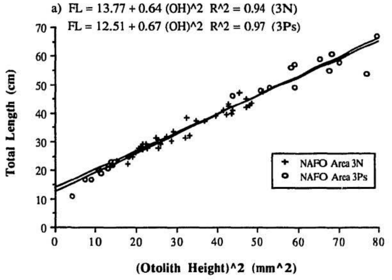
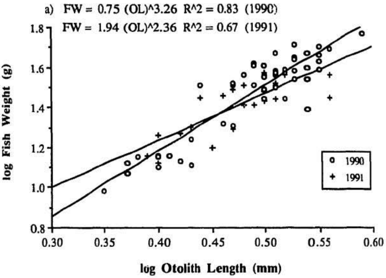

a) FL = 13.77 + 0.64 (OH)^2 R^2 = 0.94 (3N)
FL = 12.51 + 0.67 (OH)^2 R^2 = 0.97 (3Ps)
Total Length (cm)
(Otolith Height)^2 (mm^2)
NAFO Area 3N
NAFO Area 3Ps

Fig. 2.16.

Relationship between a) otolith length and total weight of capelin (*Mallotus villosus*) (p_{slope} = 0.0043, df = 67), and between b) otolith length and total weight for Atlantic herring (*Clupea harengus*) (p_{slope} = 0.1726, $p_{intercept}$ = 0.0002, df = 58), caught in 1990 and 1991.


a) FW = 0.75 (OL)^3.26 R^2 = 0.83 (1990)
FW = 1.94 (OL)^2.36 R^2 = 0.67 (1991)
log Fish Weight (g)
1.8
1.6
1.4
1.2
1.0
0.8
0.30
0.35
0.40
0.45
0.50
0.55
0.60
log Otolith Length (mm)
1990
1991

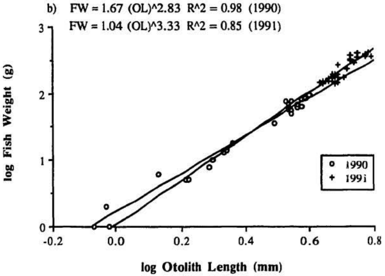
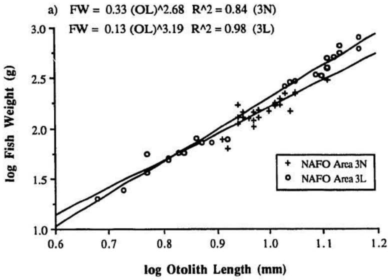
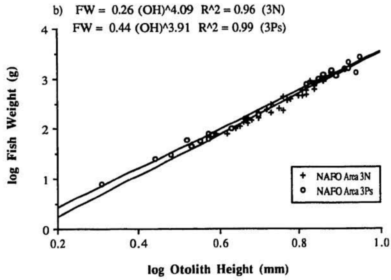

b) FW = 1.67 (OL)^2.83 R^2 = 0.98 (1990)
FW = 1.04 (OL)^3.33 R^2 = 0.85 (1991)
log Fish Weight (g)
3
2
1
0
-0.2
0.0
0.2
0.4
0.6
0.8
log Otolith Length (mm)
1990
1991

Fig. 2.17.

Relationship between a) otolith length and total weight for redfish spp. (*Sebastes spp.*) caught in 1991 in NAFO areas 3L and 3N ($p_{slope} = 0.1686$, $p_{intercept} = 0.0001$, df = 46), and between b) otolith height and total weight for Greenland halibut (*Reinhardtius hippoglossoides*) caught in 1991 from NAFO areas 3Ps and 3N ($p_{slope} = 0.2836$, $p_{intercept} = 0.0001$, df = 55).


a) FW = 0.33 (OL)^2.68 R^2 = 0.84 (3N)
FW = 0.13 (OL)^3.19 R^2 = 0.98 (3L)
log Fish Weight (g)
3.0
2.5
2.0
1.5
1.0
0.6
0.7
0.8
0.9
1.0
1.1
1.2
log Otolith Length (mm)
+ NAFO Area 3N
o NAFO Area 3L


b) FW = 0.26 (OH)^4.09 R^2 = 0.96 (3N)
FW = 0.44 (OH)^3.91 R^2 = 0.99 (3Ps)
log Fish Weight (g)
4
3
2
1
0
0.2
0.4
0.6
0.8
1.0
log Otolith Height (mm)
+ NAFO Area 3N
o NAFO Area 3Ps

John's, pers. comm.). This technique was not used in this study for two reasons. Averaging measurements from the two otoliths helped to reduce possible variance which might occur within each separate measurement if both left and right otoliths were used (S. Campana, Bedford Institute of Oceanography, Dartmouth, pers. comm.). This procedure also eliminated the possible violation of the assumption of independence of variables which results when both otolith measurements for each fish are used in the analysis.

In the present study, the mean difference between left and right Atlantic herring otoliths was 0.01 mm. Although no significant differences were found for any of the fish examined in this study, Atlantic herring did have the largest difference in measurements than any of the other species. The fact that a significant difference was found for Atlantic herring in the study by Lidster (unpublished data), and not the present one could be due to the difference in sample size used: 206 herring compared to the 43 examined in this study. Differences could also be due to differences in the precision of the instruments used to take the measurements, or from inter - experimenter reliability. Vernier calipers were used in the former study, whereas an image analyzer was used in the present one.

2.4.2. Relationship between otolith size and fish size

Otolith length is the most common criterion used in the literature for length prediction equations. It is the largest one - dimensional parameter of the otolith and may minimize the measurement error present when other morphometric parameters are used (Härkönen, 1986). For five of the six species examined, otolith length provided the best measurement for the determination of regressions to predict sizes of fish. In the case of Greenland halibut otoliths, the second largest one - dimensional parameter, otolith height, was more highly correlated to body length than otolith length. Greenland halibut otoliths are thin, and the anterior margin is extremely variable in shape, often containing long, finger - shaped tubercles at the dorso - anterior margin (Härkönen, 1986). These pointed, irregular ends may result in measurement errors, thus, lowering the correlation coefficient. There is less variability in shape of the dorsal and ventral margins, therefore, the height parameter proved to be a more appropriate parameter in this study.

Although most previous studies have used the simple linear regression equation to describe the best fit line for otolith length to body length correlations (Frost & Lowry, 1981; Finley & Gibb, 1984; Härkönen, 1986), second order polynomial regessions were also examined in this study. They provided better equations than the simple linear model to predict lengths for Atlantic cod, Greenland halibut and redfish spp.

For all but one species, coefficients of determination (r^2) for fish length regression equations were equal to or above 0.92, indicating a very high correlation between otolith size and fish length. Capelin, which are sexually dimorphic, was the only species in which the regression coefficient was considerably lower than the rest ($r^2 = 0.79$). The lower correlation likely reflects the different growth patterns generally shown by male and female capelin (B. Nakashima, Department of Fisheries and Oceans, St. John's, pers. comm.). Between age 1 - 3, there is a greater acceleration in growth of males relative to females. The size disparity between sexes increases to a maximum of 30 mm at age 3, and decreases slightly thereafter (Winters, 1982). Although ages of capelin were not recorded for this study, it is very likely that our sample contained fish within this age group as sizes of capelin were comparable to those examined in the Winter's study (1982). The ratio of females to males examined in the 1990 and 1991 samples were dissimilar indicating that there is a good possibility that gender may have caused a large proportion of the variance found. However, as sex of fish cannot be discerned from examination of otoliths alone, which is often the case when looking as stomach remains, the data were not analyzed on a gender basis.

Aside from capelin and Arctic cod, regression coefficients for equations predicting fish weight from otolith size were extremely high, ranging from 0.94 - 0.98, also indicating a high correlation between otolith size and fish weight. Again, the lower capelin values may be explained as above. In the case of Arctic cod, the lower regression coefficent could be due to a low sample size, gender or stock differences as well.

2.4.3. Spatial and temporal differences between fish

Significant differences between slopes were found in regression lines predicting both fish length and fish weight for sub - samples of capelin. As subsets of these capelin represent different years, this is an indication that possible temporal differences influence growth within this species.

Capelin growth may be affected by environmental conditions. Water temperatures in areas surrounding Newfoundland during 1991 were anomalously cold (Narayanan, Prinsenberg & Colbourne, 1992) resulting in slower maturation and later spawning of capelin in inshore waters (Carscadden, Frank & Nakashima, 1992). Colder water temperatures may have also affected the growth rate of this sample. Growth rate of capelin inhabiting cold water, such as in the Labrador region, is rather slow compared to capelin inhabiting warmer waters, such as the Grand Bank area, in which final size is approached more rapidly (Winters, 1982).

Significant differences between slopes for length predictive equations and intercepts for weight predictive equations in sub - samples of Atlantic herring from 1990 and 1991 also indicate a temporal difference in growth rate. As with capelin, it is difficult to say if growth of Atlantic herring varied yearly. Relationships between spawning time, water temperature and age structure have been reported for Atlantic herring. Different age - classes mature at different rates (Lambert, 1987). As well, data points from the two years in the present study do not overlap; all 1991 samples are larger than the 1990 samples such that each regression line alone does not represent a full size range of Atlantic herring found in the diet of seals. Yearly differences found for both capelin and Atlantic herring suggest that separate regression equations should be formulated for each year that these species are found in seal stomachs.

For redfish spp., the slopes for the otolith length to fish length relationship using a second order polynomial regression were significantly different for different areas, as were the intercepts for the weight prediction equations. This may be explained by the fact that the data points for the two subsets were not equally distributed throughout the size range examined. Samples taken from NAFO area 3N in August were clustered in the mid - section of the size range.

There is no evidence in the literature that growth rates of redfish vary by gender or age. However, there is evidence that growth rates are significantly different for at least two of the three species within this genus (Ni & McKone, 1981). Three common redfish species (*S.mentella, S. fasciatus, and S. marinus*) are found in Newfoundland waters. Due to substantial overlapping of morphological characters, it is difficult to distinguish between species (Ni, 1981). Some textbooks combine all three species into one for this reason alone (Leim & Scott, 1966; Scott & Scott, 1988). It is possible that more than one redfish species may have been included in the present study as different species were not identified.

Differences in regression lines were probably not due to spatial differences of the samples examined. Although subsets were taken from two NAFO areas, 3N and 3L, these areas are found side by side off southeastern Newfoundland (Fig. 1.2.) and are considered as one area for redfish stock assessment purposes (Parsons, 1976; Atkinson & Gavaris, 1981; Ni & McKone, 1981).

No significant differences in the otolith height - fish length relationship were found in the slopes or intercepts for Greenland halibut from two different areas, indicating that there is no difference between the relative growth rate of the otoliths between the two areas. However, differences between areas in the intercepts between the two lines were found in the otolith height - fish weight relationships indicating that there may be morphometric differences in fish between the two areas.

According to stock identification studies using meristics (Misra & Bowering, 1984), biochemical genetics (Fairbairn, 1981), blood protozoa (Khan, Dawe, Bowering & Misra, 1982), and external tagging (Bowering, 1984), there are two separate spawning populations of Greenland halibut. Greenland halibut from the Davis Strait and West Greenland area to the Labrador - eastern Newfoundland area, including the northern Grand Bank, constitutes a single biological stock, while a second genetically homogeneous stock has been suggested for Greenland halibut found in the Gulf of St. Lawrence and Fortune Bay areas off southern and western Newfoundland (Bowering, 1984; Misra & Bowering, 1984).

Since one subset of Greenland halibut in this study came from the Fortune Bay - Gulf of St. Lawrence area (NAFO area 3Ps), and the other subset came from the Grand Bank area off eastern Newfoundland (NAFO area 3N), there is the possibility that two separate stocks may have been represented.

It is evident from the results obtained that regression equations may vary within a species both spatially and temporally. Careful attention is required in selecting the appropriate equations to each fish species in the determination of fish size from otolith size. Subsets of fish within each of the capelin, Atlantic herring and redfish spp. samples examined were pooled for the final reconstructions. Sub - samples of Greenland halibut were also pooled in order to incorporate a full size range of fish in the regression. When separate equations were used to estimate fish length and weight for these two stocks, no significant differences were found between the two for length or weight estimations. Therefore, subsets were combined. To substantiate the possible stock differences, it would be necessary to examine fish growth equations from all other areas in which Greenland halibut are taken by seals.

CHAPTER 3:
Diet of hooded seals

3.1. Introduction

Knowledge oı diet is fundamental to studies of the ecology of seals and especially to any understanding of their role as predators in the northwest Atlantic marine ecosystem. Examination of hard parts of prey remains in stomachs and faeces is commonly used to obtain information on diet and to elucidate food habits in many seals (Prime & Hammond, 1987). This technique involves analysis of species - specific otoliths, eye lenses and other characteristic bony parts such as vertebrae in fishes, as well as carapaces and beaks in invertebrates.

Hard parts from prey remains are examined during different stages of digestion, depending on the most appropriate methodology. For example, examination of hard parts of prey remains found in faecal samples is applicable in situations where the killing of animals is not desired or possible. However, hard parts must pass completely through the digestive system before they become available for analysis. Therefore, the under - representation of some foods due to digestive processes is problematic (DaSilva & Nielson, 1985; Pierce et al., 1991b). An added difficulty with this technique is that faeces can only be collected seasonally on ice or land when animals have hauled - out (Pierce, Boyle & Diack, 1991). This is particularly true for hooded seals. Hooded seals rarely frequent land, and are only accessible to humans during the breeding and moulting seasons at which time they rarely eat. Thus, in this species, faecal examination is not a suitable method of diet determination.

Using the stomach lavage technique, partial samples of stomach contents may be obtained from live seals. Seals are captured, restrained, and / or chemically immobilized, and contents from the stomach are pumped by a suction tube which is inserted through the mouth. By obtaining food directly from the stomach, this method reduces the time that hard parts are subjected to digestive juices. However, stomach - flushing techniques can be very time consuming and costly. Most importantly, as with scat analysis, this method does not solve the problem of the accessibility for feeding hooded seals.

The most appropriate method of attaining dietary information and interpreting food habits of hooded seals using hard parts of prey remains is by examination of the complete stomach contents. If collection of stomachs from dead seals is not restricted to one area and / or season, there are more opportunities for securing a food record. A major limitation of this methodology is that in many cases, seal stomachs are empty, rendering this an inefficient method of collecting data (Prime & Hammond, 1990), However, many researchers claim that this method provides detailed information with fewer biases in interpretation and quantification than either the stomach lavage or scat analysis techniques (Rae, 1973; Hyslop, 1980; Murie & Lavigne, 1986).

A more recent method of evaluating feeding of marine mammals is based on stable isotopic comparisons which indicate the trophic level at which feeding occurs. Whereas the methodologies mentioned above can only provide a short - term record of recently ingested foods, carbon and nitrogen isotope ratios (delta^{13}C and delta^{15}N, respectively) reflect materials that have been assimilated over a longer period and, therefore, provide a long - term indication of diet (Ostrom, in press). The problem with this method as applied to seal diet studies is that because isotope ratios average across the variety of food ingested, it is often very difficult to infer diet composition.

Very little quantitative data are available on the feeding behaviour and dietary preferences of hooded seals. Sergeant (1976) reported that they fed on squid and redfish, although no details were given concerning methodology used for obtaining this information, the location of samples, or the numbers of seals examined. Stomach contents of juvenile and adult hooded seals collected from Greenland between 1970 - 1978 (Kapel, 1980) indicated that the most frequently occurring prey species were unidentified Gadoids, redfish, and Greenland halibut.

The first quantitative study on the diet of hooded seals examined stomachs collected opportunistically between 1982 - 1990 off the east coast of Newfoundland and Labrador (Stenson et al., 1991). Prey types and numbers of prey ingested were estimated by examination of hard parts. As with the Greenland study (Kapel, 1980), relative importance of prey in the diet was expressed as frequency of occurrence. Results indicated that the most frequently occurring prey species, in order of prevalence, were Greenland halibut, Arctic cod, capelin, squid spp., Atlantic herring, and redfish spp.

Percentage frequency of occurrence of a prey species, or the proportion of stomachs which contain a particular species, is historically, the most common method used in diet studies. This approach is quick and simple, and requires a minimum of apparatus. Although the stage of digestion has little effect on the resulting percentages, this method provides estimates which over - emphasize the importance of small prey items (Hyslop, 1980). Biases also exist in that individuals of a more rapidly digested species will be under - represented, while those resisting digestion will be over - estimated. For example, Bigg & Fawcett (1985) found that squid beaks remain in the stomach longer than fish bones, resulting in exaggeration of the importance of squid in the diet. Frequency of occurrence data do not necessarily reflect the relative energetic importance of the prey. Small, frequently occurring species appear to contribute more to the overall diet than larger, less abundant prey (Stenson et al., 1991).

Although biases inherent in using this methodology cannot be eliminated, reconstructing the actual volume and / or mass of each prey species at time of ingestion will contribute to estimating energetic importance of prey and will further improve interpretation of food consumed by seals. Actual sizes of fish and invertebrates can be determined using regression analysis. Fish size can be derived through back - calculation procedures which are based on the proportionality between fish length and some measure of otolith size. This procedure has been used to reconstruct lengths and / or weights of the prey consumed in ribbon seals in the Bering Sea (Frost & Lowry, 1980), harbour seals in the Pacific (Brown & Mate, 1983) and southern New England (Selzer et al., 1986), California sea lions (Antonelis et al., 1984), South American sea lions (George-Nascimento, Bustamente & Oyarzun, 1985), and harp seals in coastal waters of west Greenland (Kapel & Angantyr, 1989). However, no study exists which examines diet in this way for hooded seals.

The primary objective of this study was to determine the diet of hooded seals off the coast of Newfoundland and Labrador by the analysis of stomach contents. Relative importance of food items in the diet of hooded seals was expressed through reconstructing weights of prey species found in the stomach contents. These weights were determined using the regression equations established for the most common prey species in Chapter 2. Relative importance of prey, through reconstructed weights, was compared to the importance of prey estimated by relative frequency of occurrence.

3.2. Materials and Methods

3.2.1. Collection of hooded seal stomach samples

Hooded seal stomachs (n = 67) were collected in waters surrounding Newfoundland in 1991 by the Department of Fisheries and Oceans research personnel, through a shore - based collector program involving sealers and fishermen or from seals caught incidentally in offshore trawlers. Sampling locations were grouped into four different regions; the nearshore waters along the northeast coast of Newfoundland (3KL), the south coast of Newfoundland (Gulf, 3P), the whelping patch on the Front (2J3K), and offshore waters (2J3KL), both from research vessels and trawlers (Fig. 1.2.).

Stomachs were removed from seals in the field and immediately frozen, or stored in 70% ethanol until examined in the laboratory. Stomachs, jaws, and the sex of each animal were taken for all samples collected. Morphometric data (body length and weight) were collected for the seals whenever possible.

In the laboratory, stomachs were first weighed, then opened longitudinally along the greater curvature, and contents emptied into a large tray and rinsed thoroughly. Stomachs were then reweighed to obtain an estimate of wet weight of prey ingested.

Intact specimens were sorted into major prey types using visual keys (Härkönen, 1986) and reference collections at the Department of Fisheries and Oceans, St. John's, Newfoundland. Lengths and weights of fish and / or lengths of crustacean carapaces were measured when possible. Digested fish prey items were identified by sagittal otoliths. Cephalopod remains were identified to as low a taxon as possible by Dr. Malcolm Clarke, a cephalopod specialist (Ancarva, Southdown, Millbrook, Cornwall, UK).

Loose otoliths in the stomach were recovered using three sieves (500 µm, 2.00 mm, and 4.75 mm mesh diameter). Sieved contents were rinsed into glass trays, then sorted manually into categories of prey species to the lowest taxonomic level. Recovered skull cases were examined for the presence or absence of sagittal otoliths. If otoliths were retained within the skulls of fish they were removed and kept together as a 'pair', separate from the rest of the loose otoliths. Numbers of invertebrates were estimated by counting whole specimens, carapaces, and squid beaks. Otoliths were stored dry. Other material retrieved, was stored in 70% alcohol.

The total number of each fish species was calculated by adding the number of fresh fish, the number of intact skulls and the number of paired otoliths found free in the stomach. If pairing was not possible, the highest number of either left or right otoliths was reported. Squid numbers were calculated as the highest number of either upper or lower beaks, plus any fresh specimens which were present.

The age of each seal was determined by counting annual growth layers in the cementum and dentine of teeth from the jaws collected (Bowen, Sergeant & Øritsland, 1983).

The frequency of occurrence (Hyslop, 1980) of each prey type and estimated numbers of individuals were determined for each stomach examined. This information was compared to similar quantitative results described in a previous study of the diet of hooded seals in Newfoundland (Stenson et al., 1991).

3.2.2. Reconstruction of hooded seal stomach contents

According to the combined relative frequencies of occurrence of the previous (Stenson et al., 1991) and present studies, six fish species and one invertebrate species were used to reconstruct the diet of hooded seals. Greenland halibut, redfish spp., Atlantic herring, Arctic cod, Atlantic cod, capelin, and squid each represented over 5%, and together accounted for over 80% of the total diet according to relative frequency of occurrence. Although not among the six fish species most frequently eaten prey, Atlantic cod was also examined, due to its possible importance with the fishery.

To increase the sample size, otoliths and squid beaks from 65 hooded seals collected and used for species identification in our previous study (Stenson et al., 1991), and otoliths and beaks retrieved from the 67 seals from the present study were combined and re - examined in order to calculate lengths and weights of fish and squid at ingestion for each of the species listed above.

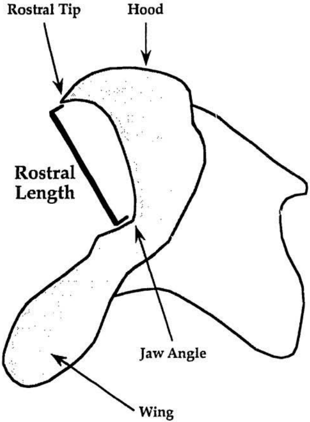
Each otolith retrieved from stomach contents was rated on a scale of 0 - 3, based on surface texture and shine, condition of edge lobulations, and degree of opacity as described by (Gales, 1988) and (Recchia & Read, 1989). A rating of 0 was given to completely undigested otoliths - those removed from intact fish or fish skulls. A rating of 1 was given to those otoliths found free in the stomach and judged to be undamaged or uneroded. If the margin crenulations had disappeared and the rostrum and sulcus acusticus (Fig. 2.1.) were less distinct, a rating of 2 was applied. A rating of 3 was given if the otolith had lost all diagnostic features. To ensure that accurate estimates of total fish length were obtained, only those otoliths which rated either 0 or 1 where used in the regression analysis. Since squid beaks do not degenerate when exposed to digestive juices, all beaks were measured.

Maximum length (anterior - posterior) and height (dorsal - ventral) was recorded for each measurable otolith using an image analysis system. Each otolith was placed under a dissecting scope, and the image projected onto a computer screen. Maximum length and height measurements were recorded using a mouse to identify the appropriate dimensions. These data were used to derive approximate lengths and weights of prey using otolith / body size regression equations derived in Chapter 2. When undigested otoliths were present, the maximum number of either left or right undigested otoliths for each species within a stomach were used to reconstruct lengths and weights of individual prey. When stomachs contained both undigested and digested otoliths of a particular species, the mean weight of the reconstructed prey for each stomach were used to estimate the weight of the digested prey in that stomach. Rostral length, the distance between the rostral tip and the jaw angle, of the lower beaks of all cephalopods were measured with vernier calipers (Fig 3.1.). Their wet weights were reconstructed using published regression equations (Clarke, 1986). From this information, average lengths and weights of prey ingested were estimated. For each stomach containing measurable otoliths, the total weight of each prey species was estimated by applying the mean weight of that species established from non - digested otoliths to all remaining otoliths of that species.

The contribution of various prey species to the total hooded seal diet based on frequency of occurrence, estimated numbers of prey ingested, and reconstructed weight estimates were compared. Gender and seasonal differences in the prey species identified in samples were compared, using mixed two - factor analyses of variance and chi square analyses (Keppel, 1989).

Fig. 3.1.

Diagram of the lower beak of a cephalopod showing the principal terms and dimensions used for measurements (after M. Clarke, 1986).



Lower beak of the squid *Gonatus*

3.3. Results

3.3.1. Collection of hooded seal stomach samples

Although an attempt was made to collect stomachs from each of the four locations described earlier, the majority of stomachs (73.1%) came from the nearshore region along the northeast coast of Newfoundland. Of the 49 stomachs collected from the northeast coast, 36 of these (73.5%) were taken in April (Table 3.1.).

A total of 64.2% of the stomachs collected came from females, and 35.8% came from males (Table 3.2.). When the animals from the whelping patch were removed, the percentage of females was reduced to 53.7 %.

The majority of seals taken (87.9%) were 4 years of age and greater. Eight stomachs (12%) came from juveniles (aged 1 - 3), whereas no samples of pups were examined. Of the 58 stomachs taken from 4+ animals, the majority (n = 46) came from the nearshore waters off the northeast coast of Newfoundland (Table 3.3.).

Food was found in 82% of the stomachs (n = 55). Most of the food - containing stomachs were taken from the nearshore area along the northeast coast (n = 45). All of the samples collected from offshore trawlers (n = 9) contained food, whereas all of the stomachs collected from the whelping

Table 3.1. Hooded seal (*Cystophora cristata*) stomach samples collected in Newfoundland waters in 1991, subdivided by month and collection area.

Month	Northeast Coast	Offshore 2J3KL	Offshore Trawler	South Coast	Whelping Patch
January	2	-	2	-	-
February	4	1	5	1	-
March	5	-	1	-	6
April	36	-	1	-	1
May	2	-	-	-	-
Total	49	1	9	1	7

Table 3.2. Sex of hooded seals (*Cystophora cristata*) taken from Newfoundland waters in 1991, subdivided by collection area.

Area	Male	Female	Total
Northeast Coast	17	32	49
Offshore 2J3KL (Research)	0	1	1
Offshore 2J3KL (Trawler)	6	3	9
South Coast (Gulf)	1	0	1
Whelping Patch	0	7	7
Total	24	43	67

Table 3.3. Age structure of hooded seals (*Cystophora cristata*) taken from Newfoundland waters in 1991, subdivided by collection area.

Area	Age 0	Age 1 - 3	Age 4+	Total
Northeast Coast	-	2	46	48
Offshore 2J3KL (Research)	-	-	1	1
Offshore 2J3KL (Trawler)	-	5	4	9
South Coast	-	1	-	1
Whelping Patch	-	-	7	7
Total	-	8	58	66 *

* One stomach with unknown age

patch were empty (n = 7) (Table 3.4.). Food was found in seven out of eight of the stomachs collected from seals aged 1 - 3, and in 47 of 58 stomachs examined from adults (Table 3.5.).

Excluding animals taken from offshore trawlers, a total of 14 prey groups were identified, 10 of which were fish and 4 invertebrates (Table 3.6.). When the relative contribution of prey to the diet was expressed as percent frequency of occurrence, Greenland halibut represented the most abundant fish prey species, occurring in 69.6% of the stomachs examined. Redfish, Atlantic herring, Arctic cod, and eelpout were also common prey items, contained in 52.2%, 39.1%, 17.4%, and 10.9% of the stomachs examined, respectively. Unidentified fish species were found in 6.5% of the stomachs examined, representing a total of 8 fish.

Squid (*Gonatus* spp.) was present in 69.6% of the stomachs collected, ranking highest in frequency of occurrence along with Greenland halibut. Most beaks were likely to be *Gonatus fabricii*, although certain physical characteristics did not exclude *G. steenstrupii*. One stomach contained beaks of a smaller *Gonatus* species probably not yet described from the north Atlantic (M. Clarke, Ancarva, Southdown, Millbrook, Cornwall, UK, pers. comm.).

The relative contribution of specific prey in the diet changed when expressed as a function of the total number of prey eaten. Squid eaten (n =

Table 3.4. Presence of food in hooded seal (*Cystophora cristata*) stomachs taken in Newfoundland waters in 1991, subdivided by collection area.

Area	Empty	Food	Total
Northeast Coast	4	45	49
Offshore 2J3KL (Research)	0	1	1
Offshore 2J3KL (Trawler)	0	9	9
South Coast	1	0	1
Whelping Patch	7	0	7
Total	12	55	67

Table 3.5. Presence of food in stomachs of hooded seals (*Cystophora cristata*) taken from waters surrounding Newfoundland in 1991, subdivided into different age groups.

Age Class	Empty	With Food	Total
Age 0	0	0	0
Age 1-3	1	7	8
Age 4 +	11	47	58
Unknown	0	1	1
Total	12	55	67

Table 3.6. Contents of hooded seal (*Cystophora cristata*) stomachs (n = 46) collected in Newfoundland waters in 1991, excluding samples obtained from offshore trawlers.

Prey Species	No. Stomachs containing prey	%	Total No. Prey Present	%
Fish				
Greenland halibut	32	69.6	125	15.7
Redfish	24	52.2	72	9.0
Atlantic herring	18	39.1	57	7.1
Arctic cod	8	17.4	64	8.0
Eelpout	5	10.9	22	2.8
Witch Flounder	4	8.7	7	0.9
Righteye flounder	4	8.7	14	1.8
Capelin	2	4.3	2	0.2
Atlantic cod	2	4.3	2	0.2
Skate eggs	1	2.2	4	0.5
Unidentified	3	6.5	8	1.0
Invertebrates				
Squid spp.	32	69.6	412	51.6
Shrimp	4	8.7	6	0.8
Hyperiid	2	4.3	2	0.2
Snow crab	1	2.2	1	0.1

412) greatly outnumbered all fish species. Greenland halibut remained the most frequently eaten fish (n = 125), however, the contribution of Arctic cod (n = 64) to the diet increased over Atlantic herring (n = 57), whereas the occurrence of eelpout (n = 22) decreased relative to the other four important species. The five most common species expressed as percent frequency of occurrence remained the most commonly eaten fish when diet was expressed as total number of prey eaten (Table 3.6.).

From seals taken incidentally by offshore trawlers, a total of four prey species, three fish and one invertebrate, were identified (Table 3.7.). Atlantic cod represented the most common prey species found in these stomachs (66.7%), followed by redfish and righteye flounder (Pleuronectidae) (22.2%, and 11.1%, respectively). One stomach contained squid remains. Redfish and Atlantic cod represented the highest total number of prey eaten (n = 13, n = 10, respectively). When the prey type found in the stomach of the seal taken by a particular trawler was compared to the fish species the trawler targeted, there was disagreement in 33.3% (n = 3) of the cases (Table 3.7). The three stomachs containing no Atlantic cod contained either redfish, righteye flounder, or squid.

3.3.2. Reconstruction of hooded seal stomach contents

Of the 132 stomachs which contained food, 72 contained measurable prey (Table 3.8.). Seventeen of these stomachs came from our previous study (Stenson et. al., 1991), while 55 came from the present study. Fish

Table 3.7. Contents of hooded seal (*Cystophora cristata*) stomachs incidentally caught in offshore trawlers in Newfoundland in 1991, showing directed species of trawl for each seal caught.

Prey Species	No. Stomachs Containing Prey	%	Total No. Prey Present	%	Directed Species of Trawl
Fish					
Atlantic cod	6	66.7	10	41.7	Atlantic cod
Redfish	2	22.2	13	54.2	Atlantic cod
Righteye flounder	1	11.1	1	4.2	Atlantic cod
Invertebrates					
Gonatus sp.	1	11.1	1	100	Atlantic cod

Table 3.8. Hooded seal (*Cystophora cristata*) stomach samples containing measurable otoliths and squid beaks, collected from 1987-1991, subdivided by month and collection area.

Month	Northeast Coast	Offshore (Research)	Offshore (Trawler)	South Coast	Whelping Patch
January	2	-	3	-	-
February	9	-	3	1	-
March	12	-	-	-	-
April	38	-	-	-	-
May	4	-	-	-	-
Total	65[1]	0	6	1	0

[1] 14 of these stomachs contained only squid beaks

length was estimated from a sample of 5 capelin, 10 Atlantic cod, 22 Atlantic herring, 23 Arctic cod, 31 redfish, and 58 Greenland halibut, whose otoliths fell under the 0 or 1 classification stage of digestion described earlier. Of these, 2 redfish, 8 Atlantic cod, and 1 Greenland halibut came from offshore trawl samples. Wet weight estimates were obtained for a total of 9 capelin, 10 Atlantic cod, 42 Atlantic herring, 190 Arctic cod, 55 redfish, 146 Greenland halibut, and 452 squid.

Although there was a wide range of prey sizes taken by the seals, the mean lengths for Atlantic herring, redfish spp., Greenland halibut, and Atlantic cod (excluding samples taken incidentally by offshore trawlers) fell between 25 - 35 cm (Fig. 3.2.). Average lengths of Arctic cod and capelin were smaller, ranging between 13 - 25 cm (Fig. 3.3.). The average lengths of Atlantic herring, redfish spp., Greenland halibut, Atlantic cod and capelin taken by the seals fall within the sizes of fish taken by the commercial fishery. Arctic cod are not commercially fished.

Estimated mean lengths of fish from animals caught incidentally in offshore trawlers were larger than all other samples (Fig. 3.2.). Atlantic cod samples were significantly larger than the rest with an estimated mean length of 49.5 cm ($t = -13.58$, $p = .0468$). Both redfish ($n = 2$) and Greenland halibut ($n = 1$) had mean lengths of 37.6 and 36.5 cm, respectively (Table 3.9.).

Fig 3.2.

Estimated prey lengths of a) redfish spp. (*Sebastes spp.*), b) Greenland halibut (*Reinhardtius hippoglossoides*), c) Atlantic herring (*Clupea harengus*), and d) Atlantic cod (*Gadus morhua*) taken from hooded seal (*Cystophora cristata*) stomachs collected from 1982 - 1991 in waters surrounding Newfoundland, excluding those taken incidentally.

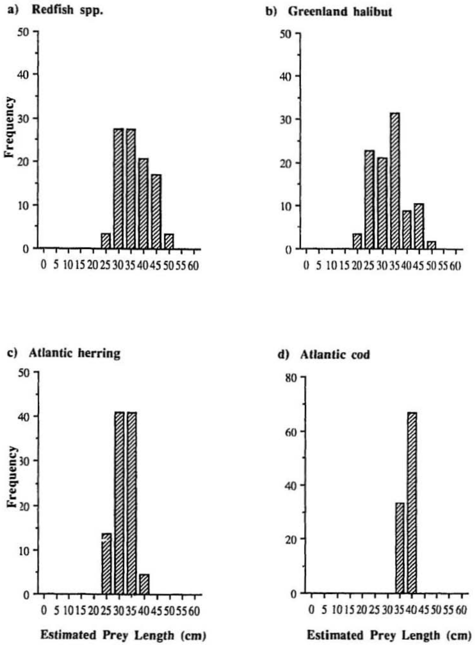

a) Redfish spp.
b) Greenland halibut
c) Atlantic herring
d) Atlantic cod
Frequency
0 5 10 15 20 25 30 35 40 45 50 55 60
Estimated Prey Length (cm)

Fig. 3.3.

Graph showing the distribution of estimated prey lenghts of a) Arctic cod (*Boreogadus saida*), and b) capelin (*Mallotus villosus*) taken from hooded seal (*Cystophora cristata*) stomachs collected from 1982 - 1991 in Newfoundland waters, excluding those taken incidentally.

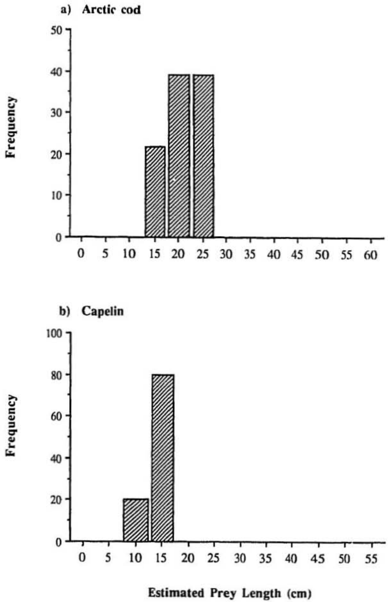

a) Arctic cod
Frequency
50
40
30
20
10
0
0 5 10 15 20 25 30 35 40 45 50 55 60
b) Capelin
Frequency
100
80
60
40
20
0
0 5 10 15 20 25 30 35 40 45 50 55
Estimated Prey Length (cm)

Table 3.9. Prey lengths of common fish prey species of hooded seals (*Cystophora cristata*) taken between 1982-1991 by collectors in inshore and offshore waters of Newfoundland (A), and taken incidentally from offshore trawlers (B), showing mean length (cm), range and standard deviation.

Prey type	Method of catch	N	Mean (cm)	Range (cm)	Std. Dev.
Atlantic herring (*C. harengus*)	A	22	28.92	21.80 — 35.62	3.44
	B	0	—	—	—
Redfish sp (*Sebastes. spp.*)	A	29	34.16	24.00 — 48.13	6.25
	B	2	37.58	34.05 — 41.11	4.99
Arctic cod (*B. saida*)	A	23	18.66	13.42 — 24.86	3.64
	B	0	—	—	—
Atlantic cod (*G. morhua*)	A	2	35.79	34.78 — 36.80	1.43
	B	8	49.51	37.55 — 72.78	11.39
Capelin (*M. villosus*)	A	5	16.18	14.83 — 16.86	0.78
	B	0	—	—	—
Greenland halibut *R.hippoglossoides*	A	57	30.21	18.61 — 45.05	6.76
	B	1	36.51	36.51	—

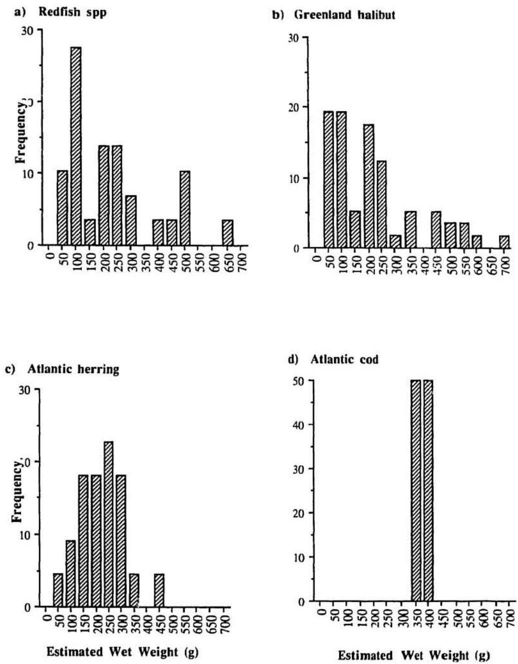
Prey weights for most species were widely distributed (Fig. 3.4. and Fig. 3.5.). Mean weights for Atlantic herring, redfish spp. and Greenland halibut fell between 235 - 250 g, while those for Arctic cod and capelin were smaller, averaging 59.4 g and 25.5 g, respectively. Again, all fish from the offshore trawlers had higher mean weights than the average inshore fish weight. Weight of Atlantic cod was significantly greater for seals caught in trawls ($t = -21.73$, $p = .0293$) ranging from 465.9 g - 3031.4 g (Table 3.10.). The average weight of squid ingested was 11.03 g (range = 0.6 g - 194.9 g).

Relative contribution of prey to the diet, expressed as the percent total wet weight of prey examined, was determined for all stomachs collected between 1982 - 1991, excluding those caught incidentally from offshore trawlers. Total wet weight was calculated using only the major prey items found. These prey accounted for > 80% of the total diet (Table 3.12.). The remaining percentage came from unknown flatfish, unidentified fish, or the odd fish or invertebrate, thus, it was not possible to get a complete total weight. Greenland halibut was by far the largest contributor, by weight, to the overall diet of hooded seals (42.2%), followed by redfish sp., Arctic cod, Atlantic herring, squid, Atlantic cod and capelin, in decreasing order of percent total weight (Table 3.11.; Fig. 3.6.).

The relative frequency of occurrence of prey of hooded seals taken between 1982 - 1990 (Stenson et al., 1991) along with the results obtained from this study is presented in Table 3.12. Five out of the six most common

Fig. 3.4.

Estimated prey weights of a) redfish sp., b) Greenland halibut, c) Atlantic herring, and d) Atlantic cod taken from hooded seal (*Cystophora cristata*) stomachs collected from 1982 - 1991 in Newfoundland waters, excluding those taken incidentally.



a) Redfish spp
b) Greenland halibut
c) Atlantic herring
d) Atlantic cod
Frequency
0
10
20
30
40
50
0
50
100
150
200
250
300
350
400
450
500
550
600
650
700
Estimated Wet Weight (g)

Fig. 3.5.

Estimated prey weights of a) Arctic cod, and b) capelin taken from hooded seal (*Cystophora cristata*) stomachs collected from 1982 - 1991 in Newfoundland waters, excluding those taken incidentally.

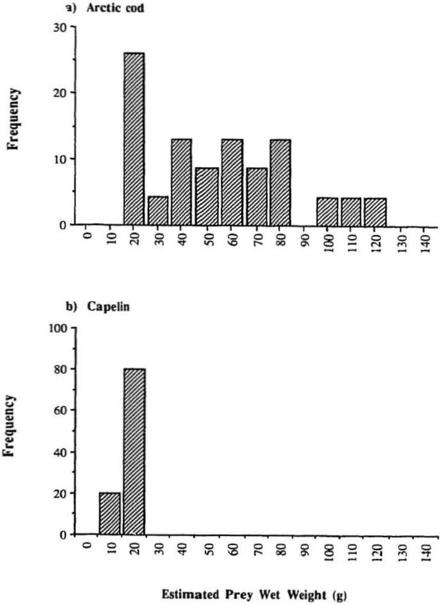

a) Arctic cod
30
20
10
0
Frequency
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
b) Capelin
100
80
60
40
20
0
Frequency
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
Estimated Prey Wet Weight (g)

Fig. 3.6.

Relative importance of six common prey species in the diet of hooded seals caught in the waters of Newfoundland between 1982 - 1991 by (a) relative frequency of ocurrence of prey, (b) percent total number of prey recovered, and (c) percent total weight of prey recovered.

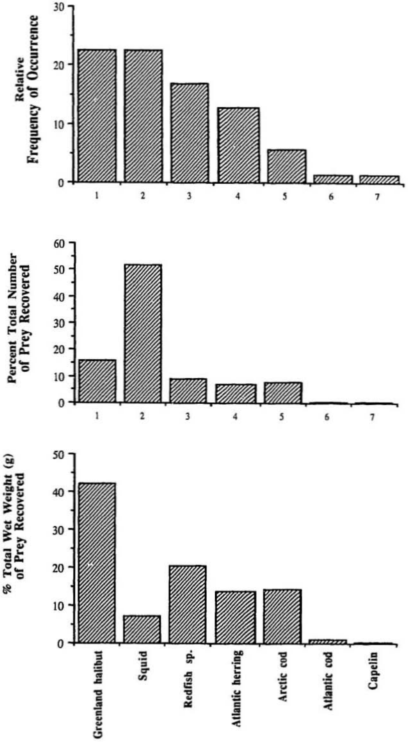

Relative Frequency of Occurrence
30
20
10
0
1
2
3
4
5
6
7
Percent Total Number of Prey Recovered
60
50
40
30
20
10
0
1
2
3
4
5
6
7
% Total Wet Weight (g) of Prey Recovered
50
40
30
20
10
0
Greenland halibut
Squid
Redfish sp.
Atlantic herring
Arctic cod
Atlantic cod
Capelin

Table 3.10. Prey weights of common fish and invertebrate prey species of hooded seals (*Cystophora cristata*) taken by collectors from inshore and offshore waters of Newfoundland (A), and taken incidentally from offshore trawlers (B), showing mean weight (g), range and standard deviation.

Prey type	Method of catch	N	Mean (g)	Range (g)	Std. Dev.
Atlantic herring (*C. harengus*)	A	22	248.23	99.44 — 452.26	87.00
	B	0	—	—	-
Redfish (*Sebastes. spp.*)	A	29	244.21	33.04 — 653.86	163.01
	B	2	321.39	223.60 — 419.18	138.30
Arctic cod (*B. saida*)	A	23	59.39	20.72 — 122.81	31.23
	B	0	—	—	—
Atlantic cod (*G. morhua*)	A	2	402.87	367.70 — 438.04	49.74
	B	8	1167.04	465.94 — 3031.38	835.51
Capelin (*M. villosus*)	A	5	25.51	19.46 — 28.75	3.53
	B	0	—	—	—
Greenland halibut *R.hippoglossoides*	A	57	236.45	46.80— 730.50	165.61
	B	1	364.76	364.76	—
Squid (*Gonatus spp.*)	A	452	11.03	0.61 — 194.90	12.05
	B	0	—	—	—

Table 3.11. Relative contributions by wet weight of common prey species of hooded seals (*Cystophora cristata*) collected from inshore and offshore waters surrounding Newfoundland, excluding those samples taken incidentally from offshore trawlers. Total weight accounts for major prey items only.

Fish Species	N of Prey	Weight (g)	% of Total Weight
Greenland halibut (***R.hippoglossoides***)	146	29024.10	42.2
Redfish sp. (***Sebastes. spp.***)	55	14178.46	20.6
Arctic cod (***B. saida***)	190	9981.43	14.5
Atlantic herring (***C. harengus***)	42	9617.40	14.0
Atlantic cod (***G. morhua***)	2	805.74	1.2
Capelin (***M. villosus***)	9	234.23	0.3
Squid (***Gonatus spp.***)	452	4987.76	7.2

Table 3.12. Comparison of the relative frequency of occurrence of prey of hooded seals (*Cystophora cristata*) taken between 1982 - 1990 (Stenson et.al., 1991) and taken in 1991, from Newfoundland (n = 132).

Prey Species	Freq. of Occurrence	1982-1990	Freq. of Occurrence	1991
	N	%	N	%
Fish				
Greenland halibut	48	27.9	32	22.5
Redfish	10	5.8	24	16.9
Atlantic herring	12	7.0	18	12.7
Arctic cod	24	14.0	8	5.6
Eelpout	2	1.2	5	3.5
Witch Flounder	-	-	4	2.8
Righteye flounder	4	2.3	4	2.8
Capelin	21	12.2	2	1.4
Atlantic cod	4	2.3	2	1.4
Skate eggs	3	1.7	1	0.7
American plaice	3	1.7	-	-
Gadoid	4	2.3	-	-
Sculpins	3	1.7	-	-
Wolffish	1	0.6	-	-
Unidentified	8	4.6	3	2.1
Invertebrates				
Gonatus sp.	16	9.3	32	22.5
Natantia	3	1.7	4	2.8
Hyperiidea	-	-	2	1.4
Amphipoda	2	1.2	-	-
Euphausiacea	1	0.6	-	-
Bivalvia	1	0.6	-	-
Octopoda	1	0.6	-	-
Snow crab	1	0.6	1	0.7

fish and invertebrate prey species found in the former study retained their significance in the present study. Greenland halibut remained the most frequently occurring species from both studies. Redfish, Atlantic herring, Arctic cod and squid were also most frequently found in both studies. However, the relative contribution of capelin to the overall diet dropped considerably in this study; eelpout were found more frequently.

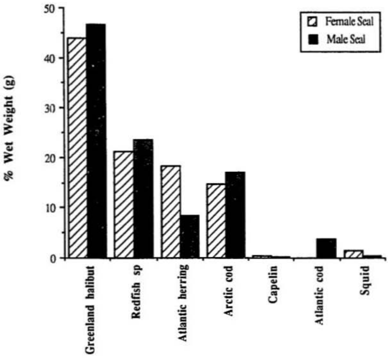
3.3.3. Differences in dietary preferences of hooded seals by sex and season

The relative contribution of common fish prey species to the overall diet of hooded seals was examined for gender and seasonal differences. Seasons were defined as winter (October - March) and summer (April - September). In order to control for variance due to geographical area, and since most measurable contents came from stomachs from the northeast coast of Newfoundland (Table 3.8.), these were the only stomachs used in all comparisons. Stomach contents from seals caught incidentally were not included in the analysis.

A chi square contingency table showed no overall significant differences between sexes in percent total weight of each prey species ($X^2 = 4.80$, $df = 5$, $p > .05$) (Fig 3.7.).

Fig. 3.7.

Proportions (% weight) of major fish prey ingested by male and female hooded seals (*Cystophora cristata*) taken from stomachs collected from 1982 - 1991 in waters surrounding Newfoundland.



% Wet Weight (g)
50
40
30
20
10
0
Female Seal
Male Seal
Greenland halibut
Redfish sp
Atlantic herring
Arctic cod
Capelin
Atlantic cod
Squid

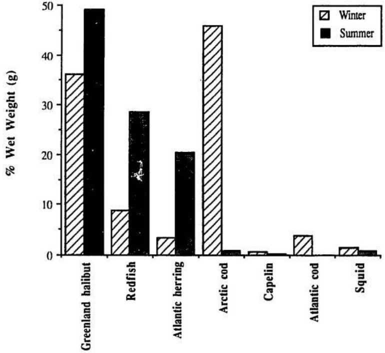
For the seasonal comparison, chi square analysis showed an overall significant difference in percent weight of prey on season that the stomach was taken ($X^2 = 68.94$, df = 5, $p < .0001$) (Fig. 3.8.). Component contingency tables were created to look for individual differences. Differences in the proportion of fish consumed per species per season by the seals were statistically significant for redfish ($X^2 = 12.18$, df = 1, $p < .001$), Atlantic herring ($X^2 = 13.66$, df = 1, $p < .001$), and Arctic cod ($X^2 = 59.36$, df = 1, $p < .001$). No significant differences were found for Greenland halibut, capelin or Atlantic cod.

Sizes of each of the six common fish prey consumed were also examined for sex and seasonal differences usign a two - way mixed factorial design. No significant differences between sexes were found for either length of prey ($F_{(1,36)} = 0.021$), or for the interaction effect between sex and prey species ($F_{(4,36)} = 0.581$), at the .05 level. Prey lengths eaten by both male and female hooded seals were very similar (Fig. 3.9.).

Lengths of the various fish prey consumed were compared for overall seasonal size differences (winter and summer) (Fig. 3.10.). The mixed two - way analysis of variance showed no overall significant differences in length of prey on season ($F_{(1,19)} = 0.124$), and no significant interaction effect between season and prey species ($F_{(4,19)} = 0.310$).

Fig. 3.8.

Proportions (% weight) of major fish prey ingested by hooded seals (*Cystophora cristata*) taken from stomachs collected from winter (October to March) and summer (April to September) between 1982 - 1991 in Newfoundland waters.



% Wet Weight (g)
50
40
30
20
10
0
Winter
Summer
Greenland halibut
Redfish
Atlantic herring
Arctic cod
Capelin
Atlantic cod
Squid

Fig. 3.9.

Mean lengths and standard deviations of major fish prey ingested by male and female hooded seals (*Cystophora cristata*) taken from stomachs collected from 1982 - 1991 in waters surrounding Newfoundland.

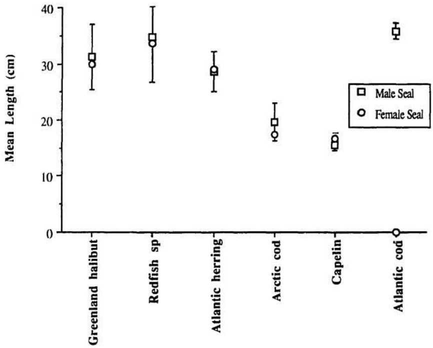
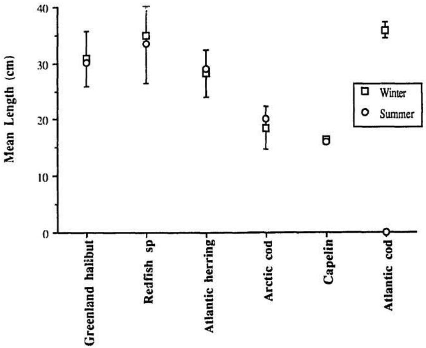

Mean Length (cm)
40
30
20
10
0
Greenland halibut
Redfish sp
Atlantic herring
Arctic cod
Capelin
Atlantic cod
Male Seal
Female Seal

Fig. 3.10.

Mean lengths and standard deviations of major fish prey ingested by hooded seals (*Cystophora cristata*) taken from stomachs collected from winter and summer between 1982 - 1991 in waters surrounding Newfoundland.



Mean Length (cm)
40
30
20
10
0
Winter
Summer
Greenland halibut
Redfish sp
Atlantic herring
Arctic cod
Capelin
Atlantic cod

3.4. Discussion

3.4.1. Seals samples

As in other studies, it was difficult to obtain a large sample size of stomachs from all areas surrounding Newfoundland. Due to the distribution of hunting effort and the temporal distribution of hooded seals in the region, most stomach samples were collected from the nearshore waters along the northeast coast of Newfoundland during March and April. Seals are most abundant in the area during this time as a large number of hooded seals congregate to breed in mid March in the area off the northern coast of Newfoundland, and/or southern Labrador (Fig. 2.1.).

Not only are hooded seals difficult to access, but stomachs obtained from the breeding grounds are typically empty. Our results agree with the behavioural observations of hooded seals at the whelping patch which suggest that females do not leave their pups during the nursing period and that hooded seal mothers do not appear to feed during lactation (Shepeleva, 1973; Bowen et al., 1987).

Although seal samples often become available when caught incidentally in fishing nets from commercial trawlers, these samples may be unrepresentative of the feeding of the population at large. Stomach contents often reflect the content of the trawl (Table 3.7.), suggesting the possibility that seals may be attracted to the trawl, and thus feed on the directed species targeted by the trawler. Although only a small sample size was available in this study, the Atlantic cod retrieved from seal stomachs taken incidentally were significantly larger, than the cod measured from seals taken elsewhere, and were roughly the same size as those taken in the nets. However, because other fish species were also found in stomachs, and as some stomachs contained no Atlantic cod, it is possible that the incidentally caught seals were not feeding directly from the fishing nets, or on Atlantic cod when they were caught.

3.4.2. Stomach contents

A large number of prey items were found in the hooded seal stomachs indicating that hooded seals feed on a wide variety of fish and invertebrate prey. However, a high percentage of the wet weight ingested was accounted for by relatively few species. The prey species which contributed most to the overall diet according to reconstructed weights, included Greenland halibut, redfish sp., Arctic cod, Atlantic herring and capelin, in decreasing order. Squid (*Gonatus spp.*) were also a widespread food source, although they did not contribute much to the total ingested wet weight. The presence of demersal fishes such as redfish spp., eelpout, Atlantic cod, Greenland halibut, and other righteye flounders in the seal stomachs, suggests that hooded seals feed in deep water areas (Sergeant, 1976; Reeves & Ling, 1981).

The large difference in relative contributions of capelin between the two studies may have been due to the variation of time and distribution of seals and prey when collections were made. Most of the capelin in the previous study came from stomachs collected in 1989 and 1990, whereas capelin from the present study all came from 1991. It is also possible that the drop in capelin found in stomachs from the present study (1991) may have been a reflection of the availability of capelin during the period of time that seals were sampled. Water temperatures in 1991 were colder than any recorded for the last 45 years, resulting in a delay of capelin migration to inshore waters for spawning by an average of four weeks (Carscadden et al., 1992). This delay in timing may also have affected the availability of capelin as prey to hooded seals. As well, 1991 showed a drastic drop of the biomass of capelin in NAFO areas 2J3KL which was thought to be influenced by the unfavourable hydrologic conditions during that year (Bakenev, 1992).

Information on the foods of hooded seals is sparse but published literature generally reports similar prey types. Kapel (1982) reported that various demersal fish species constituted the major food items, listing Greenland halibut, redfish, capelin, and gadoids as important prey items. In Canadian waters, Sergeant (1976) also reported that redfish and Greenland halibut were important prey species of hooded seals.

Food studies of harp seals collected from the same regions as the sample of hooded seals taken in this study placed Arctic cod (43.7%) and capelin (37.7%) as the most abundant prey species found (I. Ni, Department of Fisheries and Oceans, St. John's, unpublished data). Percentage frequency of occurrence of Arctic cod and capelin in this study showed presence of

Arctic cod in 17.4% of the stomachs examined, and capelin in 4.3%. Other studies have also shown that harp seals feed mainly on pelagic fishes, dominated by capelin and Arctic cod, and on a variety of invertebrates, particularly euphausids and shrimps (Finley et al., 1990; Lydersen et al., 1991). This information suggests that although harp seals and hooded seals do share a common geographical range, and some prey type preferences overlap, the prey species consumed differ in relative importance, according to frequency of occurrence. Thus, competition for food is unlikely.

3.4.3. Reconstructions of hooded seal prey

Sizes of prey estimated from stomach content remains, suggests that hooded seals eat fish within a particular size range. Mean lengths of Atlantic herring, redfish, Atlantic cod, and Greenland halibut all fell between 25 - 35 cm, and weights averaged between 235 - 250 g. As expected, Arctic cod and capelin showed smaller mean lengths and weights. No previous studies have estimated the size of prey consumed by hooded seals. However, grey seals off eastern Canada, which are of comparable size, appear to consume a similar size range of prey (Benoit & Bowen, 1990). Harp seals, which are smaller phocids, don't appear to consume the larger fish prey, however, Arctic cod and capelin are common food items. Studies have shown that harp seals consume smaller - sized Arctic cod (Finley et. al., 1990), and similar - sized capelin (Murie & Lavigne, 1991).

When mean prey lengths of fish ingested by male and female hooded seals were compared, no sex differences were found, implying that males and females eat the same sized fish. Comparisons of this sort have not been done previously on hooded seals, but studies on harp seals in the Gulf of St. Lawrence (Murie & Lavigne, 1991), and in the Barents Sea (Lydersen et al., 1991) also found no sex related differences in fish prey size. Although data indicate that hooded seals consume similar sized prey in both winter and summer, a larger sample size of seals from different months is needed to substantiate this.

As well as providing estimates of size of prey consumed, reconstructing actual weights of prey were used to describe the relative importance of prey items in the diet of hooded seals. Using reconstructed weight proportions, many of the critical problems which exist when diet is described by either the relative frequency of occurrence or the numerical method is eliminated. Figure 3.6. demonstrates how inconsistencies in the relative importance of prey to the diet can be achieved depending on which method of expression is used to present results. For example, the commonly used frequency of occurrence and numerical methods placed squid at the top in prey value, whereas squid are much less valuable when viewed as percent contribution by weight.

Comparisons of the proportions of fish consumed, by weight, for males and females suggests that hooded seals eat the same proportions of important fish prey. However, their diet may be dependent on seasonal variablilty in prey species as differences were found between the proportion of fish represented in the diet, and the season in which the stomach was taken. The proportion of redfish spp. and Atlantic herring consumed by hooded seals was significantly larger in the summer months, whereas the relative proportion of Arctic cod consumed in the winter was significantly larger. Seasonal differences in prey eaten has also been observed in both harbour (Härkönen, 1987) and harp seals (Kapel & Angantyr, 1989) in coastal waters of Greenland.

Little information is available in the literature on seasonal changes in population sizes and migratory patterns of common hooded seal fish prey. However, times and locations of spawning are available for most species. Hooded seals may feed more actively on species in the pre - spawning phase, at which time fish are more energetically rich, than in the post - spawning time when females are spent, and are of poor quality, energetically - speaking. Both redfish and Atlantic herring inhabit the waters of Newfoundland and Labrador year round (Ni & McKone, 1981; Winters, 1976; respectively). Spawning occurs primarily between April and June for redfish, and between May and June for Atlantic herring (Scott & Scott, 1988). Although there are two spawning periods for herring, those inhabiting Newfoundland's east coast are predominantly spring spawners (Winters, 1976). Arctic cod spawn primarily in the winter between December and March (Scott & Scott, 1988). A pre - spawning migration northward occurs in the early fall where Arctic cod concentrate in dense schools in nearshore waters (Bradstreet et. al., 1986).

Greenland halibut are distributed throughout the northwest Atlantic. The main spawning component occurs in the deep waters of Davis Strait. As fish approach maturity (between 6 - 9 years), they migrate northward into Davis Strait for spawning in the late winter or early spring, then move back down to the deep - water bays surrounding Newfoundland (Bowering & Brodie, 1991). Greenland halibut are slow growing animals that live in excess of 20 years and grow up to 100 cm in length (Scott & Scott, 1988). In waters surrounding Newfoundland and Labrador, most commercial and research catches have shown a scarcity of mature fish (Bowering, 1983). Since these fish are of a comparable size range to those eaten by hooded seals, it is likely that many of the fish eaten by the hooded seals are also immature, thus exhibiting no pre- or post- spawning energetic fluctuations.

The relative abundance of the fish species may also have a strong influence on the composition of the food in the diet of seals. It is possible that the difference in proportions of prey eaten in winter and summer months is simply due to the availability of certain prey in the area during those seasons. They may also be selectively choosing different prey in order to fill their energetic needs.

CHAPTER 4:
Energetic analysis of diet of hooded seals

4.1. Introduction

Information on the types of prey consumed by hooded seals and corresponding estimates of size and proportions of food ingested per meal is critical to understanding food habits of hooded seals in the northwest Atlantic. However, to more fully understand the role hooded seals play in the ecosystem, and its possible interaction with other marine resources such as commercial fish, information on the relative energetic contribution of each food item to the diet must be included. The relative contribution of prey by weight (calculated in Chapter 3) provides useful information on their diet, however, a bioenergetic approach, in which the caloric content of the fish consumed is used in conjunction with the weight of the fish, presents a more reliable measure of diet (Lavigne, Barchard, Innes & Øritsland, 1982).

By combining estimates of the daily energy requirements of hooded seals in the wild, and the proximate composition of each prey item consumed by the seals, a better idea of the biological importance of prey to the diet can be achieved. By integrating information gained through stomach content analysis (such as types and weights of the prey items ingested) with energy contents of each prey item, and energy requirements of hooded seals, the number of prey that hooded seals need to consume in order to satisfy their daily energy requirements can be estimated. Eventually, these estimates can be projected to various seal population sizes to predict annual food consumption by an entire population (Lavigne et al., 1982; Lavigne, Innes, Stewart & Worthy, 1985).

Two important assumptions must be considered when making such predictions based on stomach contents. The assumption that hooded seals consume all parts of their prey is implicit in the use of otolith analysis to assess stomach contents, and relative importance of prey to the overall diet (Murie, 1987). As well, it is assumed that contents from the stomach, with the exception of squid, are probably a product of one recent meal. A high metabolic rate, and the high water content of the digesta, allows seals to digest their food quickly (Helm, 1984; Murie & Lavigne, 1985), and many studies have consistently shown that otoliths represent recent ingestion of fish (with 24 h) (Frost & Lowry, 1980; Finley & Gibb, 1982; Murie & Lavigne, 1986; 1991). Although squid beaks may remain in stomachs indefinitely, they contribute very little by weight in the relative contribution to the overall diet.

Few studies exist which have incorporated measurement of weight of the various prey items consumed, the proximate composition of those prey items, and the estimated caloric intake of the seal. Using data on captive animals, some estimates of these factors have been made for both harp seals (Sergeant, 1973) and harbour seals (Boulva, 1973). Weight, number, and caloric content of prey species have been used to reconstruct the diet of a number of species, for example, the summer diet of harp seals in the

Canadian high Arctic (Finley & Gibb, 1984). Caloric contents of prey species have also been used to determine the relative importance of fish to the diet of wild harp seals feeding in the St. Lawrence estuary during January and February (Murie et al., 1991), and grey seals (*Halichoerus grypus*) in the northwestern Gulf of St. Lawrence (Murie & Lavigne, 1992). However, little has been documented on the caloric content of the diet of hooded seals.

The main objective of this chapter was to determine the relative importance of each of the most common prey species to the total diet of hooded seals in Newfoundland by using energetic content information of the prey species most commonly taken. Relative importance of each prey item to the total diet of the seal was defined as the percent total gross energy of prey.

4.2. Materials and Methods

4.2.1. Energetic Values of Prey and Stomach Contents

Energy densities (kJ/g) of each of the most common prey species of hooded seals, determined in Chapter 3, were obtained from the published literature, or derived from analyses done by Department of Fisheries and Oceans personnel when appropriate values were not otherwise available (Table 4.1). Seasonal or monthly values are given for each fish species whenever possible.

Table 4.1. Energy values of important prey species of hooded seals (*Cystophora cristata*) showing spatial and temporal differences whenever possible.

Fish Species	Energy Density (kJ/g)	N	Location	Season or Month	Source
Greenland halibut ***R. hippoglossoides***	4.4[1]	2	Newfoundland	Winter	1
	5.7[2]	2	Newfoundland	Winter	1
	6.6[3]	3	Newfoundland	Winter	1
	8.0[4]	4	Newfoundland	Winter	1
Redfish spp. **(*Sebastes spp.*)**	4.4	≥ 5	Gulf of Maine	Winter	2
	4.5	5	Newfoundland	Summer	1
Atlantic herring **(*C. harengus*)**	8.6	13	Newfoundland	January	3
	8.4	100	Newfoundland	February	3
	7.9	22	Newfoundland	March	3
	6.2	36	Newfoundland	April	3
Arctic cod **(*B. saida*)**	4.1	5	Newfoundland	Winter	1
	5.4	10	High Arctic	Summer	4
Capelin **(*M. villosus*)**	7.5	?	Newfoundland	March	5
	6.2	?	Newfoundland	April	5
Atlantic cod **(*G. morhua*)**	4.2	≥ 5	Newfoundland	All year	2
Squid **(*Gonatus spp.*)**	3.8	4	NE Atlantic	?	6

[1] Calculated for fish 15-20 cm
[2] Calculated for fish 25-30 cm
[3] Calculated for fish 30-35 cm
[4] Calculated for fish 35 + cm

1. N. Cheeseman, DFO, St. John's, pers. comm.
2. Steimle Jr. & Terranova (1985)
3. Hodder, Parsons, Winters & Spencer (1973)
4. Finley & Gibb (1984)
5. Montevecchi & Piatt (1984)
6. Clarke, Clarke, Holmes & Waters (1985)

Fish specimens examined at the Department of Fisheries and Oceans were collected off the east coast of Newfoundland by DFO personnel on research vessels. An attempt was made to collect fish which were directly comparable, morphometrically, temporally and spatially, to prey eaten by the hooded seals. Specimens were frozen upon capture and stored at - 20° C. Samples were thawed prior to proximal content analyses. Fish were analyzed for moisture (fresh — dried weight), protein (Kjeldahl method), lipid (diethyl ether extraction), and ash contents (combustion in muffle furnace) (see Montevecchi and Piatt, 1984).

Energetic values of each fish examined from stomach content analysis was determined by multiplying the estimated wet weight of each fish by the caloric density, according to the date of capture.

The relative importance of prey to the diet was expressed as the percent contribution to gross energy intake. These values were compared with the percent wet weight estimates obtained in the previous chapter.

4.3. Results

The mean energetic values for Atlantic herring, Atlantic cod and Greenland halibut were very similar, averaging between 1600 and 1700 kJ (Table 4.2.). Average redfish energy values were around 1100 kJ. Arctic cod, capelin and squid were considerably lower, ranging from approximately 40 - 250 kJ. Ranges in energetic values probably reflect the large range in weights of fish examined.

Relative contributions of prey, expressed as the percent total energy of prey recovered, was determined for all stomachs collected between 1982 - 1991, excluding those caught incidentally from offshore trawlers (Table 4.3.). Since it was not possible to estimate weights for all stomach contents, total gross energy throughout this study represents only the major prey items, which account for over 80% or the diet by relative frequency of occurrence determined in Chapter 3. Greenland halibut was the greatest contributor, by energy, comprising appro: .mately 53% of the total gross energy of prey recovered. Both redfish spp. and Atlantic herring contributed between 16 - 17%, while Arctic cod accounted for approximately 11% or the total energy consumed. Atlantic cod, capelin, and squid each contributed less than 1% of the total energy to the diet.

Table 4.2. Energy values (E = kJ/animal) of common prey species of hooded seals (*Cystophora cristata*) taken between 1982 - 1991 by collectors in inshore and offshore waters of Newfoundland excluding those caught incidentally by offshore trawlers.

Prey Species	No. Prey	Mean E per Individual (kJ)	Range in E value per Individual Prey (kJ)	Std. Dev.
Atlantic herring (*C. harengus*)	22	1604.48	616.53 — 2836.60	579.60
Redfish spp. (*Sebastes spp.*)	29	1094.20	148.68 — 2942.37	728.48
Arctic cod (*B. saida*)	23	256.81	84.95 — 503.52	138.61
Atlantic cod (*G. morhua*)	2	1692.05	1544.34 — 1839.77	208.90
Capelin (*M. villosus*)	5	171.93	120.65 — 201.00	32.49
Greenland halibut (*R. hippoglossoides*)	57	1642.63	205.92 — 5844.00	1422.49
Squid (*Gonatus spp.*)	452	41.93	2.32 — 740.62	45.79

Table 4.3. Relative contributions of common prey species of hooded seals (*Cystophora cristata*) collected from inshore and offshore waters surrounding Newfoundland. Samples taken incidentally from offshore trawlers are excluded. Percent total energy refers only to the major prey items examined, which accounts for over 80% of the total diet.

Prey Species	Number of Stomachs	Total Energy (kJ)	% of Total Energy
Greenland halibut *R. hippoglossoides*	30	196149.74	53.0
Redfish spp. (*Sebastes spp.*)	20	63617.50	17.2
Arctic cod (*B. saida*)	8	41478.05	11.2
Atlantic herring (*C. harengus*)	10	61068.37	16.5
Atlantic cod (*G. morhua*)	2	3384.11	0.9
Capelin (*M. villosus*)	4	1625.78	0.4
Squid (*Gonatus spp.*)	39	2694.81	0.8

4.4. Discussion

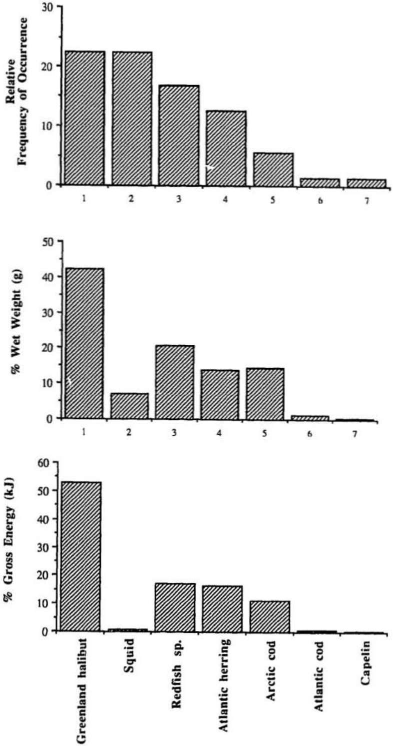
4.4.1. Energetic contribution of prey to the diet

The majority of energy consumed by hooded seals in Newfoundland throughout the year came from Greenland halibut, redfish spp., Atlantic herring, and Arctic cod, contributing a total of approximately 98% of energy estimated. Just over half was provided by Greenland halibut (53%). Little difference was observed in the relative importance of prey items in the diet when expressed both energetically and by reconstructed weights (Fig. 4.1.). The mass of fish consumed by an individual seal was, in general, proportional to its gross energy intake. Small differences were found for Atlantic herring and Arctic cod due to the fact that Atlantic herring were considerably energetically richer than Arctic cod. The importance of squid was further reduced when expressed energetically, especially compared to frequency of occurrence.

Of the seven most common prey species found in hooded seal stomachs, Atlantic herring, Greenland halibut and Atlantic cod shared equally high, and similar mean energetic values (Table 4.2.). However, in this study, approximately 53% of the energy obtained from prey came from Greenland halibut, 16.5% from Atlantic herring, and only 0.9% from Atlantic cod. Mean energy per individual may be misleading as there was a

Fig. 4.1.

Relative importance of six common prey species in the diet of hooded seals caught in the waters of Newfoundland between 1982 - 1991 by (a) relative frequency of occurrence of prey recovered, (b) percent wet weight of prey, and (c) percent gross energy of prey recovered.



30
20
10
0
Relative Frequency of Occurrence
1
2
3
4
5
6
7
50
40
30
20
10
0
% Wet Weight (g)
1
2
3
4
5
6
7
60
50
40
30
20
10
0
% Gross Energy (kJ)
Greenland halibut
Squid
Redfish sp.
Atlantic herring
Arctic cod
Atlantic cod
Capelin

large difference between Atlantic cod and Greenland halibut and Atlantic herring in the number of fish eaten, and range of energy values.

Seasonal comparisons of prey consumed (determined in Chapter 3) are contradictory to what would be expected, energetically. Although the contribution of Atlantic herring (by % weight) was significantly larger in the summer months, and the proportion of Arctic cod consumed in the winter was significantly larger, the seasonal variations in energetic densities of these two species are reversed (Table 4.1.). Change in food preference between winter and summer is, therefore, probably not due only to the energetic value of the prey, but is more likely due to the availability of these fish in the area during the time that the seals are feeding. Abundance estimates of fish occupying the same area as hooded seals, during the same time period are needed.

Obtaining appropriate energy densities of fish is critical to the analysis of the relative contribution of prey to the diet as differences in energy density of prey alone may affect the estimated biomass of food consumed by a factor of three or more (Lavigne et al., 1982; Murie et al., 1991). Although for most cases winter and summer caloric values were available for fish species, results obtained from analysis done for this study came from fish which had been frozen for an extended period of time. There was considerable moisture present in the Arctic cod and redfish sample bags when thawed which may have affected the outcome of the proximal composition analysis.

The sample sizes of fish used to obtain energy densities were low in most cases, or were not morphometrically, spatially, or temporally representative of the prey consumed by hooded seals. The size range of Greenland halibut used to discern energy densities was adequate for this study. However, in order to substantiate the claim that the energy density of Greenland halibut increases with fish length, it would be beneficial to obtain energy densities for a larger sample size of fish of varying sizes. Although a second order polynomial regression of prey length against energy density was very significant ($r^2 = .94$, $n = 10$, $p < .0001$), sample sizes from different size classes used were very low (Table 4.1.).

4.4.2. Seal / Fishery Interaction

In order to understand the potential impact that hooded seals may have on the fish stocks and commercial fisheries, information on the total energy consumption of hooded seals is important (Lavigne et al., 1982). Unfortunately, energetic requirements of hooded seals in the wild are not known.

In the past, the energy requirements of hooded seals have been estimated based on studies of other phocids and expressed as rate of food consumption. The Report of the Royal Commission (1986), estimated that hooded seals consume approximately 4% of their body weight per day. However, using percent body weight for food consumption is not strictly correct. Consumption varies seasonally, with the maturity of the animal, and with energy content of the prey species. Body mass, blubber thickness, activity, and energy requirements of hooded seals vary throughout the year. For example, during the breeding season, hooded seals undergo a period of little to no food consumption, and lose up to 20% of their body weight (Bowen et al., 1987; Kovacs & Lavigne, 1992). Therefore, they may eat more than their immediate requirements at some point during the rest of the year in order to replace the weight lost and prepare for the next breeding season. Consumption of resources must, therefore, vary seasonally. As well, hooded seals eat a variety of prey, and change the relative contributions of these prey to the diet seasonally. It is important, therefore, to obtain energetic information which corresponds to the changes seals undergo throughout the year.

Various approaches can be taken to estimate energy requirements of wild seals. Following the conventional energetic scheme (Kleiber, 1975), the caloric intake of the seal is calculated from estimates of the quantity of food ingested per meal, the frequency of feeding, measurement of the weight of various prey items consumed, and the proximate composition of those prey items (Lavigne et al., 1982). In a more complex model used to evaluate the annual energy budget of seals (SEAERG), additional factors such as seal mortality, seawater and air temperatures, and body growth for seals of each sex and age, and time - activity budgets, are incorporated into the model (Øritsland & Markussen, 1990). A sample population model is combined with a physiological model. Unfortunately, many of these parameters, such as measurements of urinary or faecal loss, estimates of the heat increment of feeding relative to the energy content of food, activity levels, and body temperatures in hooded seals or other pinnipeds are unavailable in the published literature (Lavigne et al., 1982).

Conventional estimates of metabolic rates of wild animals usually involve multiples of basal metabolic rate extrapolated from laboratory to field situations (for example, Murie & Lavigne, 1991). However, such estimates may not accurately estimate direct measurements in the wild. Doubly labeled water techniques are also used to estimate field metabolic rates of wild animals (Nagy, 1983; Birt-Friesen, Montevecchi, Cairns & Macko, 1989), although potential errors are also present using this technique (Nagy & Costa, 1980). No published information is available on metabolic rates of wild seals using this methodology.

Hooded seals in the northwest Atlantic appear to spend time in areas that are exploited by commercial fisheries. There is no doubt that they eat commercial fish species, and commercially - sized fish. It is not possible, however, to evaluate the impact of local predation on individual fish stocks before more information is collected with respect to both behavioural and physiological characteristics of seals. As well, similar temporal and spatial information on fish migrations, abundance and energetic contents in Canadian waters are needed.

CHAPTER 5:
Summary

Knowledge of diet is fundamental to studies of the ecology of seals and especially to any understanding of their role as predators in the northwest Atlantic marine ecosystem. Although hooded seals are the largest of the northern phocids, and are abundant in the North Atlantic and Arctic seas, very little quantitative data is available on their feeding behaviour and dietary preferences. Lack of information on hooded seals is most likely due to their general living environment, and inaccessibility to humans.

The main objective of this study was to determine the diet and feeding ecology of hooded seals off the coast of Newfoundland by the analysis of stomach contents. Three steps were involved. In the first part, regression equations were established to estimate fish size from otolith size for the most common prey species of hooded seals. In the second phase, stomach contents were determined by analysis of species — specific otoliths, eye lenses and other characteristic bony parts such as vertebrae in fishes, as well as carapaces and beaks in invertebrates. Sizes of fish at ingestion were then reconstructed using the equations derived from the first section. In the third phase, the caloric densities of important prey items consumed by the seals were determined, and combined with estimated sizes of the prey items ingested, established in the second section, such that the total caloric intake of each species consumed by the seal could be estimated. These energetic values were used to evaluate the relative contribution of prey to the diet in an attempt to gain a better understanding of prey choice by the hooded seals.

5.1. Summary of establishing regression equations

Sizes for six common prey species found in waters off the northeast coast of Newfoundland and Labrador were derived through growth back - calculation procedures based on the proportionality between fish size and otolith size. The regression method estimated fish length and fish weight from the measured size of the otolith into a fish length / weight - otolith length / height regression derived from samples of the population. Differences in length and height between left and right otoliths of each species, as well as spatial and temporal differences in size within each fish species were also examined.

No differences were found between measurements from left and right otoliths; therefore, the average measurement of the left and right otoliths for each fish were plotted against fish length.

For all species except Greenland halibut, the highest possible correlation between otolith size and fish length / weight was established using the maximum length of the otolith. For Greenland halibut, maximum otolith height gave a better correlation.

For Arctic cod, capelin and Atlantic herring, least squares linear regressions provided the best predictive equations of fish length from otolith size, whereas second order polynomial regressions provided a better fit for Atlantic cod, Greenland halibut and redfish. The relationships between otolith length / height and fish weight were investigated by fitting linear least squares regressions to the log - transformed data. Coefficients of determination for all equations ranged from .80 to .98.

Spatial and temporal differences within samples were examined for four of the six most important prey species which contained subsets of fish from different areas and years. Growth rates for both capelin and Atlantic herring were significantly different between 1990 and 1991. Although Greenland halibut and redfish growth rates were similar between two different areas, significantly different intercepts for redfish suggested a possible morphometric difference between subsets perhaps due to sampling of different stocks or even different species.

These results suggested that regression equations may vary within or between a species both spatially and temporally. However, because sex and stock of fish samples were not distinguished, and samples were not available from all areas and years for all species in this study, data for all fish within each species were pooled. Further studies are needed using larger sample sizes, taking gender and stocks into account, and employing samples from all appropriate areas, seasons, and years.

5.2. Summary of diet composition of hooded seals

Hard parts of prey remains found in the complete stomach contents of hooded seals were examined. A total of 132 hooded seal stomachs were collected from inshore and offshore waters surrounding Newfoundland between 1987 - 1991. The majority of stomachs (73%) came from the nearshore region along the northeast coast of Newfoundland and were taken in April. No stomachs were available from the Labrador region. No pups were taken. Over half of the samples collected were females (64.2%).

A total of 14 prey groups were identified, including 10 species of fish and 4 invertebrates. Relative importance of prey, expressed as the percent total wet weight of prey recovered, was determined for all stomachs collected between 1982 - 1991, excluding those caught incidentally from offshore trawlers. Greenland halibut was by far the most important species, followed by redfish sp., Arctic cod, Atlantic herring, squid, Atlantic cod and capelin, in decreasing order of importance. Expressing relative importance of prey to the hooded seal diet as percent total reconstructed wet weight was considered to be an improvement on the other traditional methods which include percent frequency of occurrence and numerical proportions.

Through estimating lengths and weights of fish from regression equations established in the previous section, it was discovered that hooded seals fed mainly on a particular size range of food. For the larger fishes, the average lengths ranged from 25 - 35 cm, while for the two smaller species, lengths ranged from 15 - 25 cm. Fish consumed by seals caught incidentally from offshore trawlers were larger than those taken elsewhere.

The estimated sizes (length), and proportions (% weight) of fish found per stomach did not differ significantly between male and female hooded seals, implying that males and females ate similarly - sized fish and similar proportions of fish species within their diets.

The proportions, by percent weight, of redfish and Atlantic herring consumed by hooded seals were significantly larger in the summer months, whereas the relative proportion of Arctic cod consumed was significantly larger in the winter months. No seasonal differences were found in actual lengths of fish eaten, suggesting that hooded seals ate the same - sized fish throughout the year. However, the shift in ratios of common food items consumed between winter and summer suggested either a change in food availability or preference.

Four of the five fish species significant (by weight) to the diet of hooded seals examined in this study were also important commercial species: Greenland halibut, capelin, Atlantic herring and redfish spp. Estimated sizes of these prey eaten by hooded seals are also the same sizes of fish taken by commercial fisheries. Thus, in relation to size, there is potential for direct competition between the seals and the fishery. The information given by the food of the seals in inshore waters along the northeast coast of Newfoundland suggests that Greenland halibut is the most important species by weight and frequency together with redfish spp. and Atlantic herring. Several abundant commercial fish species such as Atlantic cod, American plaice and grenadiers which share habitats with hooded seals in March and April in this area, are not found in their diet.

5.3. Summary of energetic analysis of prey consumed by hooded seals

The caloric values for six common prey species of hooded seals were determined by proximate composition analysis. As stomachs were obtained from different seasons and areas, and it is well known that caloric values of fish may vary both seasonally and temporally, an attempt was made to collect fish from locations corresponding to those from which the seals were taken.

Of the prey species examined, Greenland halibut, Atlantic herring and Atlantic cod all shared the highest average energetic values, followed by redfish, Arctic cod, capelin and squid.

Relative contribution of prey, expressed as the percent total gross energy of prey recovered, was determined for all stomachs collected between 1982 and 1991, excluding those caught incidentally offshore. Greenland halibut was by far the most important species, contributing approximately 53% of the total energy consumed, followed by redfish, Atlantic herring, Arctic cod, squid, Atlantic cod and capelin, in decreasing order of importance. These proportions corresponded with those obtained from percent total wet weight of prey recovered.

No sex differences were found in the proportion of fish eaten expressed as the percent total gross energy ingested. However, seasonal differences in energetic values for redfish, Arctic cod and Atlantic herring consumed by hooded seals were found. This corresponded with the proportions of prey eaten by hooded seals expressed as percent gross weight ingested. Since Arctic cod are more energetically rich in the summer, but comprised a higher proportion of the diet in the winter, and vice versa for Atlantic herring, it is likely that hooded seals do not rely simply on energetic value of prey, but may choose prey which are more readily available, or easier to catch.

Hooded seals in the northwest Atlantic appear to spend time in areas that are exploited by commercial fisheries. There is no doubt that hooded seals eat commercial fish species, and commercially - sized fish. It is not possible, however, to evaluate the impact of local predation on individual fish stocks before more information is collected with respect to both behavioural and physiological characteristics of seals, i.e. locations and basal metabolic rates in the wild throughout the year. As well, similar temporal and spatial information on fish migrations, abundance and energetic contents in Canadian waters are needed.

References

Antonelis, G. A., Fiscus, C. H. & DeLong, R. L. (1984). Spring and summer prey of California sea lions, *Zalophus californianus* , at San Miguel Island, California, 1978-79. Fishery Bulletin, 82, 67-76.

Atkinson, D. B. & Gavaris, C. A. (1981). Divisions 3LN redfish stock assessment. Northwest Atlantic Fisheries Organization Scientific Council Meeting Research Document, 81/VI/59(Serial No. N343), 1-3.

Beddington, J. R., Beverton, R. J. H. & Lavigne, D. M. (1985). Marine Mammals and Fisheries . George Allen and Unwin Ltd., Boston, MA. 354 pp.

Benoit, D. & Bowen, W. D. (1990). Seasonal and geographic variation in the diet of grey seals in Eastern Canada. Canadian Bulletin of Fisheries and Aquatic Sciences, 222, 215-226.

Bigg, M. A. & Fawcett, I. (1985). Two biases in diet determination of northern fur seals (*Callorhinus ursinus*). In J. R. Beddington, R. J. H. Beverton & D. M. Lavigne (Ed.), Marine Mammals and Fisheries (pp. 284-291). George Allen and Unwin Ltd. Boston, MA. 354 pp.

Birt - Friesen, V.L., Montevecchi, W.A., Cairns, D.K. & Macko, S.A. (1989). Activity - specific metabolic rates of free - living northern gannets and other seabirds. Ecology, 70(2), 357-367.

Bonner, W. N. (1982). Seals and Man, a Study of iInteractions . University of Washington Press, Seattle, WA.

Boulva, J. (1973). The harbour seal, *Phoca vitulina concolor*, in eastern Canada. PhD. Thesis, Dalhousie University, Halifax.

Bowen, W. D. (1985). Harp seal feeding and interactions with commercial fisheries in the northwest Atlantic. In J. R. Beddington, R. J. H. Beverton & D. M. Lavigne (Ed.), Marine Mammals and Fisheries (pp. 135-152). George Allen & Unwin Ltd. Boston, MA. 354pp.

Bowen, W. D., Bonness, D. J. & Oftedal, O. T. (1987). Mass transfer from mother to pup and subsequent mass loss by the weaned pup in the hooded seal (*Cystophora cristata*). Canadian Journal of Zoology, 65, 1-8.

Bowen, W. D., Myers, R. A. & Hay, K. (1987). Abundance estimation of a dispersed dynamic population: hooded seals (*Cystophora cristata*) in the Northwest Atlantic. Canadian Journal of Fisheries and Aquatic Sciences, 44, 282-295.

Bowen, W. D., Sergeant, D. E. & Øritsland, T. (1983). Validation of age estimation in the harp seal (*Phoca groenlandica*) using dental annuli. Canadian Journal of Fisheries and Aquatic Sciences, 40, 1430-1441.

Bowering, W.R. (1983). Age, growth, and sexual maturity of Greenland halibut, *Reinhardtius hippoglossoides* (Walbaum), in the Canadian Northwest Atlantic. Fishery Bulletin, 81(3), 599-611.

Bowering, W. R. (1984). Migrations of Greenland halibut, *Reinhardtius hippoglossoides* , in the northwest Atlantic from tagging in the Labrador - Newfoundland region. Journal of the Northwest Atlantic Fisheries Sciences, 5, 85-91.

Bowering, W.R. & Brodie, W.B. (1991). Distribution of commercial flatfishes in the Newfoundland - Labrador region of the Canadian Northwest Atlantic and changes in certain biological parameters since exploitation. Netherlands Journal of Sea Research, 27(3/4), 407-422

Bradstreet, M.S.W., Finley, K.J., Sererak, A.D., Griffiths, W.B., Evans, C.R., Fabijan, M.F. & Stallard, H.E. (1986). Aspects of the biology of Arctic cod (*Boreogadus saida*) and its importance in Arctic marine food chains. Canadian Technical Report of Fisheries and Aquatic Sciences, No. 1491, October.

Brown, R. F. & Mate, B. R. (1983). Abundance, movements, and feeding habits of harbour seals, *Phoca vitulina*, at Netarts and Tillamook Bays, Oregon. Fishery Bulletin, 81(2), 291-301.

Campana, S. E. (1990). How reliable are growth back-calculations based on otoliths? Canadian Journal of Fisheries and Aquatic Sciences, 47, 2219-2227.

Carlander, K. D. (1981). Caution on the use of the regression method of back-calculating lengths from scale measurements. Fisheries, 6, 2-4.

Carscadden, J., Frank, K. T. & Nakashima, B. S. (1992). Why was inshore capelin (*Mallotus villosus*) spawning delayed during 1991? Canadian Atlantic Fisheries Scientific Advisory Committee Research Document, 92/61, 14 pp.

Clarke, M. R. (1986). A Handbook for the Identification of Cephalopod Beaks. Clarendon Press, Oxford. 441 pp.

Clarke, A., Clarke, M.R., Holmes, L.J. and Waters,T.D. (1985). Calorific values and elemental analysis of eleven species of oceanic squids (Mollusca: Cephalopoda). J. mar. biol. Ass. U.K. 65, 983-986.

DaSilva, J. & Nielson, J. D. (1985). Limitations of using otoliths recovered in scats to estimate prey consumption in seals. Canadian Journal of Fisheries and Aquatic Sciences, 42(8), 1439-1442.

Fairbairn, D. J. (1981). Biochemical genetic analysis of population differentiation in Greenland halibut (*Reinhardtius hippoglossoides*) from the Northwest Atlantic, Gulf of St. Lawrence, and Bering Sea. Canadian Journal of Fisheries and Aquatic Sciences, 38, 669-677.

Finley, K. J., Bradstreet, M. S. W. & Miller, G. W. (1990). Summer feeding ecology of harp seals in relation to Arctic cod in the Canadian high Arctic. Polar Biology, 10, 609-618.

Finley, K.J. & Gibb, E.J. (1982). Summer diet of the narwhal (*Monodon monoceros*) in Pond Inlet, northern Baffin Island. Canadian Journal of Zoology, 60, 3353-3363.

Finley, K. J. & Gibb, E. J. (1984). Summer diet and feeding behaviour of harp seals in the Canadian high Arctic. In D. M. Lavigne, K. Ronald, & R. E. A. Stewart (Ed.), The Harp Seal: Perspectives in Vertebrate Science Junk Publ. The Hague.

Fitch, J. E. & Brownell, R. L. (1968). Fish otoliths in cetacean stomachs and their importance in interpreting feeding habits. Journal Fisheries Research Board of Canada, 25(12), 2561-2574.

Frost, K. J. (1980). Descriptive key to the Otoliths of Gadid Fishes of the Bering, Chukchi, and Beaufort Seas. Arctic, 34(1), 55-59.

Frost, K. J. & Lowry, L. F. (1980). Feeding of ribbon seals (*Phoca fasciata*) in the Bering Sea in spring. Canadian Journal of Zoology, 58, 1601-1607.

Frost, K. J. & Lowry, L. F. (1981). Trophic importance of some marine gadids in northern Alaska and their body-otolith size relationships. Fishery Bulletin, 79(1), 187-192.

Gales, R. P. (1988). The use of otoliths as indicators of little penguin, *Eudyptula minor*, diet. Ibis, 130(3), 418-426.

George-Nascimento, M., Bustamente, R. & Oyarzun, C. (1985). Feeding ecology of the South American sea lion *Otario flavescens* : Food contents and food selectivity. Marine Ecology Progress Series, 21, 135-143.

Hammill, M.O., Stenson, G.B., & Myers, R.A. (1992). Hooded seal (*Cystophora cristata*) pup production in the Gulf of St. Lawrence. Canadian Journal of Fisheries and Aquatic Sciences, 49, 2546-2550.

Härkönen, T. (1986). Guide to the Otoliths of the Bony Fishes of the Northeast Atlantic . Danbiu ApS. Biological Consultants, 513 pp.

Härkönen, T. (1987). Seasonal and regional variations in the feeding habits of the harbour seal, *Phoca vitulina*, in the Skagerrak and the Kattegat. Journal of Zoology, London, 213(3), 535-543.

Harwood, J. & Croxall, J. P. (1988). The assessment of competition between seals and commercial fisheries in the North Sea and the Antarctic. Marine Mammal Science, 4(1), 13-33.

Hays, W. L. (1988). Statistics (4th ed.). Holt, Rinehart and Winston, Inc., Orlando, Florida. 3054 pp.

Hecht, T. (1987). A guide to the identification of otoliths of Southern Ocean Fishes. South African Journal of Antarctic Research, 17, 1-87.

Helm, R. (1984). Rate of digestion in three species of pinnipeds. Canadian Journal of Zoology, 62, 1751-1756.

Hodder, V.M., Parsons, L.S., Winters, G.H. & Spencer, K. (1973). Fat and water content of herring in Newfoundland and adjacent waters, 1966-71. Fish. Res. Bd. of Can. Tech. Report ,No. 365.

Hyslop, E. J. (1980). Stomach contents analysis - a review of methods and their application. Journal of Fish Biology, 17, 411-429.

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

Kapel, F. O. (1980). Review of studies of hooded seals in Greenland, 1970-1979. Northwest Atlantic Fisheries Organization Scientific Council Research Document, 80/XI/170(Serial No. N257), 1-18.

Kapel, F. O. (1982). Studies on the Hooded Seal, *Cystophora cristata*, in Greenland, 1970-80. North Atlantic Fisheries Organization Science Council Studies, 3, 67-75.

Kapel, F. O., & Angantyr, L. A. (1989). Feeding patterns of harp seals in coastal waters off West Greenland, with a note on offshore feeding.

Keppel, G. (1989). Data analysis for research designs: analysis - of - variance and multiple regression / correlation approaches. W.H. Freeman, New York.

Khan, R. A., Dawe, M., Bowering, R. & Misra, R. K. (1982). Blood protozoa as an aid for separating stocks of Greenland halibut, *Reinhardtius hippoglossoides* , in the northwestern Atlantic. Canadian Journal of Fisheries and Aquatic Sciences, 39, 1317-1322.

King, J. (1983). Seals of the World . Cornell University Press, Ithaca , NY. 297 pp.

Kleiber, M. (1975). The Fire of Life: an Introduction to Animal Energetics . R.E. Krieger Publ. Co., Huntingdon, New York.

Kovacs, K. M. & Lavigne, D. M. (1986). *Cystophora cristata.* Mammalian Species, 258, 1-9.

Kovacs, K.M. & Lavigne, D.M. (1992). Mass - transfer efficiency between hooded seal (*Cystophora cristata*) mothers and their pups in the gulf of St. Lawrence. Canadian Journal of Zoology, 70, 1315-1320.

Lambert, T. C. (1987). Duration and intensity of spawning in herring, *Clupea harengus* , as related to the age structure of the mature population. Marine Ecology Progress Series, 39, 209-220.

Lavigne, D. M., Barchard, W., Innes, S. & Øritsland, N. A. (1982). Pinniped Bioenergetics. Mammals in the Sea (pp. 191-235). Food and Agriculture Organization of the United Nations. Rome.

Lavigne, D. M., Innes, S., Stewart, R. E. A. & Worthy, G. A. J. (1985). An annual energy budget for northwest Atlantic harp seals. In J. R. Beddington, R. J. H. Beverton, & D. M. Lavigne (Ed.), Marine Mammals and Fisheries (pp. 319-336). George Allen and Unwin Ltd. Boston, MA. 354 pp.

Leim, A. H. & Scott, W. B. (1966). Fishes of the Atlantic Coast of Canada. Fisheries Research Board of Canada, Ottawa.

Lien, J., Stenson, G.B. & Ni, I.H. (1988). A review of incidental entrapments of seabirds, seals and whales in inshore fishing gear in Newfoundland and Labrador: A problem for fishermen and fishing gear designers. Proceedings in World Symposium on Fishing Gear and Fishing Vessel Design. Marine Institute, St. John's, Newfoundland, 67-71.

Lydersen, C., Angantyr, L. A., Wiig, O. & Øritsland, T. (1991). Feeding habits of Northeast Atlantic harp seals (*Phoca groenlandica*) along the summer ice edge of the Barents Sea. Canadian Journal of Fisheries and Aquatic Sciences, 48(11), 2180-2183.

Messieh, S. N. (1972). Use of otoliths in identifying herring stocks in southern Gulf of St. Lawrence and adjacent waters. Journal of the Fisheries Research Board of Canada, 29, 1113-1118.

Misra, R. K. & Bowering, W. R. (1984). Stock delineation of Greenland halibut in the Northwest Atlantic using a recently developed, multivariate statistical analysis based on meristic characters. North American Journal of Fisheries Management, 4(4A), 390-398.

Montevecchi, W.A. & Piatt, J. (1984). Composition and energy contents of mature inshore spawning capelin (*Mallotus villosus*): implications for seabird predators. Comparative Biochemical Physiology, 78A(1), 15-20.

Morrow, J. E. (1979). Preliminary keys to otoliths of some adult fishes of the Gulf of Alaska, Bering Sea and Beaufort Sea. NOAA Technical Reports, National Marine Fisheries Services Circulations, 42, 32 pp.

Murie, D. J. (1987). Experimental approaches to stomach content analyses of piscivorous marine mammals. In A. C. Huntley, D. P. Casta, G. A. J. Worthy, & M. A. Castellini (Ed.), Approaches to Marine Mammal Energetics (pp. 253). Allen Press. Lawrence, KS.

Murie, D. J. & Lavigne, D. M. (1985). Digestion and retention of Atlantic herring otoliths in the stomachs of grey seals. In J. R. Beddington, R. J. H. Beverton, & D. M. Lavigne (Ed.), Marine Mammals and Fisheries George Allen and Unwin Ltd. Boston, MA. 354 pp.

Murie, D. J. & Lavigne, D. M. (1986). Interpretation of otoliths in stomach content analyses of phocid seals: quantifying fish consumption. Canadian Journal of Zoology, 64, 1152-1157.

Murie, D. J. & Lavigne, D. M. (1991). Food consumption of wintering harp seals, *Phoca groenlandica*, in the St. Lawrence estuary, Canada. Canadian Journal of Zoology, 69, 1289-1296.

Murie, D.J. & Lavgne, D.M. (1992). Growth and feeding habits of grey seals (*Halichoerus grypus*) in the northwestern Gulf of St. Lawrence, Canada. Canadian Journal of Zoology, 70, 1604-1613.

Nagy, K.A. (1983). The doubly labeled water ($^3HH^{18}O$) method: a guide to its use. University of California at Los Angeles Publication, Los Angeles, California, USA.

Nagy, K.A. & Costa, D.P. (1980). Water flux in animals: analysis of potential errors in the tritiated water method. American Journal of Physiology, 238, 454-465.

Narayanan, S., Prinsenberg, S. & Colbourne, E.B. (1992). Overview of environmental conditions in NAFO Divisions 2J + 3KL in 1991. Norwest Atlantic Fisheries Organization Scientific Council Meeting Research Document, 92/6 (Serial No. N2039), 25 pp.

Ni, I.-H. (1981). The use of vertebrae frequencies to indicate the distribution of sharp — beaked redfish *Sebastes mentella* and *S. fasciatus*. Norwest Atlantic Fisheries Organization Scientific Council Meeting Research Document, 81/VI/70(Serial No. N354), 1-9.

Ni, I.-H. & McKone, W. D. (1981). The distribution and concentration of redfish species in Newfoundland and Labrador waters. Northwest Atlantic Fisheries Organization Scientific Council Meeting Research Document, 81/VI/69(Serial No. N353), 1-5.

North, A. W., Croxall, J. P. & Doidge, D. W. (1983). Fish prey of the Antarctic fur seal *Arctocephalus gazella* at South Georgia. British Antarctic Survey Bulletin, (61), 27-37.

Parsons, L. S. (1976). Living Marine Resources of Newfoundland - Labrador: Status and Potential. Department of the Environment Fisheries and Marine Service, Ottawa, Ontario. 9-11.

Pierce, G. J., Boyle, P. R. & Diack, J. S.W. (1991a). Identification of fish otoliths and bones in faeces and digestive tracts of seals. Journal of Zoology, London, 224.

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

Pitcher, K. W. (1981). Prey of the stellar sea lion, *Eumetopias jubatus*, in the Gulf of Alaska. Fishery Bulletin, 79(3), 467-472.

Prime, J. H. & Hammond, P. S. (1987). Quantitative assessment of gray seal diet from fecal analysis. In A. C. Huntley, D. P. Costa, G. A. J. Worthy & M. A. Castellini (Ed.), Approaches to marine mammal energetics (pp. 165-181). Society for Marine Mammalogy. Lawrence, KS.

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

Rae, B. (1973). Further observations on the food of seals. Journal of Zoology, London, 169, 287-297.

Rasmussen, B. (1960). Om klapmyssbestanden i det nordlige Atlanterhav. [On the stock of hooded seals in the Northern Atlantic]. Fish oz Havet [Fish. Res. Bd. Can. Trans. Ser. No. 387].

Recchia, C. A. & Read, A. J. (1989). Stomach contents of harbour porpoises, *Phocaena phocaena*, from the Bay of Fundy. Canadian Journal of Zoology, 67, 2140-2146.

Reeves, R. R. & Ling, J. K. (1981). Hooded seal, *Cystophora cristata*. In S. H. Ridgeway & R. J. Harrison (Ed.), Handbook of marine mammals (pp. 171-194). Academic Press. London, England.

Report of the Royal Commission. (1986). Seals and Sealing in Canada. Vol. 3, Minister of Supply and Services Canada.

Reznick, D., Lindbeck, E. & Bryga, H. (1989). Slower growth results in larger otoliths: an experimental test with guppies (*Poecilia reticulata*). Canadian Journal of Fisheries and Aquatic Sciences, 46, 108-112.

Scott, W. B. & Scott, M. G. (1988). Atlantic Fishes of Canada. Canadian Bulletin of Fisheries and Aquatic Sciences, No. 219. 3249 pp.

Secor, D. H. & Dean, J. M. (1989). Somatic growth effects on the otolith-fish size relationship in young pond-reared striped bass, *Morone saxatilis*. Canadian Journal of Fisheries and Aquatic Sciences, 46, 113-121.

Selzer, L. A., Early, G., Fiorelli, P. M., Payne, P. M. & Prescott, R. (1986). Stranded animals as indicators of prey utilization by harbor seals, *Phoca vitulina concolor*, in southern New England. Fishery Bulletin, 84(1), 217-220.

Sergeant, D. E. (1973). Feeding, growth, and productivity of Northwest Atlantic harp seals (*Pagophilus groenlandicus*). 30(1), 17-29.

Sergeant, D. E. (1974). A rediscovered whelping population of hooded seals *Cystophora cristata*. Polarforschung, 44, 1-7.

Sergeant, D. E. (1976). Research on Hooded Seals *Cystophora cristata* Erxleben in 1976. 76/x/126, Ser. 4012.

Shepeleva, V. K. (1973). Adaptations of seals to life in the Arctic. In K. K. Chapskii, & V. E. Sokolov (Ed.), Morphology and Ecology of Marine Mammals (pp. 1-58). John Wiley & Sons. New York, NY.

Steimle Jr. & Terranova, R.J. (1985). Energy equivalents of marine organisms from the continental shelf of the temperate northwest Atlantic, J. Norw. Atl. fish. Sci., 6:117-124.

Stenson, G. B., Ni, I.-H., Ross, S.-A. & McKinnon, D. (1991). Hooded seal, *Cystophora cristata* , feeding and interactions with commerical fisheries in Newfoundland. Canadian Atlantic Fisheries Scientific Advisory Committee Research Document, 91/45, 1-16.

Treacy, S. D. & Crawford, T. W. (1981). Retrieval of otoliths and statoliths from gastrointestinal contents and scats or marine mammals. Journal of Wildlife Management, 45, 990-993.

Winters, G.H. (1976). Atlantic herring (*Clupea harengus*). In A.T. Pinhorn (Ed.), Living marine resources of Newfoundland - Labrador: status and potential. Bulletin of the Fisheries Research Board of Canada, Dept. of Env. Fish. and Mar. Ser., St. John's, NF.

Winters, G. H. (1982). Life history and geographical patterns of growth in capelin, *Mallotus villosus* , of the Labrador and Newfoundland areas. Journal of Northwest Atlantic Fisheries Sciences, 3, 105-114.

Øritsland, T. (1990). Seals in the Northeast Atlantic and Interactions with Fisheries. Comite Arctique International, Commentary(2), 10-13.

Øritsland, T. & Benjaminsen, T. (1975). Additional data on the sex ratio, age composition and morality of Newfoundland hooded seals, with an estimate of pup production and sustainable yield. 75/122, 3626.

Øritsland, N. A. & Markussen, N. H. (1990). Outline of a physiologically based model for population energetics. Ecological Modelling, 52, 267-288.