

Feeding habits of harp and hooded seals in Greenland waters

Finn O. Kapel

Skovvænget 10 A, DK-2970 Hørholm, Denmark.

ABSTRACT

Results of stomach contents analyses of harp and hooded seals collected in West Greenland waters in the period 1986-1993 are reviewed, and compared with published data and circumstantial information from local hunters.

The diet of harp seals in this region is variable but consists mainly of pelagic crustaceans (*Thysanoëssa* spp. and *Parathemisto libellula*) and small fish species like capelin (*Mallotus villosus*), sandeel (*Ammodytes* spp.), polar cod (*Boreogadus saida*) and Arctic cod (*Arctogadus glacialis*). Species of importance for commercial fisheries in Greenland, such as Northern prawn (*Pandalus borealis*), Atlantic cod (*Gadus morhua*), and Greenland halibut (*Reinhardtius hippoglossoides*) play a minor role in the diet of harp seals in this area.

Variation in the diet of hooded seals is less well documented, but in addition to the species also taken by harp seals, larger demersal fishes like Greenland halibut, redfish (*Sebastes* spp.), cod, and wolffish (*Anarhichas minor*) are apparently important prey items.

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Introduction

During the 1970's and 1980's, harp seals (*Phoca groenlandica*) and hooded seals (*Cystophora cristata*) were often on the front pages because of an intense debate concerning the commercial harvesting of seal pups at the whelping patches. Partly because of this debate and the following decreasing demand for seal skins, and partly because of management decisions leading to catch regulations, the commercial catches of these seals decreased dramatically (particularly off Newfoundland), and the Northwest Atlantic stock of harp seals has apparently increased (Stenson *et al.* 1993, Stenson *et al.* 1996). Also the stock(s) of hooded seals in the Northwest Atlantic may have increased, but the evidence for that is less convincing (Bowen *et al.* 1987,

Hammill *et al.* 1992, Stenson *et al.* 1997, Myers and Stenson 1996).

The rise in population size of harp seals (and other seals) may lead to another debate. The fishing industry and local fishermen are very concerned about the potential competition from consumption by these increasing seal stocks. This is not a new concern, but it is particularly relevant when seal stocks are expanding.

In Greenland, abundance of seals was previously not considered a problem, but rather a blessing, because sealing was an important and integrated way of living. In recent years, however, Greenland fishermen have also complained

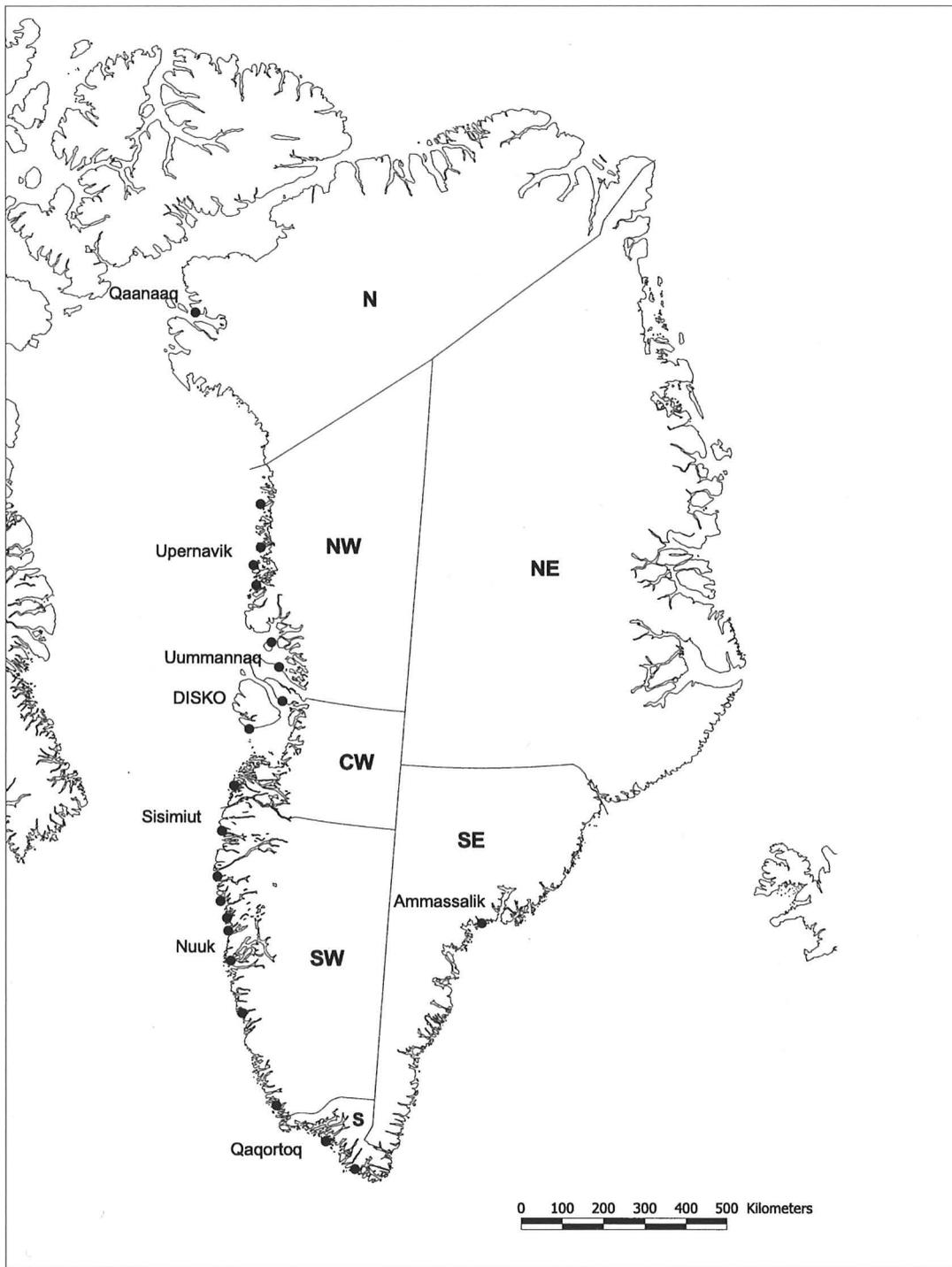


Fig. 1.
 Map of Greenland showing the geographical areas referred to and the locations from which stomach samples were obtained.

about the increasing number of seals. The concern has been about both the increasing direct interactions between local fisheries and seals, and also the possible negative effects on the commercial fisheries as a result of the consumption by the seals.

In order to examine the problem of the consumption by the seals, data on population sizes and dynamics, on the energy requirements of the seals, and on the feeding habits, are needed. The studies referred to in this paper are mainly addressing the last issue.

Table 1. Stomach samples of harp seals in Greenland, 1985-93.

DISTRICT	LOCALITY	YEAR	SEASON	N (empty)	ORIGIN ¹
THULE	Qaanaaq <i>et al.</i>	1985	(August) September	12 (2)	HMP
UPERNAVIK (n)	Nuussuaq/Kraulshavn	1985	October	12 (0)	HMP
	Nuussuaq/Kraulshavn	1989	October	8 (0)	GFR
	Nuussuaq/Kraulshavn	1990	August (September)	15 (0)	GFR
UPERNAVIK (s)	Innaarsuit	1990	August	5 (4 ²)	GFR
	Upernavik	1985	June	17 (2)	HMP
	Upernavik	1989	October	9 (0)	GFR
	Kangersuatsiaq/Prøven	1988	September	146 (4)	GFR
UUMMANNAQ	Illorsuit	1985	August	57 (2)	HMP
	Quaasut	1989	August	86 (12)	GFR
CWe (Disko Bay)	Saqqaq	1991	August-September	50 (2)	GFR
	Saqqaq	1991	September-November	47 (1)	GFR
CWw (Disko Island)	Qeqertarsuaq/Godhavn	1987	September-October	74 (3)	LAA
	Qeqertarsuaq/Godhavn	87-88	December-January	41 (1)	LAA
	Qeqertarsuaq/Godhavn	1988	June-August	98 (5)	LAA
CWw (Kangaatsiaq)	Attu	1986	February-March	24 (0)	HMP
	Attu	1988	January-February	12 (0)	LAA
OFFSHORE	St. Hellefiske Bank	1988	July	16 (0)	GFR
	St. Hellefiske Bank	1992	August	34 (5)	GFR
	Li. Hellefiske Bank	1988	October	1 (0)	GFR
SISIMIUT	Sisimiut/Holsteinsborg	1986	June	41 (3)	GFR
	Sisimiut/Holsteinsborg	92-93	August-January	14 (0)	GFR
	Sisimiut/Holsteinsborg	1993	March-April	6 (0)	GFR
MANIITSOQ	Kangaamiut	1986	June	50 (4)	GFR
	Kangaamiut	87-88	December-February	40 (2)	GFR
	Maniitsoq/Sukkertoppen	1986	June	36 (0)	GFR
	Napasog	1986	June	73 (11)	GFR
	Atammik	1986	May	10 (1)	GFR
NUUK	Nuuk/Godthåb	1986	May	6 (0)	GFR
	Qeqertarsuatsiat/Fisknenæsset	1990	May-June	38 (4)	GFR
	Qeqertarsuatsiat/Fisknenæsset	1990	November-December	10 (1)	GFR
PAAMIUT	Arsuk	1990	May-June	50 (4)	GFR
QAQORTOQ	Qaqortoq/Julianehåb	1990	June	2 (0)	GFR
	Saarloq	1990	June	30 (2)	GFR
NANORTALIK	Narsaq Kujalleq/Fr. dal	1986	May	1 (0)	HMP
AMMASSALIK	Isortoq	1987	May	1 (0)	HMP
	Isortoq	1991	September	3 (0)	GFR
TOTAL		1985-1993		1,175 (71.6%)	

¹HMP Heavy Metal Project, GFR Greenland Fisheries Research Institute, LAA Lars Anker Angantyr

²4 stomachs not analysed

Information on the qualitative composition of the diet of harp and hooded seals in Greenland was previously presented by several authors, e.g. Fabricius (1780, 1790), Winge (1902), and Vibe (1950), supplemented by Sergeant (1973), Kapel (MS 1973), Kapel and Geisler (MS 1979) and Kapel (1982).

However, there were few quantitative analyses of seal diet in Greenland, and with limited temporal or regional coverage. In order to improve the knowledge, material from harp seals has been collected since 1985 as part of three parallel projects: The 'Heavy Metal Project' (HMP) by Greenland Environment Research Institute, a

Table 2. Food items identified in harp seal stomachs sampled in Greenland

<u>Scientific name</u>	<u>English name</u>
<i>Salvelinus alpinus</i>	Char
<i>Mallotus villosus</i>	Capelin
<i>Benthoosema glaciale</i>	Arctic lanternfish
<i>Notoscopelus kroeyeri</i>	Kroyer's lanternfish
<i>Gadus morhua</i>	Atlantic cod
<i>Gadus ogac</i>	Greenland (Rock) cod, uvaq
Gadidae	Unidentified codfish
<i>Boreogadus saida</i>	Polar cod
<i>Arctogadus glacialis</i>	Arctic cod
<i>Ammodytes</i> ssp.	Sandeel, sand lance
<i>Anarhichas minor</i>	Spotted wolffish
<i>Lumpenus/Leptoclinus</i> sp.	Snake blennies
<i>Lycodes</i> ssp.	Eelpouts
<i>Sebastes marinus/mentella</i>	Redfish
Cottidae	Sculpins
<i>Liparis/Careproctus</i> sp.	Seasnails
<i>Reinhardtius hippoglossoides</i>	Greenland halibut
<i>Hippoglossoides platessoides</i>	Long rough dab
<i>Hippoglossus hippoglossus</i>	Atlantic halibut
	Unidentified fish
<i>Pandalus borealis/(montagui)</i>	Northern prawn
<i>Eualus gaimardi/Argis lar/</i>	
<i>Lebbeus polaris/Pasiphaeidae</i>	Other prawns (shrimps)
<i>Chionoecetes opilio/Hyas</i> sp.	Crabs
Mysidacea spp.	Mysids
<i>Thysanoessa/Meganyctiphanes</i>	Euphausiids
<i>Parathemisto libellula</i>	Arctic pelagic amphipod
Gammaridae	Gammarid amphipod
<i>Gonatus fabricii/ Rossia</i> sp.	Squids, octopods
	Other invertebrates

graduate study project by L.A. Angantyr at the University of Copenhagen, and a special project under the seal study program of Greenland Fisheries Research Institute (GFRI). This material was examined and analysed in GFRI's laboratories and results were presented by Kapel and Angantyr (MS 1989), Angantyr and Kapel (1991), Kapel (MS 1994) and Kapel (1995). Similar material for quantitative analysis of hooded seal diet is limited (Kapel 1982, 1995).

The purpose of this presentation is to summarize the information available in these earlier reports and meeting documents on the feeding habits of harp and hooded seals in Greenland waters during their migrations and stay in these regions, i.e. outside of the whelping and moulting seasons.

MATERIAL AND METHODS

In connection with collection of jaws of harp and

hooded seal for analyses of age composition of catches in Greenland, hunters provided written information on stomach contents of thousands of harp and hooded seals in Greenland in the period 1970-1983 (Kapel MS 1973, Kapel and Geisler MS 1979, Kapel 1982). The hunters' information was not particularly specified, and it is not known how they evaluated the stomach contents, but their reports were used for comparison with results of analyses of stomach samples, or as indication of food preferences when samples were lacking.

During the period 1985-1993 stomachs were sampled from 1,175 harp seals caught in Greenland (Table 1, Fig. 1). In connection with this sampling program, stomachs from 44 hooded seals were also obtained.

All samples were frozen as soon as possible for later shipment to the laboratory in Copenhagen. In the laboratory the material was treated as described in previous papers (Kapel and Angantyr MS 1989, Angantyr and Kapel 1991, Kapel MS 1994):

For all species or taxonomic groups (Table 2) the number of specimens were either counted or estimated. The total number of each fish species was calculated by adding the number of fresh fishes to the number of intact skulls and half the number of free otoliths in the stomach. For cephalopods the total number was calculated by adding the number of fresh specimens to the highest number of either lower or upper beaks. For larger species of crustaceans (crabs, prawns), the number of specimens was counted. When small species (euphausiids, amphipods, mysids) were present in large numbers the amount was estimated by counting a subsample.

The fresh weight of the stomach contents was sometimes calculated using otolith-fresh weight equations (e.g. Härkönen 1986), but most often standard values for each species were used. Details on the values used were given in previous reports (e.g. Angantyr and Kapel 1991).

The composition of the diet was expressed in terms of mean estimated weight percentage ("calculated biomass") calculated on the basis of the number and average weight of each species or taxonomic group identified in the stomach.

Table 3. Harp seal food composition in Greenland in terms of calculated biomass (Weight %), by area and month; subareas (s) southern, (n) northern, (w) western, and (e) eastern part.

Areas	Months	N	capelin	Gadus sp.	Polar cod	other fishes	prawns	krill	amphipods	other crust.	squid
Southwest (s)	May	25	14.1	0.1		0.9	2.0	82.1	0.7		0.1
Southwest (s)	June	52	45.5	1.5		0.1	1.2	49.7	<0.1	1.9	
Southwest (n)	May	33	20.2	6.4		6.9	4.3	62.1			
Southwest (n)	June	198	85.1	2.8		4.2	0.8	7.2		<0.1	<0.1
Southwest (n)	Aug.-Nov.	23	76.1	2.8		7.8	6.9	4.6	<0.1	0.1	0.7
Southwest (n)	Dec.-Apr.	44	40.6	12.1		19.3	5.4	20.9		1.8	0.1
Centr. W. (w)	June-July	79	31.8	0.1		4.8	10.7	28.8	23.4		0.4
Centr. W. (w)	Aug.-Jan.	125	83.4	6.7	0.1	6.7	1.6	0.6	0.7	+	0.7
Centr. W. (w)	Feb.-Mar.	36	3.3	1.3	0.1	54.9	1.0	17.3	3.0	+	19.1
Centr. W. (e)	August	48	26.8		50.7		1.0	14.6	2.3	4.1	0.5
Centr. W. (e)	September	46	59.6	1.5	20.5	10.4	1.4	<0.1	1.1	<0.1	5.4
Uummanaq	August	129	0.1	+	18.0	9.8	0.4	59.4	11.0	+	1.3
Upernavik (s)	June	15	0.2		81.0	10.9	6.3	<0.1	0.4	<0.1	1.2
Upernavik (s)	September	152	58.1	2.3	33.3	2.0	0.9	<0.1	1.2	1.3	0.8
Upernavik (n)	August	15			85.8	0.6	0.3	13.3			
Upernavik (n) & Thule	September	30			87.5	5.0	0.1		5.1		2.3
Offshore SW	July	16				86.5	7.9		<0.1	<0.1	0.6
Offshore SW	August	29				64.6	1.1	3.9	30.4	<0.1	
Southeast	July	1	1.5		4.2	93.3					
Southeast	September	3	62.2					33.3	1.1		3.4

Weight percentages are presented in this paper for harp seal only. Samples from several sampling localities are pooled to give an overview of variations between regions and seasons. For hooded seal, hunters' information, expressed as per cent occurrence (i.e. the proportion of stomachs in which a species is recorded) is compared with the limited stomach analysis material, expressed as calculated biomass or mean per cent volume (the visually estimated volume of a prey species in relation to the volume of all food items found in the stomach).

RESULTS

Harp seal feeding in Greenland

Considerable geographical and seasonal variation was demonstrated, but some general patterns in feeding habits emerged. These are illustrated in Table 3 and Fig. 2, and can be summarized as follows:

In the coastal waters of Southwest Greenland two prey items dominate the diet of harp seals: capelin (*Mallotus villosus*) and "krill" (euphausiids). In the early summer (May) krill appears to be the predominant food; later, in June and in the autumn months, capelin constitutes the major part of the food. Codfishes, mostly cod (*Gadus morhua*) and Greenland cod

(*G. ogac*), other fish species, and prawns (particularly Northern prawn *Pandalus borealis*) are also taken but altogether they account for less than 20% of the diet in terms of biomass. In the winter months, however, these 'secondary prey species' appear to contribute with more than one third of the food biomass, although capelin is still the most important prey item.

In the western part of Central West Greenland, i.e. the region around the southern entrance to the Disko Bay, the pattern resembles that found in Southwest Greenland: In June-July pelagic crustaceans (euphausiids and amphipods, *Parathemisto* sp.) dominate the diet, followed by capelin, and prawns. In the autumn, however, capelin is the predominant prey item, whereas the winter diet is composed of a number of other fish species, pelagic crustaceans, and squid (mainly *Gonatus fabricii*).

Few samples were obtained from offshore waters in Southwest and Central West Greenland (Table 3). They show considerable variation between areas and months, with sandeel (*Ammodytes* sp.) as a very important food item, supplemented by *Parathemisto*, *Pandalus*, redfish (*Sebastes* sp.), and squid (Kapel MS 1974).

In the northeastern part of the Disko Bay

Table 4a. Hooded seal food composition in Greenland, information from hunters expressed as % occurrence in all reports, and in reports of stomachs with contents

	South Greenland			Northwest Greenland			Southeast Greenland		
	reports	% of all	% of food	reports	% of all	% of food	reports	% of all	% of food
	N	reports	reported	N	reports	reported	N	reports	reported
All reports	1236	100		614	100		236	100	
Empty stomachs	386	31.2		153	24.9		206	87.3	
Stomachs with food	850	68.8	100	461	75.1	100	30	12.7	100
Capelin	58	4.7	16.3	26	4.2	5.7	1	0.4	3.4
Codfishes	131	10.6	36.9	15	2.4	3.3	1	0.4	3.4
Greenland halibut	13	1.0	3.7	278	45.3	61.1	2	0.9	6.9
Redfish	101	8.2	28.4	6	1.0	1.3	24	10.2	82.8
Wolffish	28	2.3	7.9	49	8.0	10.8	1	0.4	3.4
Other fish	15	1.2	4.2	22	3.6	4.8	-	-	-
Unspecified fish	482	39.0	*	5	0.8	*	1	0.4	*
FISH TOTAL	828	67.0	97.4	401	65.3	87.0	30	12.7	100
Decapods	14	1.1	1.6	4	0.6	0.9	-	-	-
Other crustaceans	2	0.2	0.2	55	9.0	11.9	-	-	-
CRUST. TOTAL	16	1.3	1.9	59	9.6	12.8	-	-	-
Cephalopods	6	0.5	0.7	1	0.2	0.2	-	-	-

*The percentages of the various fish species are adjusted proportionally to account for "unspecified fish".

Table 4b. Hooded seal stomach contents in Greenland samples in terms of estimated volume per cent (Vol. %) and calculated biomass (Weight %).

	Southwest Greenland		Central West Greenland	Northwest Greenland		Southeast Greenland		
	Vol. %	Weight %	Weight %	Uummannaq	Upernavik	Isortoq 1991		
Stomachs examined (N)	6	5	1	3	5	4	29	20
Empty stomachs (%)	16.7	.	.	.	20.0	.	31.0	.
Capelin	82.5	93.1	64.0	-	-	-	-	-
Polar/Arctic cod	-	-	31.9	-	17.6	25.4	1.9	2.1
Greenland halibut	-	-	-	86.6	61.0	65.3	-	-
Redfish	-	-	-	4.4	-	-	2.4	33.4
Wolffish	0.2	6.4	-	-	-	-	-	-
Other fish	0.5	0.5	3.9	7.9	0.4	7.0	1.7	3.8
Pandalus	-	-	0.3	0.6	-	-	15.4	9.2
Other crust.	0.2	<0.1	<0.1	-	-	-	2.1	0.1
Cephalopods	-	-	-	0.2	0.4	1.9	42.0	50.3
Other molluscs	-	-	-	0.4	0.6	0.3	-	-
Unidentified items	-	-	-	-	-	-	3.4	0.9

(‘Vaigat’), polar cod (*Boreogadus saida*) was the predominant prey in August, followed by capelin and krill. In September-November, capelin took the leading role followed by polar cod, other fish species, and crustaceans.

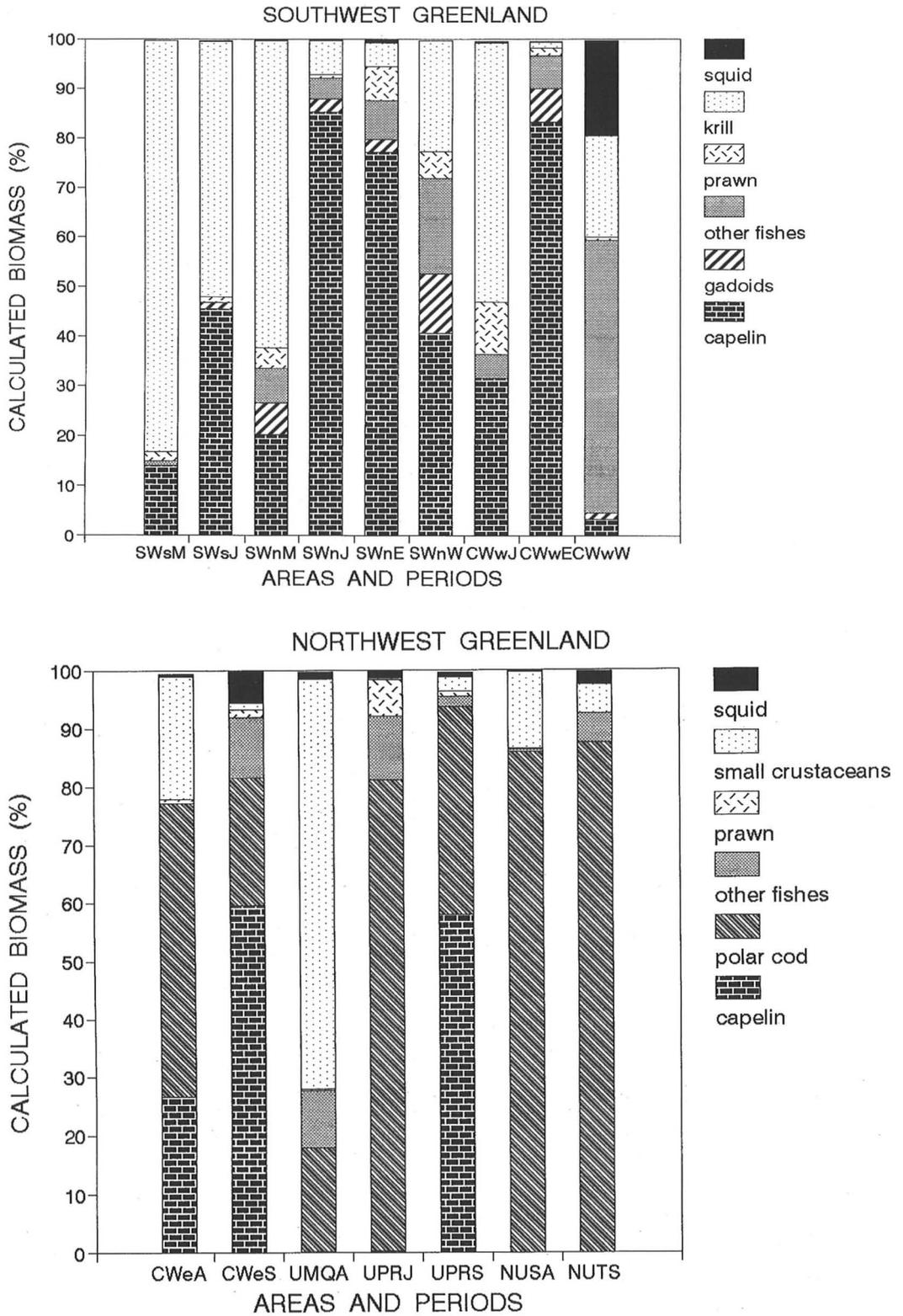
In most of the samples from Northwest Greenland, polar cod and to some extent Arctic cod (*Arctogadus glacialis*) dominated the harp seal diet. In the Uummannaq district, however,

krill was the predominant prey in August, and in the southern part of Upernavik district capelin constituted more than half of the calculated biomass of the diet in September.

Very few stomachs collected in Southeast Greenland (Ammassalik district) have been analysed (Table 3). One specimen sampled in May contained mainly redfish (94%), whereas three young harp seals caught in September had

Fig. 2.

Food composition (weight %) of harp seals in Southwest (upper part) and Northwest Greenland (lower part). Areas: SW Southwest Greenland, CW Central West Greenland, s, n, w, e southern, northern, western and eastern part, respectively, UMQ Uummannaq, UPR Upernavik (southern part), NUS northern part of Upernavik, NUT same (NUS) and Thule. Month: M May, J June(-July), A August, S September(-October), E autumn, W winter.



been feeding on capelin (62%) and krill (33%).

In addition to the above-mentioned species, the diet of harp seals feeding in inshore waters of West Greenland includes a number of other fish species, prawns, and squid (see Table 2). Some samples indicate that the relative importance of these 'secondary food items' is greater in the autumn and winter, but other samples demonstrate that capelin is the predominant prey also at this time of the year.

Hooded seal feeding in Greenland

Much less information is available on hooded seal diets in Greenland than for harp seals. Accounts in the literature, and information gathered from hunters were reviewed by Kapel (1982), and are summarised in Table 4a and Fig. 3. Results of examination of the contents of the few hooded seal stomachs obtained in connection with sampling of harp seal stomachs are presented in Table 4b and Fig. 3).

South Greenland hunters provided information on the stomach contents of 1,236 hooded seals taken during the spring hunt, 386 of which (31.2%) were empty. Of the 850 stomachs with contents, 828 (97.4%) contained fish, whereas crustaceans and squid were reported in only 16 and 6 stomachs - less than 2% and 1%, respectively. For many stomachs, the contents were only given as "fish", but the fish species reported most frequently were redfish, cod or Greenland cod, and capelin.

Six stomachs of hooded seals caught in Southwest Greenland have been examined in the laboratory. One was empty, and in the remaining five capelin was the predominant food. Three of the seals were taken in April, two in June, and one in November; they were all very young animals (0-1 year old) - in contrast to the above mentioned hunters' samples that were dominated by seals of age 2 or older (Kapel 1982).

Hunters' information on stomach contents is available for 236 hooded seals caught in Southeast Greenland (Ammassalik district) 1970-74. Of 215 caught in late July-early August, 201 (93.5%) were empty. This is not surprising because the seals were in the late stage of moulting, during which hooded seals are known to have reduced feeding activity (Rasmussen

1960, Potelov *et al.* this volume). Of the 21 reports from this district later in the year (autumn and winter), only 5 (24%) stomachs were empty. The prey species reported most frequently by the Ammassalik hunters was redfish (in 83% of the stomachs with contents), followed by Greenland halibut (*Reinhardtius hippoglossoides*, 7%). Neither crustaceans nor squid were reported by the hunters.

In Southeast Greenland, 29 hooded seal stomachs were collected in early September 1991. Laboratory examination revealed that 9 (31%) were empty, and that the rest contained only small amounts of food remains. The predominant prey item was squid, particularly identified by the eyes found in 80% of these stomachs, and constituting about 50% (calculated biomass) of the stomach contents. Prawns (*Pandalus sp.*) dominated in five stomachs (25% occurrence, 9% of biomass). The stomach contents of a three year old seal were dominated by redfish, and fish otoliths (most frequently polar cod) were found in five other stomachs. Most of the seals in this sample were young of the year (70%), whereas these constituted only a minor part (3%) of the 1970-74 samples.

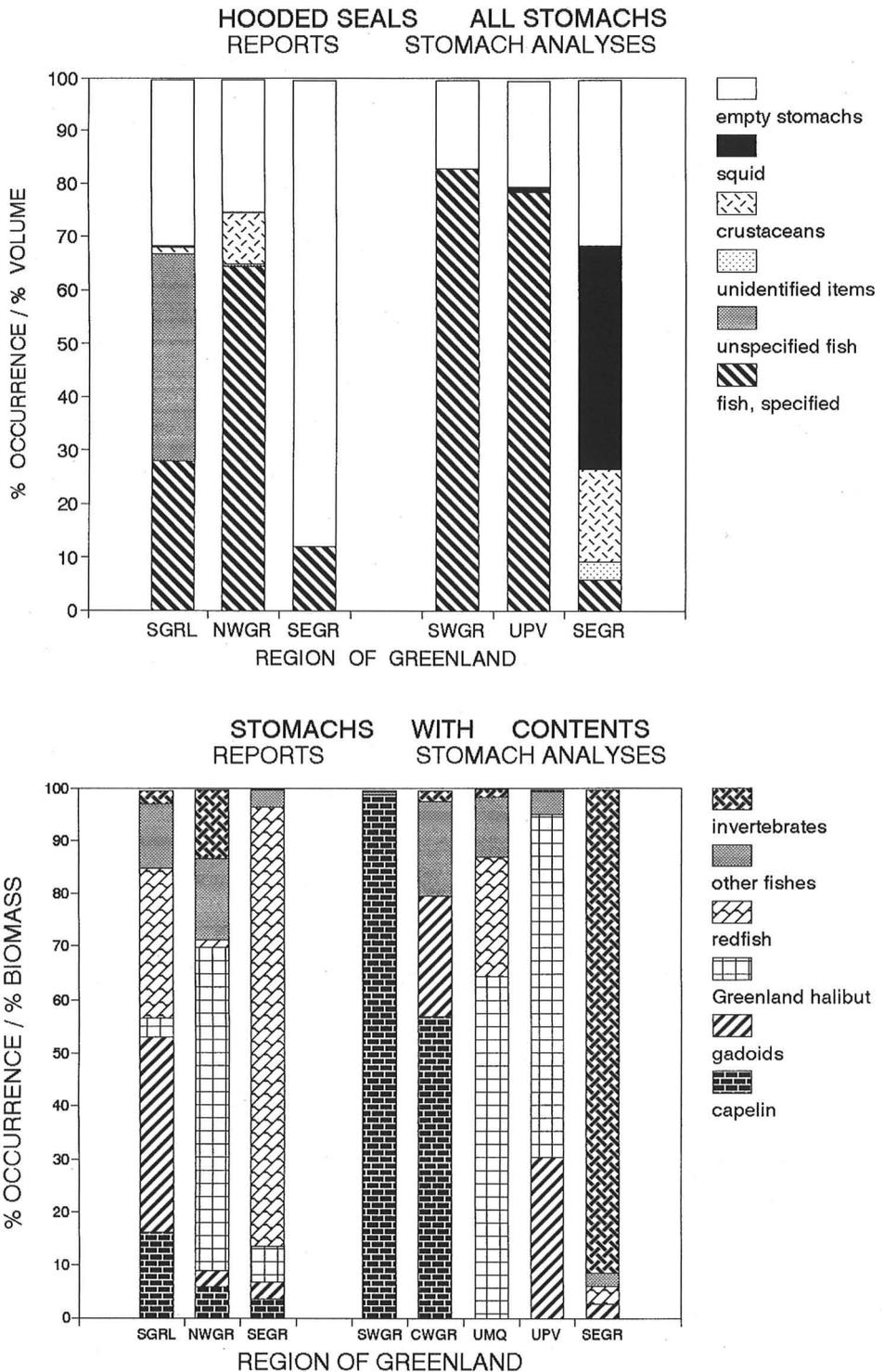
From Northwest Greenland, hunters' information is available for 614 hooded seals, of which 153 (25%) had empty stomachs. The highest proportion of empty stomachs (42%) was found in July, which probably relates to recent moulting condition, the lowest in late autumn (18%)(Kapel 1982). In this region, Greenland halibut was the prey reported most frequently (in 61% of the stomachs with contents), followed by wolffish (*Anarhichas sp.*) (11%), and pelagic crustaceans (12%).

Laboratory analyses of stomach contents of hooded seals caught in the northern part of West Greenland are few: One stomach from Vaigat (Central West Greenland) contained 64% capelin, 32% polar cod, and 4% other fish remains (calculated biomass); the contents of seven stomachs from Ummannaq and Upernavik were dominated by Greenland halibut (87% and 65%, respectively), followed by redfish (Ummannaq, 4%) or polar cod (Upernavik, 25% biomass).

Little information is available on the feeding of

Fig. 3.

Food composition of hooded seals in Greenland: All stomachs (upper part) and stomachs with contents (lower part), based on hunters' reports (% occurrence, left side columns) and stomach analyses (weight %, right side columns). Areas: SEGR Southeast Greenland, SGRL South Greenland, SWGR Southwest Greenland, CWGR Central West Greenland, NWGR Northwest Greenland, UMQ Uummannaq, UPV Upernavik.



hooded seals in offshore areas. A seal taken as by-catch during longline fishery off Central West Greenland (appr. 69° N 59° W) at depths exceeding 650 m had two (900 and 950 g)

Greenland halibut in the stomach (Søren A. Pedersen, Greenland Fisheries Research Institute, pers. com.).

DISCUSSION

Sergeant (1973) reviewed available information on harp seal feeding in the Northwest Atlantic, and included more recent studies in his monograph on harp seals (Sergeant 1991). Another review of studies of harp seal feeding in the Northwest Atlantic was presented by Wallace and Lavigne (1992).

In recent years, a considerable amount of additional data on harp seal feeding patterns in Canadian waters have been published or presented at meetings in international fora:

Murie and Lavigne (1991) and Beck *et al.* (1993) studied the diet of harp seals collected in the Gulf of St. Lawrence, Lawson *et al.* (1995, 1998) and Lawson and Stenson (1997) reviewed a large material of stomach contents of harp seals in nearshore and offshore waters around Newfoundland and Labrador, and Lawson and Stenson (1995) discussed historic variation in the diet of harp seals in this region. The present knowledge on the diet of harp seals during their stay in Atlantic Canada is thus based on extensive sampling, and is well documented.

Less is known on harp seal feeding in Arctic Canada. Sergeant (1973) presented stomach contents data on 16 harp seals caught in the Canadian Arctic (at four different localities). Polar cod occurred in 6 of these, mysids in 5, *Parathemisto* in 4, and euphausiids in 3 stomachs.

Foy *et al.* (1981, cited in Sergeant 1991) reported on harp seal feeding along the Labrador coast. They found that immature and adult harp seal feeding in bays at the Labrador north coast in late May-June were taking mainly capelin, whereas the diet of juveniles feeding near the offshore archipelago consisted mainly of euphausiids. Immatures and adults feeding further offshore had a more varied diet including fish, euphausiids, and bottom living decapods. In November-January harp seals feeding in the bays were feeding on a variety of small Gadidae, polar cod, and capelin, whereas invertebrates were of secondary importance.

Smith *et al.* (1979) working in southeastern Baffin Island (63-64° N) in July-September found that the diet of four young-of-the-year

harp seals consisted of 64% pelagic crustaceans (mysids and *Parathemisto*), and 36% fish (mainly polar cod). One adult female harp seal was feeding on the pelagic shrimp *Sergestes arcticus*.

In the western Hudson Strait, Beck *et al.* (1993) found that the stomachs of 14 harp seal caught in September-October near the south coast were dominated by capelin, with polar cod, Greenland cod, sculpins, and flatfishes as secondary elements. One seal feeding offshore, near Salisbury Island, had taken *Parathemisto* and polar cod in almost equal amounts.

In the High Arctic, Finley *et al.* (1990) analysed 63 stomachs of harp seals at Pond Inlet (73° N) and Grise Fiord (76° N) between mid-August and early October. Polar cod occurred in all of them, and accounted for 84% of all food items found in the stomachs (% frequency). Arctic cod was found in 63% of the stomachs, but in low numbers (5% frequency). In terms of biomass, however, polar cod and Arctic cod contributed with 66% and 33%, respectively. Other fish species and invertebrates were also found, but accounted for only a minor part of the diet (altogether 16% frequency, and about 1% by weight).

The analyses of the material collected in Greenland is in accordance with a general conclusion that can be drawn from the studies in coastal areas of the Canadian Arctic, namely that capelin is a predominant prey in the southern part of the range, polar cod in the northern part, and that krill and *Parathemisto* make significant contributions to the diet in some seasons or areas.

Sergeant (1973, 1991) stated that small crustaceans were taken particularly by young harp seals. In some of the summer samples from Southwest Greenland crustaceans seem to constitute a greater part of the diet of young animals, but in other samples no indication of an age dependent difference in diet was found (Angantyr and Kapel 1991). In general, the analyses of the Greenland samples indicate that the relative importance of the 'primary' food items (pelagic crustaceans vs. pelagic fish species) in the diet of harp seals in West Greenland depends on the season and locality, rather than on the age of the seals (Kapel MS 1994). Some of the samples indicate, however,

that the food items referred to above as 'secondary' may constitute a larger fraction of the diet of adult seals than of immature seals.

All these studies indicate great seasonal and regional, and probably also year-to-year or long-term variation in the feeding of harp seals, and thus stress the need for continued sampling and analyses in order to document the feeding patterns better and elucidate any short- or long-term changes in food preference or availability. For some seasons or areas, e.g. offshore waters, the present knowledge is based on a very limited data set.

In order to translate the knowledge on feeding patterns to an evaluation of the consumption at the population level, information on population size and dynamics, on the spatial distribution of the seal during the year and on the energy requirements of harp seals, is also needed.

The present population size of the Northwest Atlantic stock is fairly well known (Stenson *et al.* 1993, Stenson *et al.* 1996), and its composition and dynamics can be modelled. A crucial point may be the question on the spatial distribution of the stock within its general distribution area. The general distribution and migration pattern of harp seals is fairly well known (see e.g. Sergeant 1991), but when it comes to estimating the number occurring in a given area at a given time our knowledge is far from satisfactory, and ways to improve that knowledge are not easy to find - or extremely resource demanding. Satellite telemetry of harp seals has already revealed new details about the movements of a number of individuals (Stenson and Sjøre MS 1997), but a major effort in satellite tagging is required to illustrate the dispersal of the entire population all the year round. An alternative approach may be to make reasonable guesses and check the ranges of the results by simulations.

A fair amount of data on the energy requirements of harp seals, and calculations of the energy budget of harp seal populations has been published (e.g. Lavigne *et al.* 1985, Keiver *et al.* 1984), which may be applicable in the present context. But again, the allocation to certain regions or seasons is highly speculative.

Using available knowledge on diet, abundance, and energy requirements, Stenson *et al.* 1997 estimated the consumption by harp seals during their stay in the southern range of the distribution, and Hammill and Stenson (forthcoming) made similar calculations for all seal species occurring in the waters of Atlantic Canada. They made assumptions of the part of the seal populations present in these waters during winter and summer, and using similar assumptions one could attempt to calculate the consumption by harp and hooded seals during their stay in the Arctic. A next step would be to make assumptions on distribution in Arctic Canada, offshore waters and coastal Greenland.

Questions relating to possible interactions between an increasing population of harp seals and commercial fisheries in Greenland is part of the background for conducting the studies on harp seal diet reported in this and previous papers. The most important species for the commercial fishing fleet in Greenland are Northern prawn, cod, and Greenland halibut. According to the present analysis, none of these species constitute a significant fraction of the stomach contents of harp seals in Greenland waters.

It is known that other seals sometimes eat parts of larger fish without taking the head with the otoliths (Boulva and McLaren 1979, Härkönen 1986). If harp seals often feed that way, this analysis is biased. However, it is generally believed that they take their prey by suction, i.e. swallow the items whole (Ronald and Healey 1981). It appears, therefore, that harp seals in Greenland waters were of little importance as direct competitors to the commercial fishery in the late 1980's. Whether the diet of harp seals in Greenland waters has changed in recent decades is not known; but it is likely that the fraction of Atlantic cod in the diet was higher previously, when that species was extremely abundant off West Greenland.

An evaluation of the role harp seals play in the marine ecosystem by eating large quantities of prey species at lower trophic levels (euphausiids, amphipods, capelin, polar cod) is very difficult to conduct because knowledge about the total biomass of these species in Greenland waters is extremely limited.

The role of hooded seals is perhaps even more difficult to assess, because the knowledge on population size and distribution is far from complete, and quantitative data on feeding very limited. Besides the information from Greenland presented here, Ross (MS 1993) analysed the contents of 67 hooded seal stomachs collected around Newfoundland. Seven seals taken at the whelping patch had empty stomachs. The four most important fish species were Greenland halibut, redfish, Atlantic herring (*Clupea harengus*) and polar cod, accounting for 96% of the stomach contents (expressed as both per cent occurrence and as calculated biomass); squid occurred in 70% of the stomachs and constituted 52% of the number of all items found, but only 1% of the

biomass. Hammill *et al.* (1997) and Hammill and Stenson (forthcoming) used this information to estimate the consumption by hooded seals in the Gulf of St. Lawrence and the entire Atlantic Canada region.

It is worth noting that although the number of hooded seals in the Northwest Atlantic is only about one tenth of that of harp seals, the average body mass is 2-3 times as large and their diet appears to include a much higher fraction of fish species exploited commercially in Greenland. It is quite possible that the consumption by hooded seals in some areas of Greenland constitutes a more direct conflict with fisheries than in the case of harp seals.

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