Feeding habits of harp and hooded seals in drift ice waters along the east coast of Greenland in summer and winter

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Results of analyses of stomach and intestinal contents from hooded (*Cystophora cristata*) and harp (*Phoca groenlandica*) seals captured in the pack ice belt of the Greenland Sea in summer (July–August) in 2000 and winter (February–March) in 2001 revealed that the diet of both species were comprised of relatively few prey taxa. Pelagic amphipods of the genus *Parathemisto*, the squid *Gonatus fabricii*, polar cod (*Boreogadus saida*) and capelin (*Mallotus villosus*) constituted 63 - 99 % of the observed diet biomass in both seal species, irrespective of sampling period, but their relative contribution to the diet varied both with species and sampling period/area. For hooded seals, *G. fabricii* and capelin were the dominant food items in winter 2001, but the summer 2000 diet comprised a mixture of this squid and polar cod. *Parathemisto* was most important for the harp seals during summer 2000; in winter 2001 the contribution from krill and capelin were comparable to that of *Parathemisto*. Multivariate analyses revealed differences in the intestinal contents of hooded and harp seals in areas where the two species' occurrence spatially overlapped. Different foraging depths of the two species may have contributed to the observed differences in diets.

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Harp (*Phoca groenlandica*) and hooded (*Cystophora cristata*) seals co-occur in the drift ice waters of the Greenland Sea along the east coast of Greenland during breeding and moulting (March–June; see Sergeant 1991; Folkow & Blix 1995; Folkow et al. 1996; Haug et al. 2000; Potelov et al. 2000). In this area, previous studies of the two species have concentrated mainly on stock size estimation, reproduction and migration patterns (Øritsland 1959, 1964; Øien & Øritsland 1995; Øritsland & Øien 1995; Folkow & Blix 1995, 1999; Folkow et al. 1996; ICES 1998, 2004; Frie et al. 2003; Folkow et al. 2004). Little attention has been paid to the feeding habits of the seals. While a few observations on diets have been made in the Greenland Sea during breeding and moult, known to be periods with low feeding intensity (Haug et al. 2000; Potelov et al. 2000), only occasional information, mostly from coastal areas of eastern Greenland and northern Iceland, is available from other times of the year (Gray 1889; Pedersen 1930; Rasmussen 1957, 1960; Surkov 1960; Hauksson & Bogason 1997).

Recent information, obtained by satellite tagging, about the migratory patterns of the two seal species, indicate that they may co-occur in the Greenland Sea pack ice also outside the breeding and moulting period (Folkow et al. 1996; Folkow et al. 2004). This was further confirmed during research surveys in July–August in 2000 and February–March in 2001. These cruises were carried out as part of a Norwegian project aimed to assess the feeding habits of the Greenland Sea stocks of harp and hooded seals in the period July–February, i.e. the intensive feeding period between moulting and breeding (Rasmussen 1960; Kovacs

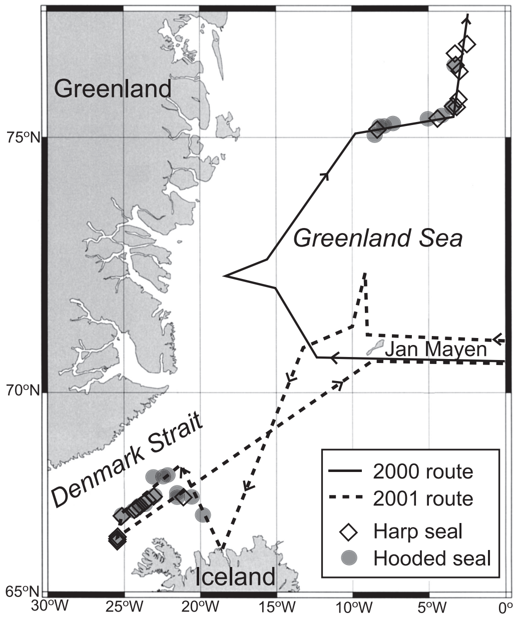

Fig. 1. Sailing routes and seal catch positions during the July–August 2000 and February–March 2001 expeditions with the RV *Jan Mayen* to the open drift ice areas along the east coast of Greenland.

& Lavigne 1986; Nilssen et al. 2000). Sampling of co-occurring specimens of the two species made it feasible to describe and compare their diets in periods and areas where such data were previously unavailable. That is the purpose of this paper.

Materials and methods

Sampling of seals

A research vessel was used to search for harp and hooded seals along the drift ice edge areas off the east coast of Greenland (Fig. 1). Seals were shot on ice floes or in the water and brought on board the vessel for dissection; entire stomachs and large intestines were frozen. The lower jaw (with teeth) was collected from each seal for age determination. Positions of the seals at the time of shooting were recorded using GPS.

Age estimation of individual seals

One lower canine tooth was extracted after boiling the lower jaw. From each tooth, a 10 - 12 µm transverse section was mounted on a glass slide. Sections were examined under transmitted light and ages estimated from counts of growth layers in the cementum for hooded seals (Born 1982) and the dentine for harp seals (Bowen et al. 1983).

Analyses of stomach and intestinal contents

In the laboratory the stomachs and intestines were cut open after thawing. Stomach contents were weighed and, after flushing the intestine with fresh water, the contents sorted. Most of the stomach and intestinal contents were partly or completely digested; prey organisms were identified to the lowest possible taxonomic level, preferably species, with references to Enckell (1980), Breiby (1985), Pethon (1985), Clarke (1986) and Härkönen (1986). Estimates of the number of crustaceans present were obtained by counting fresh animals and the carapaces of each species. Approximate average weights of crustaceans were obtained from fresh prey specimens found in the stomachs or from published values (Haug et al. 1996; Potelov et al. 2000), and these were used to reconstruct the original biomass of crustaceans. Numbers of upper and lower squid beaks were recorded—the most numerous category was used to estimate the total number of squid consumed. Back-calculation of squid biomass from lower rostral lengths were performed using regression equations given by Clarke (1986). The total number of each fish species in stomachs was estimated by adding the number of whole specimens, the number of intact skulls and half the number of "free" otoliths. Otolith length to fish length and fish wet weight correlations were used to estimate the initial mass of the polar cod (*Boreogadus saida*) consumed by the seals (Lindstrøm et al. 1998). Unidentifiable gadoid otoliths, most likely polar cod, were treated similarly. Due to a general lack of published otolith length correlations for Arctic fishes, the biomass of a few observed Cottidae (sculpins) and Liparidae individuals were calculated using correlations based on our own unpublished material. No corrections were made for otolith erosions.

Feeding indices

The frequency of occurrence of each prey item (FO_i) was calculated as a binary measure (i.e. prey were either present or absent in a sample): $FO_i = (s_i/s_t) \bullet 100$, where s_i is the number of examined seals with stomachs and/or intestines containing species i, and s_t is the total number of seals examined.

A bulk biomass index (B_i) was calculated for each seal. This index standardized the proportion that each prey species contributed to each individual seal's gut contents. For each individual seal, we divided the estimated biomass of each prey species by the estimate of total biomass for that seal's stomach or intestine. In this way, each prey item was represented as a proportion of the prey present in each seal, with all proportions for each seal summing to 1, that is: $B_i = (b_{ij}/b_j)$, where b_{ij} is the mass of prey category i in the sample from seal j, and b_j is the estimated mass of all prey in the sample from animal j. Mean values and associated measures of variability for the bulk biomass index were calculated for gut contents by species, using individual seals as independent samples.

Data analyses

Each seal intestine was treated as a separate sample in which each prey species occurred, so the table of species in intestines was treated as a matrix of species-in-sites, conceptually similar to Q-mode analyses in classical community ecology (Legendre & Legendre 1998). These matrices, with individuals in rows and species in columns, were then row-standardized (equivalent to calculating the "bulk biomass index"; Legendre & Legendre 1998). Data analyses were carried out using R (Ihaka & Gentleman 1996) version 1.7.0. Libraries used were MASS version 7.1-4, vegan version 1.4-3, cluster version 1.7.0 and gregmisc version 0.8.4.

Results

Seals sampled

During the period 30 July to 1 August 2000, 28 hooded seals and 20 harp seals were caught in areas with species co-occurrence in the Greenland Sea along a south–north cruise track between 75 and 77° N (Fig. 1). Most sampling was performed in areas with sea depths ranging between 1000 and 3000 m. During the period 25 February to 1 March 2001, co-occurring hooded and harp seals were observed in the Denmark Strait, where 57 hooded and 54 harp seals were taken in ice-filled waters with depths ranging between 800 and 1200 m. Most of the sampled seals were young: only 26 % of the harp seals and 20 % of the hooded seals were estimated to be six years of age or older.

Far more samples of intestines had identifiable prey items than stomachs (Table 1). Intestines also showed a greater diversity of prey items than did stomachs. Therefore, intestines were considered most appropriate for further examination.

Summer 2000 gut content

In July–August 2000, 4 % and 71 % of the 28 examined hooded seal intestines and stomachs, respectively, were empty (Table 1). At least nine different prey items were identified, of which two appeared to be of particular importance. The cephalopod *Gonatus fabricii* occurred in more than 82 % of the intestines, and in 18 % of the stomachs, while polar cod occurred in 71 % and 21 % of the intestines and stomachs, respectively. The frequency of occurrence of both sandeels and amphipods of the genus *Parathemisto* was also considerable. In terms of reconstructed prey biomass, polar cod (on average 45 %) and *G. fabricii* (on average 36 %) contributed most to the intestine but the contributions from other fish species were also considerable (Fig. 2a). Variable contributions of these prey items to individual seal diets are illustrated by the large confidence intervals.

Of the 20 harp seals sampled in 2000, 65 % had empty stomachs, but only 5 % had empty intestines. The identified prey remains included at least six different categories (Table 1). *Parathemisto* (35 - 90 %), *G. fabricii* (25 - 55 %) and polar cod (30 - 60 %) occurred most frequently. In the estimated intestinal prey biomass, the contribution from *Parathemisto* was by far the largest (on average 76 %; Fig. 2b). The contribution from polar cod was also considerable (on average 14 %).

Winter 2001 gut contents

Of the 57 hooded seal intestines and stomachs examined in February–March 2001, 30 % and 86 %, respectively, were empty (Table 1). At least 11 different prey items were identified. *Gonatus fabricii* occurred in 28 % of the intestines, and in 10.5% of the stomachs, and capelin (*Mallotus villosus*) occurred in 42 % of the intestines. In terms of reconstructed prey biomass, *G. fabricii* dominated the intestinal contents with a point estimate of more than 80 %, whereas contributions from all other prey items (including capelin) were less than 10 % (Fig. 2a).

The majority (96.3 %) of the 54 harp seals sampled in 2001 had empty stomachs, but only 3.7 % had empty intestines. The identified prey remains included at least nine different categories (Table 1). *Parathemisto* (ca. 70 %), krill (55 %) and capelin (35 %) were most frequently observed. In estimated intestinal prey biomass, the contribution from *Parathemisto,* capelin and krill were all about 30 % (Fig 2b). Variation among individual seals was large, as seen from the confidence intervals.

Prey composition differences in intestines of harp and hooded seals

To assess whether the prey composition of samples from harp and hooded seals differed, we selected for analysis the intestines of animals sampled in the one site where overlapping samples of both species were obtained in winter 2001. This provided 43 samples from hooded seals and 44 from harp seals. One harp seal sample was selected at random and removed from the data set to create equal-sized matrices for analysis. Prey species used in analysis were capelin, polar

Table 1. Frequency of occurrence of empty stomachs and intestines, and identified taxa in stomachs and intestines of hooded and harp seals caught in drift ice east of Greenland, July–August 2000 and February–March 2001. N = number of seals examined.

	Percentage occurrence							
	July–August 2000				February–March 2001			
	Stomachs		Intestines		Stomachs		Intestines	
	Hooded n=28	Harp n=20	Hooded n=28	Harp n=20	Hooded n=57	Harp n=54	Hooded n=57	Harp n=54
Empty	71.4	65.0	3.6	5.0	86.0	96.3	29.8	3.7
Crustacea								
Amphipoda								
Parathemisto libellula	3.6	35.0	10.7	90.0	0	1.9	1.8	27.8
Parathemisto sp.	10.7	10.0	39.3	85.0	1.	3.7	1.8	70.4
Gammarus sp.	3.6	0	14.3	10.0	0	0	0	14.8
Unident. amphipod remains	0	0	10.7	0	0	0	1.8	0
Euphausiacea								
Thysanoessa sp.	0	5.0	0	0	0	1.9	0	55.6
Decapoda	0	0	0	0	0	0	3.5	1.9
Unident. crustacean remains	0	0	0	0	0	0	0	3.7
Mollusca								
Cephalopods								
Gonatus fabricii	17.9	25.0	82.1	55.0	10.5	0	28.1	3.7
Pisces								
Osmeridae								
Mallotus villosus	0	0	0	0	1.7	0	42.1	35.2
Gadidae								
Gadus morhua	0	0	3.6	0	0	0	0	0
Boreogadus saida	21.4	30.0	71.4	60.0	0	0	3.5	7.4
Unident. gadoid remains	3.6	5.9	39.3	0	0	0	0	0
Ammodytidae								
Ammodytes sp.	14.3	10.0	32.1	20.0	0	0	0	0
Zoarcidae								
Unident. zoarcid remains	0	0	0	0	0	0	7.0	3.7
Liparidae								
Unident. liparid remains	0	0	0	0	0	0	1.8	1.9
Scorpaenidae								
Unident. scorpaenid remains	0	0	0	0	0	0	1.8	0
Pleuronectidae								
Hippoglossoides platessoides	0	0	0	0	0	0	3.5	0
Unident. fish remains	3.6	0	10.7	5.0	1.7	0	12.3	3.7

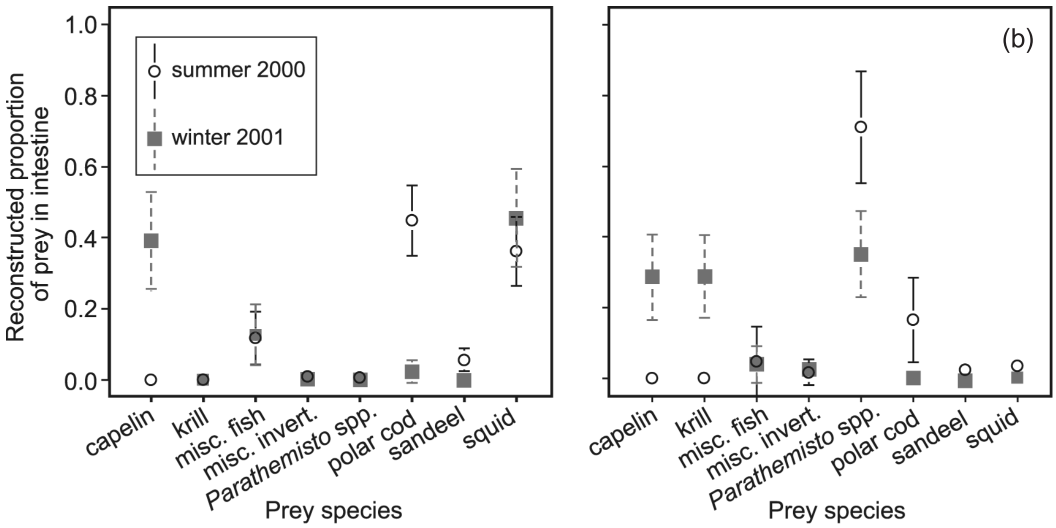

Fig. 2. Estimated proportion of eight prey types by estimated biomass, from (a) hooded seal and (b) harp seal intestines during summer 2000 and winter 2001 in drift ice waterrs in the Greenland Sea. Points indicate means and lines indicate 95 % confidence intervals for each prey category. The prey category miscellaneous fish includes cod, Ammodytidae, Zoarchidae, Liparidae, Scorpenidae and Pleuronectidae. Miscellaneous invertebrates include amphipods of the genus *Gammarus* and decapods.

cod, miscellaneous fish (including other gadoids, Ammodytidae, Zoarchidae, Liparidae, Scorpenidae and Pleuronectidae), squid, *Parathemisto*, krill and miscellaneous invertebrates (including amphipods of the genus *Gammarus* and Decapodae).

Harp and hooded seal matrices were combined. Dissimilarity coefficients of the standardized data were calculated using the Bray-Curtis index (Legendre & Legendre 1998). A dendrogram was computed using average-link clustering (Venables & Ripley 2002). This revealed five clusters in the data (Fig. 3), of which two were comprised entirely of harp seals and one entirely of hooded seals. Two clusters included members of both species (13 harp seals and 20 hooded seals).

Discussion

The gut contents of both hooded and harp seals in the Greenland Sea pack ice included few prey taxa. The dominant role of four particular items—pelagic amphipods of the genus *Parathemisto,* most probably almost exclusively *P. libellula*, the squid *Gonatus fabricii*, polar cod and capelin—was conspicuous. Although their relative contribution to the diet varied both with species and sampling period/area, these five prey items constituted 63 - 99 % of the observed diet biomass in both seal species. The two invertebrate taxa contributed importantly during both sampling periods (the amphipods mainly in harp seals, squid mainly in hooded seals), whereas the relative contribution of polar cod was confined mainly to the July–August 2000 period, and capelin exclusively to the January–February 2001 period.

This study identified *G. fabricii* as a major food constituent for Greenland Sea hooded seals. This was also the conclusion of Potelov et al. (2000) in their study of Greenland Sea hooded seal diets during March–June. *G. fabricii* is the most abundant squid of the Arctic and sub-Arctic waters of the North Atlantic (Kristensen 1981, 1983). Their biomass production in the Nordic seas represents a considerable food resource, particularly in the Arctic waters (Dalpadado et al. 1998) and the consumption of them by a variety of deep diving predators is assumed to be substantial (Bjørke 2001). *G. fabricii* and capelin were observed as the most important food items for hooded seals in winter 2001, whereas the summer 2000 diet was dominated by polar cod, but with an important contribution from *G. fabricii*.

Satellite tracking data have revealed that hooded seals from the West Ice stock were based in the ice-covered waters off the east coast of Greenland, from where they made long excursions to distant waters (Folkow & Blix 1995, 1999; Folkow et al. 1996;). From their teleme-

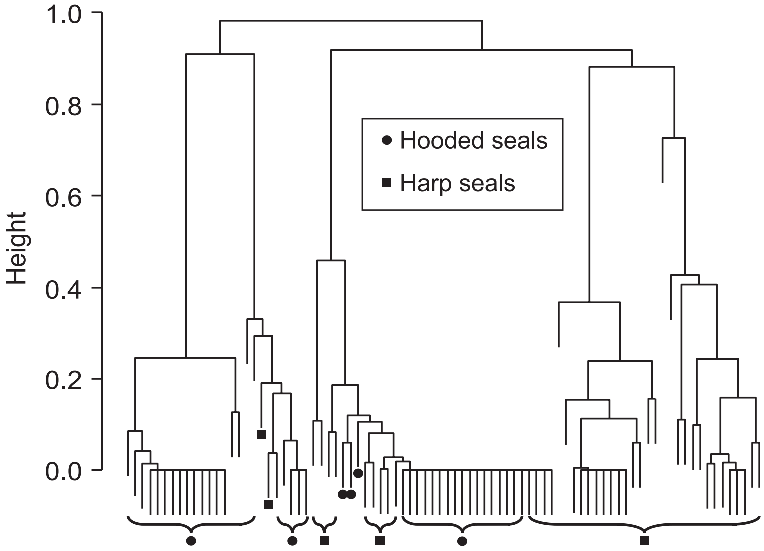

Fig. 3. Dendrogram of estimated biomass of harp and hooded seal intestinal contents, from one area sampled in winter 2001 where the spatial distribution of harp and hooded seals overlapped. The dendrogram was produced using average linkage clustering of Bray-Curtis dissimilarities of row-standardized data.

try-based observations of diving behaviour and published information about potential prey species, Folkow & Blix (1999) suggest that the diet of hooded seals along the ice edge in the northern Greenland Sea might be comprised of Greenland halibut (*Reinhardtius hippoglossoides*), redfish species of the genus *Sebastes*, polar cod and the squid *G. fabricii*. We found no evidence for Greenland halibut or redfish as important hooded seal food in the study area, whereas polar cod and *G. fabricii* were present.

G. fabricii was nearly absent from the harp seal samples which were characterized by pelagic crustaceans. Pelagic amphipods of the genus *Parathemisto* and polar cods were very important for the harp seals during summer 2000, whereas in winter 2001 krill, capelin and *Parathemisto* dominated. Polar cod was virtually absent from the harp seal diet in winter when capelin and other fish species were present. In their studies of harp seal diets in the Greenland Sea in April–June, Potelov et al. (2000) observed that the seals had fed mainly on pelagic amphipods, krill and polar cod, i.e. the same items as observed in this study. Pelagic amphipods of the genus *Parathemisto* include several species, but *P. libellula* is the only species that is confined exclusively to Arctic waters (Dalpadado et al. 2001; Dalpadado 2002). Previous investigations in the Greenland Sea during summer revealed that this amphipod species completely dominated the plankton communities in the upper Arctic water layers (Dalpadado et al. 1998). Similar observations have been made both in the north-west Atlantic (Percy 1993) and in the Barents Sea, where abundance may reach a peak in early autumn (Dalpadado et al. 2001; Dalpadado 2002). *P. libellula* is assumed to be an important link in the Arctic marine food chain between herbivorous zooplankton and fish, birds and mammals (Dunbar 1957; Bradstreet & Cross 1982; Mehlum & Gabrielsen 1993; Nilssen, Haug, Potelov & Timoshenko 1995; Dalpadado et al. 2001). In the Arctic parts of the Barents Sea, Dalpadado et al. (2001) suggest strong predator–prey interactions between macrozooplankton species such as *P. libellula* and predators such as capelin, cod and harp seals, and that the amphipod population appears to be largely controlled by predation.

Very little is known about fish stocks such as sandeels and polar cod in the study area. However, capelin is fairly well known (Vilhjalmsson 1997, 2002). Capelin spawn in areas south of Iceland, and their feeding areas are the northern parts of the Denmark Strait and shelf areas between Iceland and the island Jan Mayen (see Fig. 1). This restricted distribution explains both their appearance in hooded and harp seal diets in the Denmark Strait during winter in 2001 and their absence in seal diets during summer in 2000, when sampling of seals occurred far to the north of the distributional areas for capelin.

Many of the examined stomachs were empty, a common feature in harp seals when the species is sampled while hauled out on ice (see Nilssen, Haug, Potelov, Stasenkov et al. 1995; Nilssen, Haug, Potelov & Timoshenko 1995; Lindstrøm et al. 1998), and it may reflect rapid digestion (Helm 1984; Markussen 1993; Berg et al. 2002) and/or some migratory distance between feeding grounds and the haul-out sites on the ice. In passing through the gastrointestinal tract of the predator, otoliths of different species and sizes erode at different rates, and some are completely digested (e.g. Tollit et al. 1997; Berg et al. 2002; Tollit et al. 2003). Furthermore, whilst cephalopod beaks appear to be less susceptible to digestion, they may accumulate in the stomach (Pitcher 1980; Bigg & Fawcett 1985; Tollit et al. 1997), causing additional bias. The effect of passage through the pinniped gastrointestinal tract of crustaceans, as compared with fish, for example, is unknown. Despite these methodological problems, however, the presented results suggest that the ecology and distribution of the observed prey species can be related to known predator distribution and diving behaviour to give an account of how these seals fit into the Greenland Sea ecosystem. Obviously, the relative contribution of the most important prey species to the diet varied between the two seal species. Hooded seal diet was characterized by squid *G. fabricii* and polar cod, but pelagic crustaceans (amphipods and krill) were important for harp seals. When the relative intestinal prey composition were compared quantitatively among co-occurring harp and hooded seals in the winter 2001 sample, differences were observed. These are probably the result of different foraging depths of the two seal species. Studies of diving behaviour of harp and hooded seals in the Greenland Sea have revealed that both species usually perform more shallow dives during summer than during winter, and that hooded seals dive to deeper waters than harp seals in both periods (Folkow & Blix 1999; Folkow et al. 2004). Except for the youngest stages, which may occur in the upper water layers during summer, the major hooded seal prey *G. fabricii* has a typical mesopelagic distribution with occurrence mainly at depths greater than 400 m (Bjørke 2001). This is in contrast to the distribution of the major food of harp seals: the observed krill and amphipod species are usually confined to the more upper water layers (<200 m depth; Dalpadado et al. 1998; Dalpadado et al. 2001).

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References

Berg, I., Haug, T. & Nilssen, K. T. 2002: Harbour seal (*Phoca vitulina*) diet in Vesterålen, north Norway. *Sarsia 87*, 451–461.

Bigg, M. A. & Fawcett, I. 1985: Two biases in diet determination of northern fur seals (*Callorhinus urinus*). In J. R. Beddington et al. (eds): *Marine mammals and fisheries*. Pp. 284–291. London: George Allen & Unwin.

Bjørke, H. 2001: Possible predators of *Gonatus fabricii* (Lichtenstein) in its deep-water habitat. *Fish. Res. 52*, 113–120.

Born, E. W. 1982: Reproduction in the female hooded seal, *Cystophora cristata* Erxleben, at south Greenland. *J. Northwest Atl. Fish. Sci. 3*, 57–62.

Bowen, W. D., Sergeant, D. E. & Øritsland, T. 1983: Validation of age estimation in harp seals, *Phoca groenlandica*, using dental annuli. *Can. J. Fish. Aquat. Sci. 40*, 1430–1441.

Bradstreet, M. S. W. & Cross, W. E. 1982: Trophic relationships at High Arctic edges. *Arctic 35*, 1–12.

Breiby, A. 1985: Otolitter fra saltvannsfisker i Nord Norge. (Otoliths from salt water fishes in north Norway.) *Tromura Nat.vitensk. 53*, 1–30.

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

Dalpadado, P. 2002: Inter-specific variations in distribution, abundance and possible life-cycle patterns of *Themisto* spp. (Amphipoda) in the Barents Sea. *Polar Biol. 25*, 656–666.

Dalpadado, P., Borkner, N., Bogstad, B. & Mehl, S. 2001: Distribution of *Themisto* (Amphipoda) spp. in the Barents Sea and predator–prey interactions. *ICES J. Mar. Sci. 58*, 876–895.

Dalpadado, P., Ellertsen, B., Melle, W. & Skjoldal, H. R. 1998: Summer distribution patterns and biomass estimates of macrozoplankton and micronekton in the Nordic seas. *Sarsia 83*, 103–116.

Dunbar, M. J. 1957: The determination of production in northern seas: a study of the biology of *Themisto libellula* Mandt. *Can. J. Zool. 35*, 797–819.

Enckell, P. H. 1980. *Kräftdjur. (Crustaceans.)* Lund: Bokförlaget Signum.

Folkow, L. P. & Blix, A. S. 1995: Distribution and diving behaviour of hooded seals. In A. S. Blix et al. (eds): *Whales, seals, fish, and man*. Pp. 193–202. Amsterdam: Elsevier.

Folkow, L. P. & Blix, A. S. 1999: Diving behaviour of hooded seals (*Cystophora cristata*) in the Greenland and Norwegian seas. *Polar Biol. 22*, 61–74.

Folkow, L. P., Mårtensson, P. E. & Blix, A. S. 1996: Annual distribution of hooded seals (*Cystophora cristata*) in the Greenland and Norwegian seas. *Polar Biol. 16*, 179–189.

Folkow, L. P., Nordøy, E. S. & Blix, A. S. 2004: Distribution and diving behaviour of harp seals *Pagophilus groenlandica* from the Greenland Sea stock. *Polar Biol. 27*, 281–298.

Frie, A. K., Potelov, V. A., Kingsley, M. C. S. & Haug, T.

2003: Trends in age at maturity and growth parameters of female northeast Atlantic harp seals, *Pagophilus groenlandicus* (Erxleben, 1777). *ICES J. Mar. Sci. 60*, 1018–1032.

Gray, R. W. 1889: Notes on a voyage to the Greenland Sea in 1888. *Zoologist 3(13)*, 1–9, 42–51, 95–104.

Härkönen, T. 1986: *Guide to the otoliths of the bony fishes of the northeast Atlantic*. Hellerup, Denmark: Danbiu.

Haug, T., Lindstrøm, U., Nilssen, K. T., Røttingen, I. & Skaug, H. J. 1996: Diet and food availability for northeast Atlantic minke whales *Balaenoptera acutorostrata*. *Rep. Int. Whaling Comm. 46*, 371–382.

Haug, T., Nilssen, K. T. & Lindblom, L. 2000: First independent feeding of harp seal (*Phoca groenlandica*) and hooded seal (*Cysophora cristata*) pups in the Greenland Sea. *NAMMCO Sci. Publ. 2*, 29–39.

Hauksson, E. & Bogason, V. 1997: Comparative feeding of grey (*Halichoerus grypus*) and common seals (*Phoca vitulina*) in coastal waters of Iceland, with a note on the diet of hooded (*Cystophora cristata*) and harp seals (*Phoca groenlandica*). *J. Northwest Atl. Fish. Sci. 22*, 125–135.

Helm, R. C. 1984: Rate of digestion in three species of pinnipeds. *Can. J. Zool. 62*, 1751–1756.

ICES (International Council for the Exploration of the Sea) 1998: *Report of the Joint ICES/NAFO Working Group on Harp and Hooded Seals*. ICES Headquarters, Copenhangen, 28 August–3 September 1997. ICES CM 1998 / Assess: 3.

ICES (International Council for the Exploration of the Sea) 2004: *Report of the Joint ICES/NAFO Working Group on Harp and Hooded Seals*. Arkhangelsk, Russia, 2–6 September 2003. ICES CM 2004 / ACFM: 6.

Ihaka, R. & Gentleman, R. 1996: A language for data analysis and graphics. *J. Comput. Graph. Stat.* 5, 299–314.

Kovacs, K. M. & Lavigne, D. M. 1986: *Cystophora cristata*. *Mamm. Species 258*, 1–9.

Kristensen, T. K. 1981: The genus *Gonatus* Gray, 1849 (Mollusca, Cephalopoda) in the North Atlantic. A revision of the North Atlantic species and description of *Gonatus steenstrupi* n. sp. *Steenstrupia 7*, 61–99.

Kristensen, T. K. 1983: 10 *Gonatus fabricii*. In P. R. Boyle (ed.): *Cephalopod life cycles. Volume 1. Species accounts*. Pp. 159–173. London: Academic Press.

Legendre, P. & Legendre, L 1998: Numerical ecology. Second English edition. Amsterdam: Elsevier.

Lindstrøm, U., Harbitz, A., Haug, T. & Nilssen, K. T. 1998: Do harp seals *Phoca groenlandica* exhibit particular prey preferences? *ICES J. Mar. Sci. 55*, 941–953.

Markussen, N. H. 1993: Transit time of digesta in captive harbour seals *(Phoca vitulina). Can. J. Zool. 71*, 1071–1073.

Mehlum, F. & Gabrielsen, G. W. 1993: The diet of High-Arctic seabirds in coastal and ice-covered pelagic areas near the Svalbard archipelago. *Polar Res. 12*, 1–20.

Nilssen, K. T., Haug, T., Potelov, V., Stasenkov, V. A. & Timoshenko, Y. K. 1995: Food habits of harp seals (*Phoca groenlandica*) during lactation and moult in March–May in the southern Barents Sea and White Sea. *ICES J. Mar. Sci. 52*, 33–41.

Nilssen, K. T., Haug, T., Potelov, V. & Timoshenko, Y. K. 1995: Food habits and food availability of harp seals (*Phoca groenlandica*) during early summer and autumn in the northern Barents Sea. *Polar Biol. 15*, 485–493.

Nilssen, K. T., Pedersen, O.-P., Folkow, L. P. & Haug, T. 2000: Food consumption estimates of Barents Sea harp seals. *NAMMCO Sci. Publ. 2*, 9–28.

Øien, N. & Øritsland, T. 1995: Use of mark–recapture experiments to monitor seal populations subject to catching. In A. S. Blix et al. (eds): *Whales, seals, fish, and man.* Pp. 35–45. Amsterdam: Elsevier.

Øritsland, T. 1959: Klappmyss. (Hooded seal.) *Fauna (Oslo) 12*, 70–90.

Øritsland, T. 1964: Klappmysshunnens forplantingsbiologi. (Reproductive biology of female hooded seals.) *Fisken og Havet 1964(1)*, 1–15.

Øritsland, T. & Øien, N. 1995: Aerial surveys of harp and hooded seal pups in the Greenland Sea pack-ice. In A. S. Blix et al. (eds): *Whales, seals, fish, and man.* Pp. 77–87. Amsterdam: Elsevier.

Pedersen, A. 1930: Fortgesetzte Beitrage zur Kenntnis der Saugetiere und Vogelfauna der ostkuste Grønlands. (Contributions to the knowledge of mammals and birds from the east coast of Greenland.) *Meddelser om Grønland 77*, 344–506.

Percy, J. A. 1993: Reproduction and growth of the Arctic hyperiid amphipod *Themisto libellula* Mandt. *Polar Biol. 13*, 131–139.

Pethon, P. 1985: *Aschehougs store fiskebok. (Fishes.)* Oslo: Aschehoug and Company.

Pitcher, K. W. 1980: Stomach contents and faeces as indicators of harbour seal, *Phoca vitulina,* foods in the Gulf of Alaska. *Fish. Bull. 78*, 797–798.

Potelov, V., Nilssen, K. T., Svetochev, V. & Haug, T. 2000: Feeding habits of harp *Phoca groenlandica* and hooded seals *Cystophora cristata* during late winter, spring and early summer in the Greenland Sea. *NAMMCO Sci. Publ. 2*, 40–49.

Rasmussen, B. 1957: Exploitation and protection of the east Greenland seal herds. *Norsk Hvalfangsttidende 46*, 45–59.

Rasmussen, B. 1960: Om klappmyssbestanden i det nordlige Atlanterhav. (The hooded seal stock in the North Atlantic.) *Fisken og Havet 1*, 1–23.

Sergeant, D. E. 1991: *Harp seals, man and ice. Can. Spec. Publ. Fish. Aquat. Sci. 114*.

Surkov, S. S. 1960: Dannye po biologii i promyslu Yan Maienskogo Lysuna i Kohklacha v Zapadynkh L'dyakh. (Data on the biology and hunting of the Jan Mayen harp and hooded seals of the West Ice.) *Trudy PINRO, Murmansk 12*, 88–106. (Transl. 538, US Naval Oceanographic Office, Washington D.C. 20390,1972.)

Tollit, D. J., Steward, M. J., Thompson, P. M., Pierce, G. J., Santos, M. B. & Hughes, S. 1997: Species and size differences in the digestion of otoliths and beaks: implications for estimates of pinniped diet composition. *Can. J. Fish. Aquat. Sci. 54*, 105–119.

Tollit, D. J., Wong, M., Winship, A. J., Rosen, D. A. S. & Trites, A. W. E. 2003: Quantifying errors associated with using prey skeletal structures from fecal samples to determine the diet of Stellar's sea lion (*Eumetopias jubatus*). *Mar. Mamm. Sci. 19*, 724–744.

Venables, W. N. & Ripley, B. D. 2002: *Modern applied statistics with S.* Fourth edition. New York: Springer.

Vilhjalmsson, H. 1997: Interactions between capelin (*Mallotus villosus*) and other species and the significance of such interactions for the management and harvesting of marine ecosystems in the northern North Atlantic. *Rit Fiskideildar 15*, 31–63.

Vilhjalmsson, H. 2002: Capelin (*Mallotus villosus*) in the Iceland–East Greenland–Jan Mayen ecosystem. *ICES J. Mar. Sci. 59*, 870–883.