

DIETS OF HOODED SEALS IN COASTAL AND DRIFT ICE WATERS ALONG THE EAST COAST OF GREENLAND

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ABSTRACT

To provide data on the feeding habits of hooded (*Cystophora cristata*) seals in the Greenland Sea, seals were collected for scientific purposes on expeditions with R/V "Jan Mayen", conducted in the pack ice belt east of Greenland in September/October 1999 and 2002 (autumn), July/August in 2000 (summer), and February/March in 2001 and 2002 (winter). Results from analyses of stomach and intestinal contents from captured seals revealed that the diet was comprised of relatively few prey taxa. The squid *Gonatus fabricii* and polar cod *Boreogadus saida* were particularly important, whereas capelin *Mallotus villosus*, and sand eels *Ammodytes* spp contributed more occasionally. *G. fabricii* was the most important food item in autumn and winter, whereas the observed summer diet was more characterized by polar cod, however with important contribution also from *G. fabricii* and sand eels. The latter was observed on the hooded seal menu only during the summer period, while polar cod, which contributed importantly also during the autumn survey, was almost absent from the winter samples. During the latter survey, also capelin contributed to the hooded seal diet. Samples obtained in more coastal waters indicated a more varied and fish based (polar cod, redfish *Sebastes* sp., Greenland halibut *Reinhardtius hippoglossoides*) hooded seal diet.

INTRODUCTION

Hooded seals *Cystophora cristata* occur in the drift ice waters of the Greenland Sea along the east coast of Greenland during breeding and moult (March/April, see Rasmussen 1957, 1960; Folkow & Blix 1995; Folkow et al. 1996; Haug et al. 2000; Potelov et al. 2000). Recent information, obtained in satellite tagging programs, about the migratory patterns of the species, has indicated that hooded seals may occur in the Greenland Sea pack ice also in considerable periods outside the breeding and moulting period (Folkow et al. 1996). In total, they appeared to be based in the ice-covered waters off the east coast of Greenland in around 40% of the year; from these areas they made long excursions to distant waters (such as the waters off the Faroe Islands, the Irminger Sea, north/northeast of Iceland, areas in the Norwegian Sea, and along the continental shelf edge from Norway to Bear Island), presumably to feed, before returning to the ice edge again (Folkow & Blix 1995, 1999; Folkow *et al.* 1996). During excursions, which could last for more than 3 months, the seals apparently never hauled out, even if they sometimes stayed very close to coastal areas.

In the Greenland Sea, previous hooded seal studies have been concentrated mainly on stock size estimation, reproduction and migrational patterns (Rasmussen 1957, 1960; Øritsland 1959, 1964, Rasmussen & Øritsland 1964; Jacobsen 1984; Øien & Øritsland 1995; Øritsland & Øien 1995; Folkow & Blix 1995, 1999; Folkow *et al.* 1996; ICES 1998). Little attention has been paid to the feeding habits of the seals, and our knowledge about the ecological significance of this stock is, therefore, very poor. Except for some observations made in the West Ice during breeding and moult (i.e., spring, see Haug *et al.* 2000; Potelov *et al.* 2000), which are known to be periods with low feeding intensity (Rasmussen 1960; Kovacs & Lavigne 1986), only occasional information, mostly from coastal areas of eastern Greenland and northern Iceland were available (Hauksson & Bogason 1997; Kapel 2000). Although hooded seal migrational patterns outside the West Ice breeding and moulting periods are fairly well known from the recent satellite tagging program (Folkow & Blix 1995, 1999; Folkow *et al.* 1996), the diet of these animals in the same period has remained rather undocumented.

To enable an assessment of the ecological role of hooded seals during the considerable period

they occur in drift ice waters along the east coast of Greenland, a project aimed to study their feeding habits in the area was initiated in 1999. The project intended to pay special attention to the period July-February (i.e., between moulting and breeding), which is known to be a period of intensive feeding for the seals (Rasmussen 1960). Dedicated expeditions, using the ice going vessel R/V "Jan Mayen" along the east Greenland pack ice edge, were conducted during summer (July-August, 2000), autumn (September/October 1999, 2002) and winter (February-March, 2001, 2002). Additionally, some historical samples were obtained from coastal hunters that operated in the Ammassalik area on the southeastern coast of Greenland in May in 1987.

Hooded seals have long been known to co-occur with harp seals *Phoca groenlandica* in the drift ice waters of the Greenland Sea along the east coast of Greenland during spring, when both species breed (March/April, see Wollebæk 1907; Iversen 1927; Rasmussen 1957; Folkow & Blix 1995; Folkow *et al.* 1996, 2004; Haug *et al.* 2000; Potelov *et al.* 2000). Recent information, obtained in satellite tagging programs 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 period (Folkow *et al.* 1996, 2004). The latter was further confirmed in the research surveys performed during during summer (July/August) in 2000 and winter (February/March) in 2001, when it was observed that, although they co-occurred, the diets varied remarkably between the two seal species (Haug *et al.* 2004). These observed differences were probably the result of different foraging depths: 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).

Based on the entire data set, collected in 1987 and 1999-2002, it is the aim of this paper to give a more thorough description of the diet of hooded seals during all periods they occur in coastal and more offshore drift ice waters along the east coast of Greenland.

MATERIAL AND METHODS

Sampling of seals

Data from 20 hooded seals taken by local hunters in the Ammassalik area on the southeast coast of Greenland (Fig. 1) in May 1987 is included. The stomachs were frozen by the hunters and later transferred to a laboratory for analyses.

The remaining material originate from five dedicated research expeditions performed in 1999-2002, using the ice-going research vessel "Jan Mayen", to open drift ice areas along the east coast of Greenland from the Denmark Strait (between Iceland and Greenland) to approximately 78° N (Fig. 1). The sampling was allocated to three periods of the year: Summer (July/August), autumn (September/October) and winter (February/March). The cruise track generally followed the ice edge as an *a priori* planned "transect" line – all seals spotted along this edge were attempted shot and sampled. The seals were shot in the water or on ice floes and immediately brought on board the research vessel for dissection where samples of digestive tracts were frozen. The lower jaw (with teeth) were collected from each seal for age determination (see Born 1982; Haug *et al.* 2004).

During the period 2 – 6 October 1999, 15 hooded seals were sampled in the Greenland Sea along a north-to-south cruise track, starting in position 76° 40'N; 7° 07'W and ending in position 75° 21'N; 9° 07'W. Most sampling were performed over deep waters (1500-2800 m). On one occasion two hooded seals were taken in pack ice located over more shallow waters (c. 330 m) on the Greenland continental shelf (approximate position 76° 45'N; 8° 00'W).

In 2000, 65 hooded seals were sampled in the Greenland Sea during the period 22 July – 1 August along a south-to north cruise track, starting to the west of the island Jan Mayen, between positions 70° 58'N; 14° 30'W and 76° 54'N; 3° 55'W. Most sampling were performed in areas with sea depths ranging between 1000-3000 m. Two hooded seals were taken in pack ice located over more shallow waters (c. 250 m) on the Greenland continental shelf (approximate position 72° 20'N; 18° 10'W).

The 2001 survey, performed during 18 February – 1 March, covered areas of the Greenland Sea north of Jan Mayen (as far north as to 72° 24'N; 8° 50'W) and of the Denmark Strait northwest and west of Iceland, as far to the south-west as to 66° 41'N; 22° 29'W. A total of 13 hooded seals were sampled in the Greenland Sea area pack ice (depths ranging between 600-800 m). In the Denmark Strait, 57 hooded seals were taken in ice-filled waters with depths ranging between 800 – 1200 m.

In 2002, samples were obtained from two different surveys: During the first cruise, 25 hooded seals were obtained along the ice edge in the Greenland Sea between 71° 25'N; 11° 24'W and 69° 00'N; 17° 59'W in the period 17 – 28 February. Later in the same year, during the period 30 September – 4 October, 38 hooded seals were caught in the Greenland Sea along a cruise track which first went from north to south between positions 78° 11'N; 4° 39'W and 76° 43'N; 6° 20'W, and then turned in a northwestward direction up to 78° 18'N; 17° 24'W. The seals were taken in areas overlaying the Greenland continental shelf (250 – 1000 m depths).

Digestive tract contents analyses

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, and the prey organisms were identified to the lowest possible taxonomic level, preferably species, with references to Enckell (1980), Pethon (1985), Breiby (1985), Clarke (1986), and Härkönen (1986).

Estimates of the number of crustaceans present in the entire digestive tract (stomach and intestines combined) were obtained by counting the carapaces and/or tails of each species. In cases with large contents, subsamples were taken. Approximate average weights of crustaceans were obtained from fresh prey specimens found in the stomachs or from previously published values (see Haug *et al.* 1996, 2004; Potelov *et al.* 2000), and these were used to reconstruct the original biomass of crustaceans. Number of upper and lower squid beaks were recorded – the most numerous category decided the estimate of total squid number in the digestive tract. Apparently, only one squid species (*Gonatus fabricii*) was recorded. Due to the importance of this particular prey item in the hooded seal diets, a subsample of beaks were sent to Dr Thomas K. Kristensen (present head of The Mandal-Barth Research

Center for Biodiversity and Health, DBL – Institute for Health Research and Development, Charlottenlund, Denmark) for control. Dr Kristensen, an expert on squid of the genus *Gonatus* (e.g., Kristensen 1981, 1983), confirmed the species identifications. Backcalculation of squid biomass and mantle lengths from lower rostral lengths were performed using regression equations given by Clarke (1986).

The total number of each fish species in the digestive tract were estimated by adding the number of whole specimens, the number of intact skulls and half the number of "free" otoliths. Otoliths were measured, and published otolith length to fish length and fish wet weight correlations were used to reconstruct the initial weight of the most numerous fish species: polar cod *Boreogadus saida*, capelin *Mallotus villosus*, sand eels *Ammodytes* sp., redfish *Sebastes* sp., and flatfish, see Härkönen (1986) and Lindstrøm *et al.* (1998). Unidentifiable gadoid otoliths, most likely also from polar cod, were treated similarly. No corrections were made for otolith erosions, but only otoliths that were little or moderately digested were used in the biomass back-calculations. Due to a general lack of published otolith guides for Arctic fishes, the biomass of sculpins (Cottidae) and snailfishes (Liparidae) individuals were calculated using correlations based on our own unpublished material (see also Haug *et al.* 2004).

Feeding indices

The following two feeding indices were used to analyse the dietary data (see also Hyslop 1980; Pierce & Boyle 1991):

- 1) The frequency of occurrence of each prey item, FO_i :

$$FO_i = (s_i / s_t) \cdot 100$$

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.

- 2) The bulk biomass index, B_i :

$$B_i = (b_i / b_t) \cdot 100$$

where b_i is the total mass of prey category i in all seals and b_t is the total mass of all prey categories.

3) The combined index, C_i :

$$C_i = \frac{B_i \cdot F_i}{\sum_{i=1}^k B_i \cdot F_i}$$

where B_i and F_i is percentage weight and occurrence, respectively, and k is number of prey groups.

To construct 95% confidence intervals for the relative importance, as the combined index, of each prey group the diet data was bootstrapped 1000 times. All confidence intervals were corrected for possible acceleration and bias (see Efron & Tibishirani 1993). Pairwise bootstrapped based hypothesis testing was used to test for possible differences in diet composition between years and age groups (Efron & Tibishirani 1993). Because multiple testing tend to lead to exaggerated p-values, all p-values were Bonferroni corrected. A Friedman test, a nonparametric counterpart of the two-way analysis of variance, was run to test for possible temporal differences in length (mantle) composition of squid.

RESULTS

Prey occurrence

Most seals (95%) taken by local hunters in East Greenland coastal waters of the Ammassalik area had well filled stomachs, whereas the majority of stomachs (60-80%) from animals taken in the off shore drift ice areas were empty (Table 1). Intestine material was not available from the local hunter sample, but intestines from the drift ice samples generally contained food

remains (only 6-24% were empty).

At least 22 different prey items were identified – of these there were 4 crustaceans, one mollusc and at least 17 fish species (Table 1). Not all items appeared to be of equal importance – of particular importance in all periods in the off shore samples were the cephalopod *G. fabricii* (occurred in 34-82% of the intestines, and in 13-32% of the stomachs). Polar cod also occurred quite frequently in intestines in all periods (6-68%), while other fish species occurred more sporadic in particular periods (e.g., sand eels in summer, cottids in autumn, and capelin in winter, see Table 1). The frequency of occurrence of amphipods of the genus *Parathemisto* was considerable in all periods. Seals sampled in coastal areas were not observed to have eaten cephalopods, whereas fish species such as polar cod and redfish *Sebastes* sp., to some extent also Greenland halibut *Reinhardtius hippoglossoides*, appeared to be important.

Prey biomass

Polar cod and redfish contributed with 66% and 29%, respectively, to the prey biomass found in stomachs of the seals taken by local hunters in East Greenland coastal waters of the Ammassalik in May 1987. The combined contribution from other fish, particularly Greenland halibut *Reinhardtius hippoglossoides*, Arctic cod *Arctocephalus glacialis*, and sculpins were 5%, whereas the contribution from invertebrates were negligible.

In terms of relative biomass, *G. fabricii* dominated the digestive tract contents in all autumn (1999 and 2002) and winter (2001 and 2002) samples obtained from the open drift ice areas (58-94%, see Fig. 2). In the summer 2000 samples, the contribution from *G. fabricii* (32%) was significantly lower than in the autumn 1999 and in both the winter samples (74-94%, pairwise bootstrap-based testings, all $P < 0.05$). The summer sample in 2000 was particularly characterized by a large contribution from polar cod (54%) - this value was significantly higher for this species than in all other periods/areas (pairwise bootstrap-based testings, all $P < 0.05$), although polar cod contributed considerably also in the autumn samples in 1999 (19%). Sand-eels and capelin contributed with 11% and 14% in the summer (2000) and winter (2001) samples, respectively, but were otherwise more or less absent. The contribution from other fish, primarily bottom living sculpins, were significantly higher (39%) in the autumn 2002 samples than in any other samples (pairwise bootstrap-based testings, all $P < 0.05$). The

contributions from crustaceans were low in all periods.

The entire material included digestive tract contents from 170 hooded seals, of which 109 were in their first or second year of life, whereas the remaining 61 were two years old or older. Apparently, there were no significant differences (paired bootstrap-based testings, all $\hat{A} > 0.05$) in the diets observed for the youngest (< 2 years old) seals as compared with those two years old or older (Fig. 3).

Size of prey

Estimated mantle lengths for *G. fabricii*, the most common prey found in the hooded seal digestive tracts, ranged from less than 5 mm to 200 mm (Fig. 4). Small squid (length groups 0-50 and 50-100 mm) were, however, significantly more numerous than larger squid (Friedman test; $\chi^2_{3,0.01} = 14.1$, $P = 0.003$). The smallest size groups (0-50 mm) appeared to dominate the samples from summer (July-August) and autumn (September-October), whereas in the winter samples (February-March) there seemed to be an increased contribution from larger squids, particularly the size groups 50-100 mm mantle lengths. This apparent change was, however, not statistically significant (Friedman test; $\chi^2_{4,0.01} = 3.6$, $P = 0.46$).

DISCUSSION

The observed diet of hooded seals in the Greenland Sea pack ice appeared to be comprised of relatively few prey taxa, and the dominant role of the squid *Gonatus fabricii* was conspicuous. Although the relative contribution from polar cod, capelin and sand eel varied both with species and sampling period/area, these four prey items (one squid, three fishes) constituted 60-97% of the observed diet biomass, irrespective of sampling period. *G. fabricii* appeared to contribute importantly during all sampling periods, whereas polar cod was confined mainly to the summer 2000 (July/August) and autumn 1999 (September/October) periods, sand eels to the summer period, and capelin to the winter 2001 (January/February) period (Table 1, Fig. 2). When interpreting the results from the presented digestive tract contents analyses, one

must of course take into consideration that the sample sizes were small. The material contained a considerable larger number of younger (less than 2 years old) than of older seals – no significant change were, however, observed with increasing age of the seals in the material (Fig. 3).

Satellite tracking data have revealed that hooded seals from the West Ice stock appeared to be based in the ice-covered waters off the east coast of Greenland, from where they made long excursions to distant waters (such as the waters off the Faroe Islands, the Irminger Sea, north/northeast of Iceland, areas in the Norwegian Sea, and along the continental shelf edge from Norway to Bear Island), presumably to feed, before returning to the ice edge again (Folkow & Blix 1995, 1999; Folkow *et al.* 1996). During excursions, which could last for more than 3 months, the seals apparently never hauled out, even if they sometimes stayed very close to coastal areas. The present observations indicated that hooded seals both fed and hauled out regularly when they occurred along the ice edge in the northern Greenland Sea. From their satellite tag based observations of diving behaviour and available published information about potential prey species, Folkow & Blix (1999) suggested that the diet of hooded seals along the ice edge in the northern Greenland Sea might be comprised of Greenland halibut, redfish species of the genus *Sebastes*, polar cod and the squid *G. fabricii*. The present investigations did not give any evidence for demersal species such as Greenland halibut or redfish as important hooded seal food in the offshore drift ice area, whereas the more pelagic polar cod and particularly *G. fabricii* did prove to be major food items for the seals. The presented coastal samples from Greenland, on the other hand, confirmed the importance of redfish and Greenland halibut. It is also worth to notice that the autumn 2002 samples contained a larger proportion of demersal fishes (sculpins in particular) than any other drift ice samples. A large number of the autumn 2002 samples were taken over the Greenland shelf (see Fig. 1) – this may have made demersal fish species more available to the seals and suggest that hooded seals may well feed on bottom fishes in areas where they can obtain them, e.g., when the seals occur closer to coastal waters.

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 represent a considerable food resource, and the consumption of them by other top predators such as sperm whales *Physeter macrocephalus*, northern bottlenose whales *Hyperoodon ampullatus* and long finned pilot whales *Globicephala melaena* is assumed to be substantial (Bjørke

2001). Based on information from stranded animals, sperm whales have been suggested to feed primarily on adult specimens (mantle lengths generally more than 200 mm, see Santos *et al.* 1999, 2002; Simon *et al.* 2003), in particular mature females which after mating undergo comprehensive ontogenetic changes which implies that they lose their swimming ability and presumably become floatation devices for their negatively buoyant eggs (Kristensen 1981, Arkhipin & Bjørke 1999). This seems not to be the case with hooded seals for which the majority of the squid eaten had mantle lengths less than 50 mm during summer and autumn, and less than 100 mm in winter (Fig. 4). In his study of the life history of *G. fabricii* from West Greenland waters, Kristensen (1983, 1984) concluded that the juveniles (< c. 50 mm mantle length) lived in shoals in the uppermost 80 m of the water column. At increasing size they would live deeper, and as sub-adults and adults they would live above the bottom from 200m and downwards. Apparently, the main source of squid as food for the hooded seals were the juveniles (Fig. 4). There was an increased occurrence of larger specimens (in particular individuals with mantle lengths ranging between 50-100 mm) in the observed winter diets, as compared with summer and autumn. A general increase in size of squid specimens due to their natural individual growth from summer to winter may have contributed to this (Kristensen 1983, 1984). However, there are important differences in the habitats where the seals were sampled during summer and autumn (north of Jan Mayen, primarily in areas with water depths exceeding 1000 m) as compared with the winter samples which were obtained south of Jan Mayen in water depths ranging primarily between 250-1000 m (see Fig. 1). The larger depths north of Jan Mayen may simply have made the older, near-bottom dwelling squid unavailable for the seals.

Although hooded seals are known to feed much less intensively during breeding and moult than in other periods of the year (Rasmussen 1960), they have been shown to perform some food intake on their breeding and moulting grounds in pack ice areas of the Greenland Sea in April-June. As in the present investigations, *G. fabricii*, to some extent also polar cod, dominated their diet (Potelov *et al.* 2000). The diet of hooded seal pups during their first independent feeding excursions in April has been observed to be mainly *Parathemisto* sp. (Haug *et al.* 2000).

Hooded seal stomachs examined further to the south in the Nordic Seas (southern Greenland Sea, Iceland Sea) and in more coastal waters seems to indicate a more varied and fish based diet. Animals taken by local hunters in southeastern Greenland in June-July suggested low

feeding intensity in this period when particularly redfish and Greenland halibut were consumed (Kapel 1995). Later in the year (September), however, a few samples seem to indicate that hooded seal feeding was more intensive in the area, the diet now being comprised of squid, shrimp *Pandalus* sp., polar cod and redfish. The importance of polar cod and redfish, to some extent also Greenland halibut, was confirmed by the present Greenland coast samples (from May 1987). Hooded seals examined south of the breeding and moulting lairs (in coastal waters of northern Iceland) during the period April-October were observed to feed mainly on redfish, cod *Gadus morhua* and various other fishes, occasionally also shrimps and squid (Hauksson & Bogason 1997).

Very little is known about fish stocks such as sand eels 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 seal diets in the Denmark Strait during winter in 2001, and their absence in all diets of seals taken to the north of the distributional areas for capelin.

Many of the examined stomachs were empty, a common feature in seals when they are sampled while hauled out on ice (see Nilssen *et al.* 1995a, b; Lindstrøm *et al.* 1998; Haug *et al.* 2004), 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, 2003; Berg *et al.* 2002; Christiansen *et al.* 2005). The present recalculations of fish biomass were based only on little or very moderately eroded otoliths. 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 e.g., fish 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.

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REFERENCES

- Arkhipin, A.I. & Bjørke, H. 1999. Ontogenetic changes in morphometric and reproductive indices of the squid *Gonatus fabricii* (Oegopsida, Gonatidae) in the Norwegian Sea. *Polar Biol.* 22: 357-365.
- 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. Northw. Atl. Fish. Sci* 3: 57-62.
- Breiby, A. 1985. Otolitter fra saltvannsfisker i Nord Norge. *Troms Naturvitensk.* 53: 1-30.
- Christiansen, J.S., Moen, A.-G.M., Hansen, T.H., Nilssen, K.T. 2005. Digestion of capelin, *Mallotus villosus* (Müller), herring, *Clupea harengus*., and polar cod, *Boreogadus saida* (Lepechin), otoliths in a simulated seal stomach. *ICES J. mar. Sci.* 62: 86-92.
- Clarke, M.R. 1986. *A handbook for the identification of cephalopod beaks*. Clarendon Press, Oxford.
- Efron, B. & Tibshirani, R.J. 1993. *An introduction to bootstrap*. New York: Chapman and Hall. 436 pp.
- Enckell, P.H. 1980. *Kräftdjur*. Bokförlaget Signum i Lund. 685 pp.
- Folkow, L.P. & Blix, A.S. 1995. Distribution and diving behaviour of hooded seals. Pp. 193-202 in Blix, A.S., Walløe, L. & Ulltang, Ø. (eds) *Whales, seals, fish, and man*. Elsevier Science B.V.
- 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.
- Härkönen, T. 1986. *Guide to the otoliths of the bony fishes of the northeast Atlantic*. Danbiu ApS, Hellerup, Danmark: 256 pp.
- 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. Whal. Commn* 46: 371-382.
- Haug, T., Nilssen, K.T. & Lindblom, L. 2000. First independent feeding of harp seal (*Phoca groenlandica*) and hooded seal (*Cystophora cristata*) pups in the Greenland Sea. *NAMMCO Sci. Publ.* 2: 29-39.
- Haug, T., Nilssen, K.T. & Lindblom, L. 2004. Feeding habits of harp and hooded seals in drift ice waters along the east coast of Greenland in summer and winter. *Polar Res.* 23: 35-42.
- 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. Northw. Atl. Fish. Sci.* 22: 125-135.
- Helm, R. C. 1984. Rate of digestion in three species of pinnipeds. *Can. J. Zool.* 62: 1751-1756.
- Hyslop, E.J. 1980. Stomach content analysis - a review of methods and their application. *J. Fish Biol.* 17: 411-429.
- International Council for the Exploration of the Sea (ICES). 1998. Report of the Joint ICES/NAFO Working Group on Harp and Hooded Seals, ICES Headquarters, 28 August-3 September 1997. ICES CM 1998 / Assess: 3: 35 pp.
- Iversen, T. 1927. Drivis og selfangst. *Årsber. vedk. Norges Fiskerier* 1927(2): 1-84. (In Norwegian).
- Jacobsen, N.O. 1984. Estimates of pup production, age at first parturition and natural mortality for hooded seals in the West Ice. *FiskDir. Skr. Ser. HavUnders.* 17: 483-498.
- Kapel, F.O. 1995. Feeding ecology of harp and hooded seals in the Davis Strait - Baffin Bay region. Pp. 287-304 in Blix, A.S., Walløe, L. & Ulltang, Ø. (eds) *Whales, seals, fish, and man*. Elsevier Science B.V.
- Kapel, F.O. 2000. Feeding habits of harp and hooded seals in Greenland waters. *NAMMCO Sci. Publ.* 2: 50-64.
- Kovacs, K. M. & Lavigne, D. M. 1986. *Cystophora cristata*. *Mammalian 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*. Pp. 159-173 in Boyle, P.R. (ed.) *Cephalopod Life Cycles. Volume 1 Species Accounts*. Academic Press.
- Kristensen, T.K. 1984. Biology of the squid *Gonatus fabricii* (Lichtenstein, 1818) from West Greenland waters. *Meddr. Grønland, Biosci.* 13: 3-17.
- 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.
- Nilssen, K.T., Haug, T., Potelov, V., Stasenkov, V.A. and Timoshenko, Y.K. 1995b. 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. and Timoshenko, Y.K. 1995a. 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.
- Øien, N. & Øritsland, T. 1995. Use of mark-recapture experiments to monitor seal populations subject to catching. Pp. 35-45 in Blix, A.S., Walløe, L. & Ulltang, Ø. (eds) *Whales, seals, fish, and man*. Elsevier Science B.V.
- Øritsland, T. 1959. Klappmyss. *Fauna (Oslo)* 12: 70-90.
- Øritsland, T. 1964. Klappmysshunnens forplantingsbiologi. *Fisken Hav*. 1964(1): 1-15.
- Øritsland, T. & Øien, N. 1995. Aerial surveys of harp and hooded seal pups in the Greenland Sea pack-ice. Pp. 77-87 in Blix, A.S., Walløe, L. & Ulltang, Ø. (eds) *Whales, seals, fish, and man*. Elsevier Science B.V.
- Pethon, P. 1985. *Aschehougs store fiskebok*. Aschehoug, H. and Company (Nygaard, W.) A/S.
- Pierce, G.J. and Boyle, P.R. 1991. A review of methods for diet analysis in piscivorous marine mammals. *Oceanogr. Mar. Biol. Annu. Rev.* 29: 409-486.
- Pitcher, K. W. 1980. Stomach contents and faeces as indicators of harbour seal, *Phoca vitulina*, foods in the Gulf of Alaska. *Fish. Bulle.* 78: 797-798.
- Potelov, V., Nilssen, K.T., Svetochov, 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 Hvalfangsttid.* 46: 45-59.
- Rasmussen, B. 1960. Om klappmyssbestanden i det nordlige Atlanterhav. *Fisken Hav*. 1: 1-23.
- Rasmussen, B. & Øritsland, T. 1964. Norwegian tagging of harp and hooded seals in North Atlantic waters. *FiskDir. Skr. Ser. HavUnders.* 13: 43-55.
- Santos, M.B., Pierce, G.J., Boyle, P.R., Reid, R.J., Ross, H.M., Patterson, I.A.P., Kinze, C.C., Tougaard, S., Lick, R., Piatkowski, U. & Hernandez-Garcia, V. 1999. Stomach contents of sperm whales *Pyseter macrocephalus* stranded in the North Sea 1990-1996. *Mar. Ecol. Prog. Ser.* 183: 281-294.
- Santos, M.B., Pierce, G.J., Garcia-Hartmann, M., Smeenk, C., Addink, M.J., Kuiken, T., Reid, R.J., Patterson, I.A.P., Lordan, C., Rogan, E. & Mente, E. 2002. Additional notes on stomach contents of sperm whales *Pyseter macrocephalus* stranded in the north-east Atlantic. *J. Mar. Biol. Ass. U.K.* 82: 501-507.
- Simon, M.J., Kristensen, T.K., tendal, O.S., Kinze, C.C. & Tougaard, S. 2003. *Gonatus fabricii* (Mollusca, Theuthida) as an important food source for sperm whales (*Physeter macrocephalus*) in the Northeast Atlantic. *Sarsia* 88: 244-246.
- 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.
- 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 Fiskideild.* 15: 31-63.
- Vilhjalmsson, H. 2002. Capelin (*Mallotus villosus*) in the Iceland-East Greenland-Jan Mayen ecosystem. *ICES*

J. mar. Sci. 59: 870-883.

Wollebæk, A. 1907. Über die Biologie der Seehunde und die Seehundjagd im Europäischen Eismeer. *Rapp.t
proc.-verb. Réunion. Cons. Int. l'Explor. Mer* 8: 109–119.

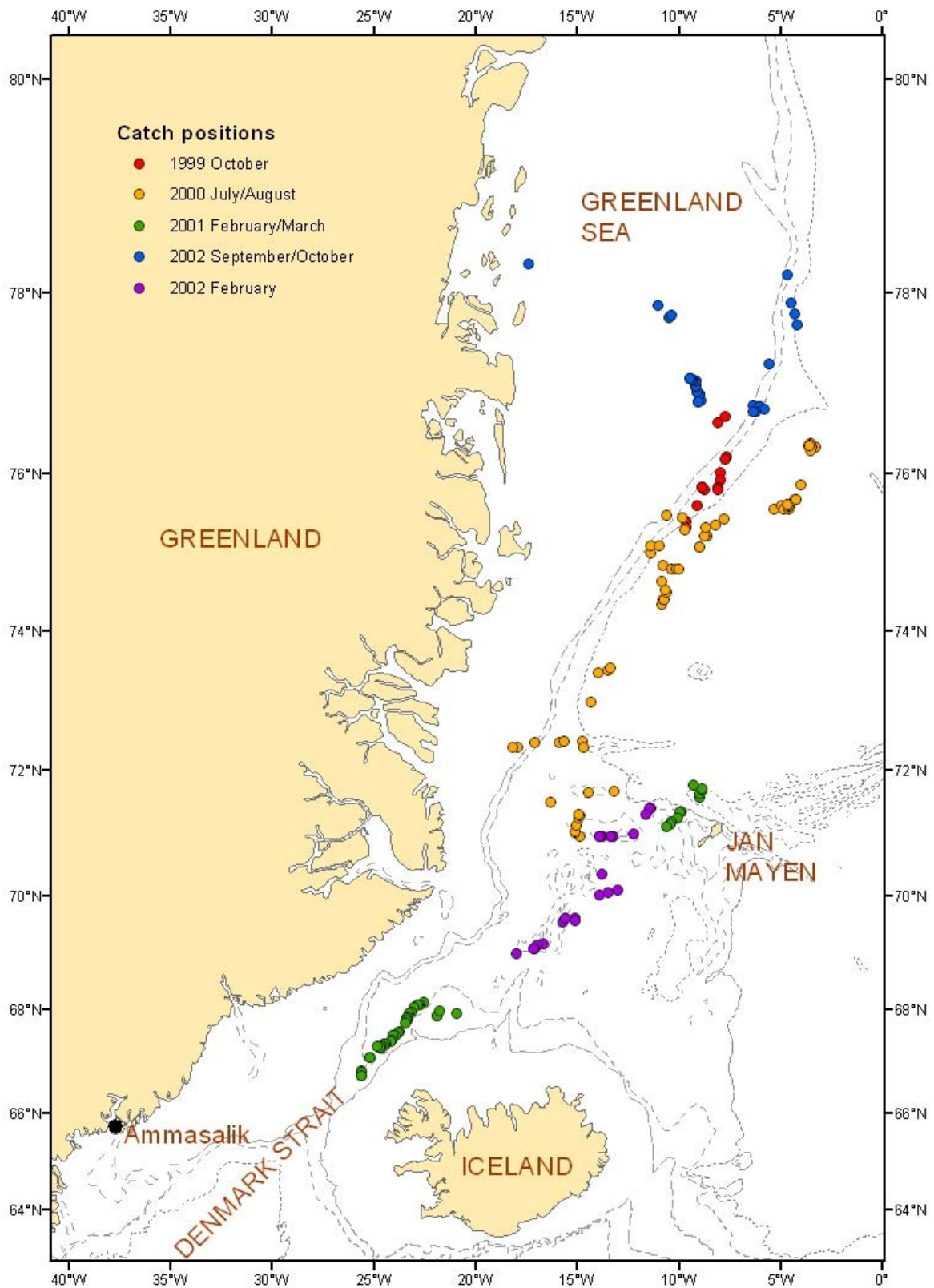


Fig. 1. Catch positions for hooded seals taken for scientific purposes east of Greenland in 1999-2002.

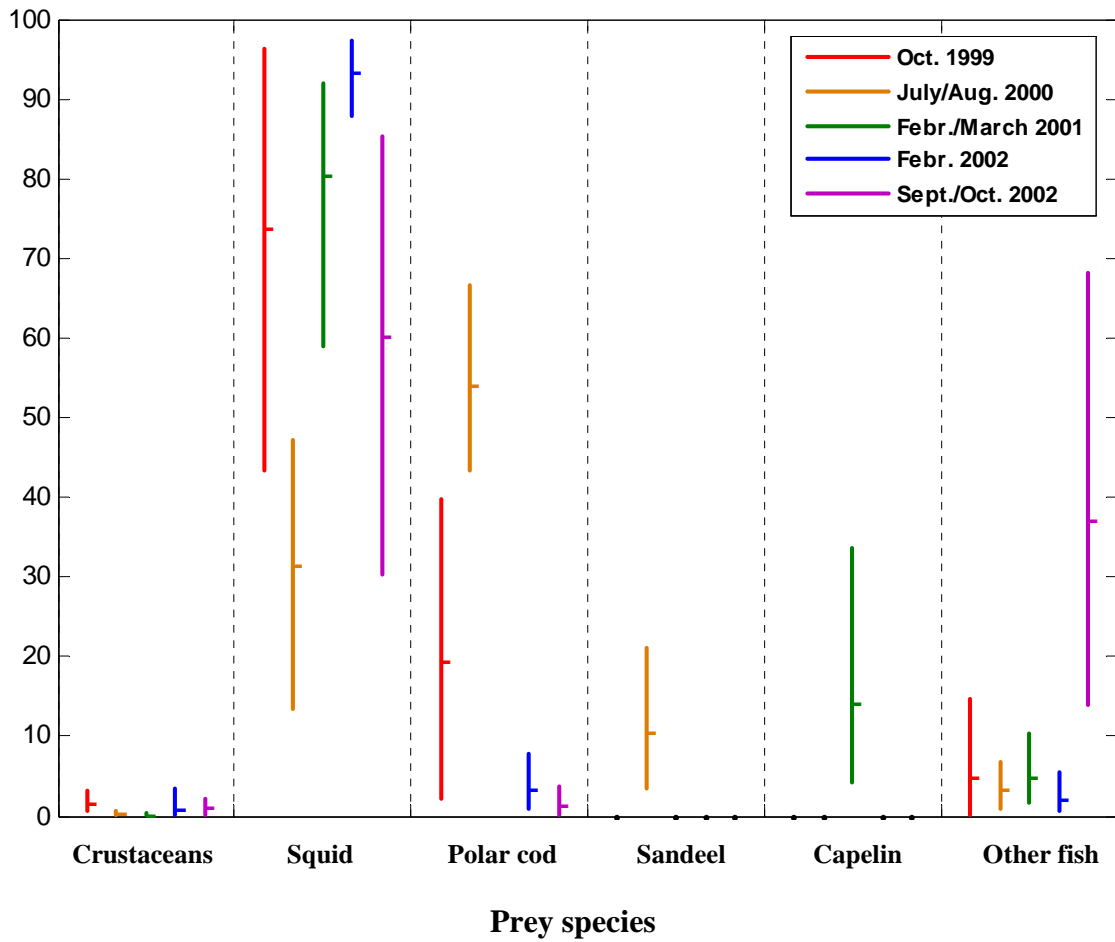


Figure 2. Relative prey importance, as percentage combined index (see text for explanation), in hooded seal diets east of Greenland in the period 1999-2002. The mean relative biomass estimates are plotted with 95% confidence interval, determined from 1000 bootstrap replicates, and corrected for possible acceleration and bias.

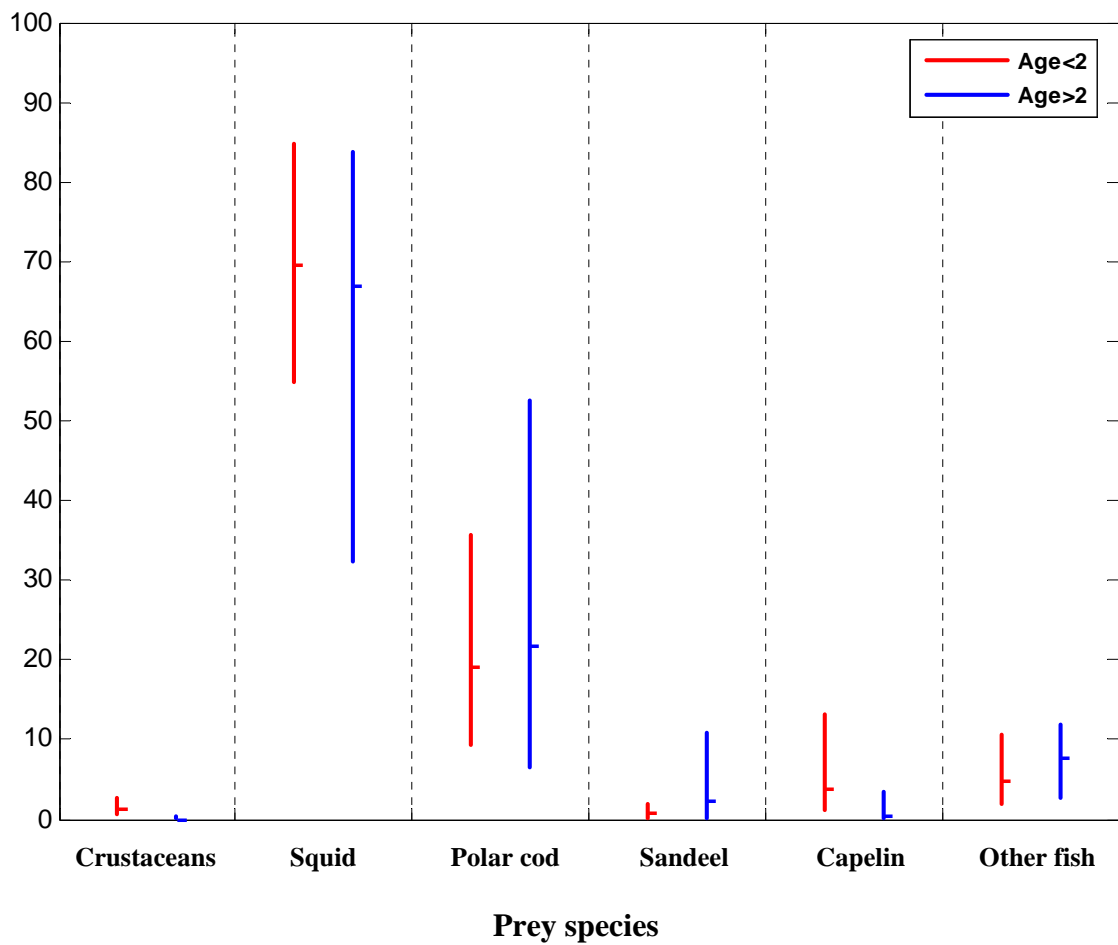


Figure 3. Relative prey importance, as percentage combined index, in hooded seal diets east of Greenland in the period 1999-2002. The mean relative biomass estimates are plotted with 95% confidence interval, determined from 1000 bootstrap replicates, and corrected for possible acceleration and bias.

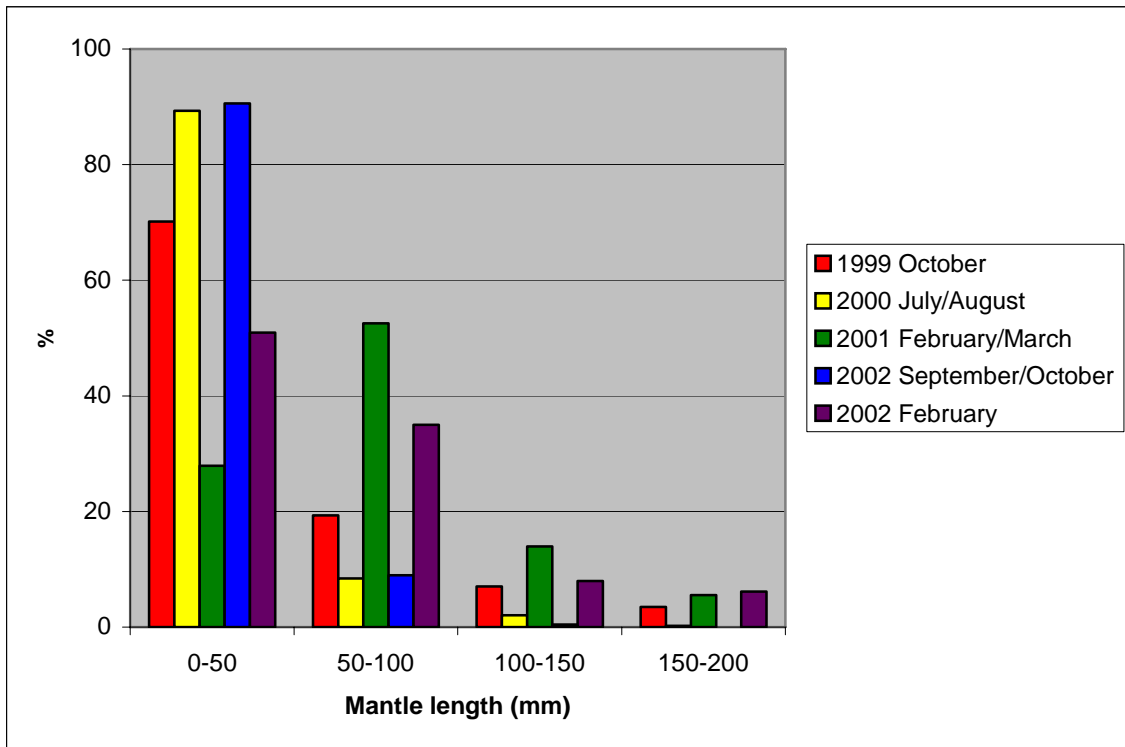


Fig. 4. Size distribution (mantle lengths) of squid (*Gonatus fabricii*) found in digestive tracts of hooded seals taken for scientific purposes east of Greenland in 1999-2002.

Table 1.

Frequency of occurrence of empty stomachs and intestines, and identified species in stomachs and intestines of hooded seals caught in drift ice areas east of Greenland in May (1987), July/August (2000), September/October (1999 and 2002), and in February/March (2001 and 2002). N = number of seals examined. n = number of stomachs/intestines with content.

	PERCENTAGE OCCURRENCE										
	MAY		JUL/AUG		SEP/OCT		FEB/MAR				
	1987 N=20 Stomachs N=19	2000 N=65 Stomachs n=26	Intestines n=61	1999 N=15 Stomachs n=4	Intestines n=13	2002 N=38 Stomachs n=17	Intestines n=31	2001 N=70 Stomachs n=14	Intestines n=53	2002 N=25 Stomachs n=7	Intestines n=21
Empty	5.0	60.0	6.2	73.3	13.3	55.3	18.4	80.0	24.3	72.0	16.0
Crustacea											
Amphipoda											
<i>Parath. libellula</i>	10.0	12.3	13.8	13.3	40.0	15.8	15.8	1.4	4.3	8.0	28.0
<i>Parathemisto</i> sp.	45.0	13.8	33.8	20.0	66.7	13.2	21.1	4.3	10.0	8.0	40.0
<i>Gam. wilkitzkii</i>	0	0	0	6.7	0	7.9	0	0	0	0	0
<i>Gammarus</i> sp.	0	6.2	10.8	0	6.7	2.6	0	0	1.4	0	0
Unid. Amph.	0	0	7.7	0	6.7	2.6	2.6	0	1.4	0	0
Euphausiacea											
<i>Thysanoessa</i> sp.	0	3.1	1.5	0	0	2.6	0	1.4	0	0	0
Decapoda	10.0	3.1	1.5	0	0	0	0	1.4	7.1	0	4.0
Unid. Crust.	0	3.1	6.2	6.7	0	0	7.9	0	0	0	0
Mollusca											
Cephalopods											
<i>Gonatus fabricii</i>	0	32.3	81.5	13.3	73.3	21.1	34.2	17.1	40.0	20.0	60.0
Pisces											
Clupeidae											
<i>Clupea harengus</i>	0	0	1.5	0	0	0	0	0	0	0	0
Osmeridae											
<i>Mallotus villosus</i>	0	0	0	0	0	0	0	1.4	34.3	0	16.0
Paralepididae											
Unid. Paralepididae	0	0	0	0	0	0	7.9	0	0	0	0
Gadidae											
<i>Boreogadus saida</i>	80.0	24.6	67.7	13.3	46.7	5.3	7.9	0	5.7	8.0	24.0
<i>Gadus morhua</i>	5.0	0	0	0	0	0	2.6	0	0	0	0
<i>Pollachius virens</i>	0	0	0	0	0	0	5.3	0	0	0	0
<i>Melanog. aeglefinus</i>	5.0	0	0	0	0	0	0	0	0	0	0
Unid. Gadoids	0	7.7	30.6	6.7	13.3	0	2.6	0	0	4.0	0
Ammodytidae											
<i>Ammodytes</i> sp.	0	10.8	30.8	0	0	0	0	0	0	0	0
Lumpenidae											
Unid. Lumpenids	0	0	3.1	0	0	0	0	1.4	0	0	0
Zoarcidae											
Unid. Zoarcids	0	0	0	0	0	0	0	0	7.1	0	0
Scorpaenidae											
<i>Sebastes marinus</i>	35.0	0	0	0	0	0	0	0	0	0	0
Unid. Scorpaenids	0	0	0	0	0	0	0	0	1.4	0	0
Cottidae											
Unid. Cottids	10.0	0	0	6.7	6.7	2.6	26.3	0	0	0	0
Cyclopteridae											
Unid. Cyclopterids	5.0	0	0	0	0	0	0	0	0	0	4.0
Liparidae											
Unid. Liparids	0	1.5	3.1	0	6.7	0	2.6	0	1.4	0	0
Pleuronectidae											
<i>Hippogl. platessoides</i>	0	0	0	0	0	0	0	0	2.9	0	0
<i>Reinh. hippoglossoides</i>	20.0	0	0	0	0	0	0	0	0	0	0
Bothidae											
Unid. Bothidae	5.0	0	0	0	0	0	0	0	0	0	0
Unid. Fish remains	0	10.8	9.2	0	6.7	10.5	23.7	1.4	11.4	0	0