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INVASIONS OF HARP SEALS *PHOCA GROENLANDICA* ERXLEBEN TO COASTAL WATERS OF NORWAY IN 1995: ECOLOGICAL AND DEMOGRAPHIC IMPLICATIONS

KJELL T. NILSSEN, TORE HAUG, TORGER ØRITSLAND, LOTTA LINDBLOM & STEN A. KJELLQWIST

SARSIA



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Since 1978, and in particular in 1986-1988, large numbers of harp seals *Phoca groenlandica* ERXLEBEN have invaded coastal waters of North Norway during winter and spring. After 1988 the harp seal invasions have been restricted to the northeasternmost parts of the coast of Norway. In 1995, however, a significant increase occurred in both the magnitude and the spatial extent of the harp seal invasions. Diet composition, age structure and body condition parameters were examined on seals taken incidentally in Norwegian gill net fisheries during winter and spring in 1995. In early winter immature animals were taken, while mature females dominated in the spring. Analyses of stomach contents suggested that the diet mainly contained fish, in particular saithe *Pollachius virens* (L.), haddock *Melanogrammus aeglefinus* (L.) and cod *Gadus morhua* (L.). Body condition parameters revealed that the one year old seals taken in February 1995 were in significantly poorer condition than harp seals of the same age taken in the southeastern Barents Sea in February 1993. Also the mature females taken in April 1995 had significantly lower condition compared to adult females collected in April 1992. Recaptures of 39 tagged harp seals showed that some of the invading immature seals in the winter of 1995 belonged to the Barents Sea stock. Comparisons of age compositions of the Barents Sea harp seals based on material collected during Norwegian commercial sealing in the East Ice moulting lairs in the period 1978-1993 with samples from 1995 could suggest a low recruitment to this stock of the 1993 and in particular the 1994 year classes.

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KEYWORDS: Northeast Atlantic; harp seals; invasions; condition; diet; age compositions.

INTRODUCTION

In winter and spring (December to May) the entire stock of Barents Sea harp seals *Phoca groenlandica* ERXLEBEN is usually concentrated at the southern end of its range, in the southeastern parts of the Barents Sea and in the White Sea (HAUG & al. 1994). Whelping takes place in the White Sea mainly from 20 February to 5 March, and is followed by a twelve days lactation period after which the females mate and desert their pups (CHAPSKII 1961). After a lapse of four more weeks the adults and immatures moult on the drifting ice in the White Sea and in the southeastern Barents Sea (SERGEANT 1991). After completed moult, the seals migrate north and northwest in the Barents Sea where they are distributed in open waters and in relation to the drifting pack ice during summer and autumn. During November-December the seals return to the southeastern parts of the Barents Sea and the White Sea (HAUG & al. 1994).

Beginning in 1978, large numbers of harp seals started to appear along the coast of North Norway during early winter and spring. During the early 1980s, pregnant females and immature seals began to appear on the coast of eastern Finnmark (BJØRGE & al. 1981). The females left the coast in early March but reappeared in April, whereas males were present from mid-March onwards. During 1986-1988 both the magnitude and the geographic extent of the seal invasions increased dramatically, and substantial numbers of seals were taken as by-catches in coastal gill net fisheries in northern Norway, some animals as far south as Skagerrak (HAUG & al. 1991). The total number of seals drowned may have been up to ten thousand per year in the early 1980s and perhaps as many as one hundred thousand in 1987. From 1989 onwards the numbers seem to have returned to the level of the early 1980s. In recent years the harp seal invasions have again been confined mainly to the eastern coast of Finnmark county and have characteristically

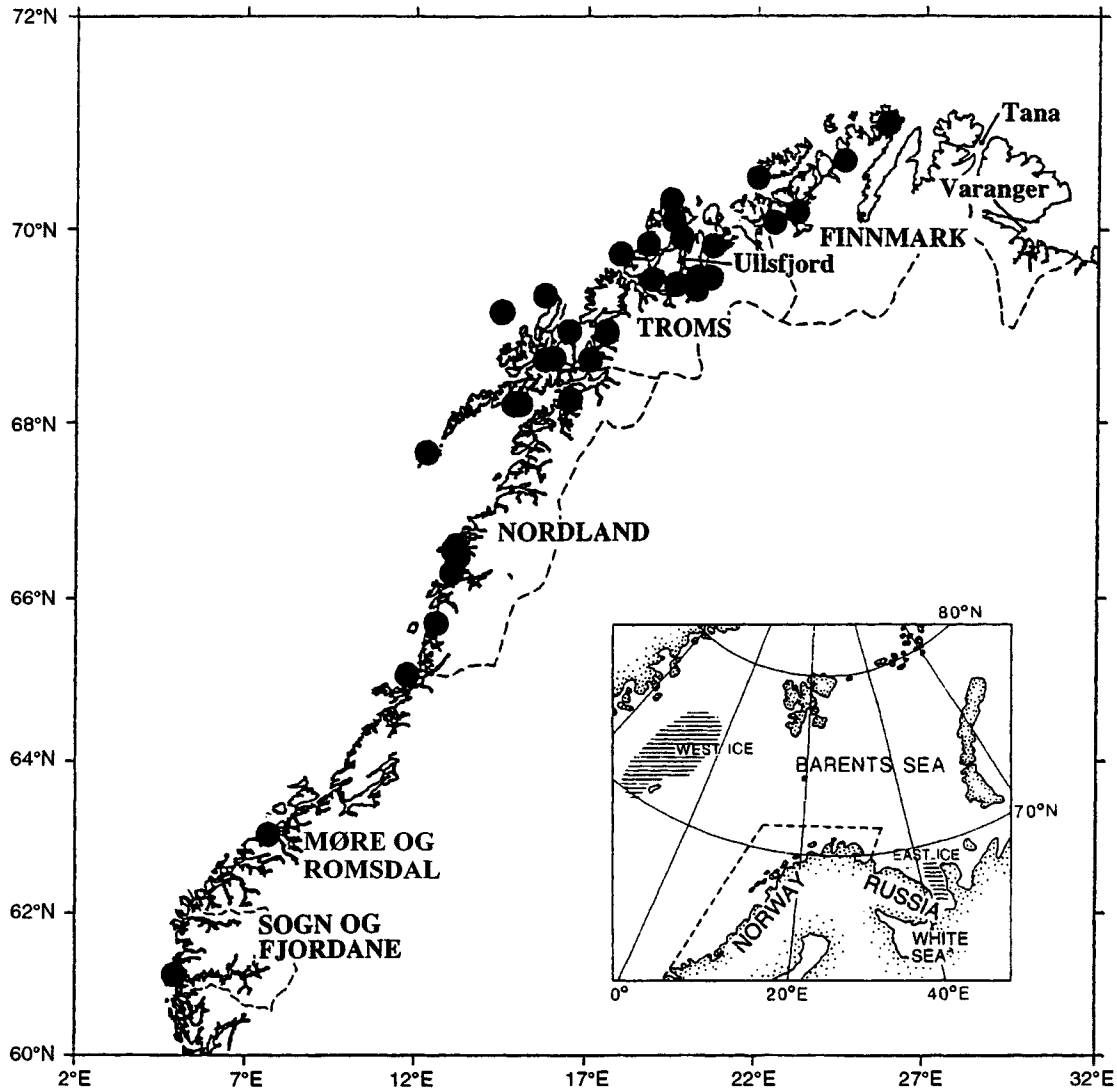


Fig. 1. Sampling areas of harp seals and recaptures (black circles) of tagged harp seals along the Norwegian coast and in the East Ice during winter 1994/1995.

included females performing feeding migrations in the period between breeding and moult (March–April) (HAUG & NILSEN 1995; NILSEN & al. 1995a).

In 1978, the total stock size of Barents Sea harp seals was estimated to number c. 800 000 animals with an annual increase of about 5 % (BENJAMINSEN 1979). This increasing trend may have persisted until the mid-1980s, whereafter substantial changes, including failed recruitment, seems to have occurred (KJELLQWIST & al. 1995; HAUG & NILSEN 1995; ØRITSLAND 1995, 1996). Recent stock size estimates are lacking, but the pup production in the White Sea was estimated to be 142 000 pups in 1991, which could be equivalent to a stock size of approximately 600 000 seals (1+) (ØIEN 1994).

The marine ecosystem of the Barents Sea has undergone substantial changes during the course of the past 30 years. The most conspicuous changes relate to variations in abundance of the two pelagic shoaling fish species: the Norwegian spring spawning herring *Clupea harengus* (L.) stock collapsed in the late 1960s but is now recovering, whereas the Barents Sea capelin *Mallotus villosus* (MÜLLER) stock collapsed in the mid-1980s, recovered to some extent in the early 1990s but is once more at a very low level (ANON. 1996a). Both species are consumed by Barents Sea harp seals (HAUG & al. 1991; NILSEN 1995; NILSEN & al. 1994, 1995a, b) and their collapses, combined with increasing numbers of seals, may have contributed to the seal invasions, in

particular the extensive 1986-1988 invasions which followed the 1985/1986 capelin stock crash (HAUG & NILSEN 1995). Observations of effects (poor condition, decreased growth rate, increased age at maturity and reduced female fecundity) that could indicate density-dependent responses within the seal stock (KJELLQWIST & al. 1995; NILSEN & al. 1997) support the hypothesis that food shortage may have contributed to the seal invasions. A substantial temporary increase in the abundance of immature Norwegian spring spawning herring after 1988 in the southeastern Barents Sea may have provided a suitable alternative winter food resource for the harp seals until the strong herring year-classes of 1991 and 1992 migrated out of the southern parts of the Barents Sea and into the Norwegian Sea during 1994 and 1995 (ANON. 1996a).

In 1995, an increase again occurred in both magnitude and geographic extent of harp seal invasions to the Norwegian coast. Sampling of stomach contents for diet analyses, teeth for age determinations and body condition parameters were carried out on invading seals incidentally caught in Norwegian gill net fisheries during winter and spring in 1995. Furthermore, collection of data on the age composition of the Barents Sea harp seals were continued during Norwegian commercial sealing in the East Ice moulting areas in April-May 1995 (ØRITSLAND 1996). Results from analyses of these data are presented in this paper along with data on recaptures along the Norwegian coast in late 1994 and early 1995 of harp seals tagged in the White Sea. The objectives of the study are to use the collected parameters to evaluate possible reasons for the observed increase in seal invasions and potential impact on the seal stock.

MATERIAL AND METHODS

Norwegian by-catches of harp seals

Due to damage to gill nets and reduced catches caused by the invading seals, Norwegian authorities paid a compensation to fishermen who caught seals in their nets. As documentation, the fishermen had to deliver the front flippers from the dead seals. Payments were organized by Norges Råfisklag (Norwegian Fishermen's Sales Organisation). In the absence of a direct census of the invading seals, it is assumed that the number of seals recorded for compensation payments provides an index of the magnitude of the invasion along the coast of Norway during the winter of 1995. This method was also used to evaluate the size of seal invasions during the 1980s, including the large invasions in 1986-1988 (HAUG & al. 1991; UGLAND & al. 1993; HAUG & NILSEN 1995).

Recaptures of tagged harp seals

In a joint Norwegian-Russian program, substantial numbers of harp seals have been tagged annually in the White Sea since 1989 (ØIEN & ØRITSLAND 1995). In 1992, 1993 and 1994, a

total number of 2315, 1730 and 4860 harp seal pups were tagged, respectively. The Institute of Marine Research, Bergen, Norway, have provided the tags, while Russian scientists from SevPINRO, Arkhangelsk, Russia, have performed the taggings of pups during the breeding season (February-March). Seal pups were tagged in one of their rear flippers, using yellow plastic Rototags. All taggings and recaptures have been recorded in a database at the Institute of Marine Research, Bergen. The results from recaptures of harp seals given in this paper are provided from this database.

Collection of biological material

Samples from harp seals taken incidentally in gill net fisheries were collected in coastal areas of North Norway in 1995. On the coast of Troms county 87 animals were sampled during January-February, and 27 seals were sampled in Tana, Finnmark county, in April. Biological material from harp seals was also collected during Norwegian commercial sealing in the East Ice in April-May 1995 where lower jaws (for age determination) were collected from 1697 seals. Samples from by-caught seals were taken as soon as possible after the seals were landed. Due to low winter temperatures some animals were frozen and had to be thawed before sampling. Condition measurements were performed on all seals. The measurements include total weight to the nearest kg; standard body length, measured to the nearest cm in a straight line from the tip of snout to the tip of tail, with the animal lying on its back; axillary girth, measured to the nearest cm; dorsal blubber thickness to the nearest mm (in a knife-cut at the mid-line between the front flippers). The stomachs of the seals were collected and frozen for laboratory examination of the contents. Lower jaws with teeth were collected for age determination.

Age determination

The ages of the seals were determined by incremental growth layers in the dentine of the lower canine teeth, examined in transverse sections using transmitted light (BOWEN & al. 1983).

Analyses of body condition

Measurements of dorsal blubber thickness, and a condition index (C), based on RYG & al. (1990), expressed as

$$C = \sqrt{L/W} \times d,$$

where L is standard body length in cm, W is total body mass in kg and d is dorsal blubber thickness measured in cm in the mid-line between the front flippers, were used to describe the body condition of the sampled seals. Both parameters were tested using student's t -test for possible differences between seals sampled in coastal areas of Troms county in February 1995 and animals of equal age sampled in the southeastern Barents Sea in February 1993. The condition measurements of harp seals sampled in Tana during the first part of April 1995 were compared with similar data collected in April 1992 in Varangerfjord, Finnmark county, and in the East Ice (NILSEN & al. 1997).

Stomach contents analyses

In the laboratory the stomachs were cut open after thawing, the contents removed and the total weight of the contents recorded. Fish and crustaceans were separated and the wet weight of each group recorded. All fresh specimens of fish and crustaceans

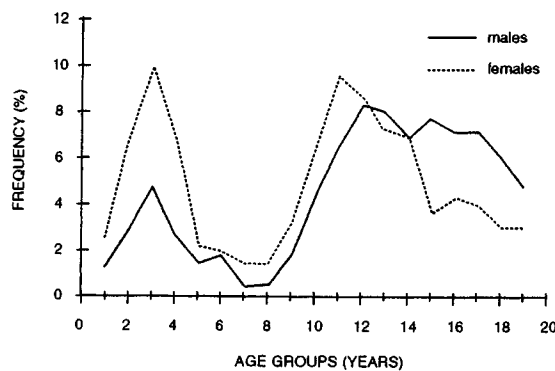


Fig. 2. Age-composition of 1189 male and 508 female harp seals (one year and older) sampled in the East Ice in the period 4 April - 1 May 1995.

were identified using standard identification keys (PETHON 1985; ENCKELL 1980). Feathers from seabirds were identified at Tromsø Museum, University of Tromsø, Norway, using reference material (Wim Vader, Tromsø Museum, University of Tromsø, pers. commn).

The total, or a subsample of crustaceans in each seal stomach, was weighed and the species composition determined. The wet weights and numbers of each crustacean species were recorded and used to estimate the numerical frequencies of crustaceans in the seal diet. By counting carapaces the numbers of partly digested crustaceans were obtained. Mean wet weights of undigested crustaceans were used to calculate the initial weight of crustacean remains found in the seal stomachs.

Otoliths were separated from the remainder of the stomach contents (TREACY & CRAWFORD 1981; MURIE & LAVIGNE 1985), and were identified to the lowest possible taxon, using reference material (BREIBY 1985; HÄRKÖNEN 1986). All otoliths were measured, and otolith length to fish wet weight correlations, based on a published guide (HÄRKÖNEN 1986), were used to estimate the initial weights of the fish in the seal diet. For herring, the otolith length (OL) (mm) - fish weight (FW) (g) correlation: $FW = 0.634 \times OL^{4.034}$, based on material sampled during minke whale *Balaenoptera acutorostrata* (LACÉPÈDE) in-

vestigations in the southern Barents Sea in 1992 (HAUG & al. 1995), were used. The total number of each fish species was estimated by adding the number of fresh specimens, the number of intact skulls and half the number of free otoliths.

Three indices were used to estimate the dietary contribution of the different prey items (HYSLOP 1980; PIERCE & BOYLE 1991): (1) the frequency of occurrence of a given prey was defined as the percentage of stomachs that contained one or more individuals of the prey species; (2) the numerical frequency of a species was calculated as a numerical fraction of total numbers of all prey categories; and (3) the biomass was recorded as the relative contribution of each prey species to the total seal diet expressed in terms of calculated wet weight.

RESULTS

By-catches

According to data provided from Norges Råfisklag, the number of harp seals drowned in gill nets at the Norwegian coast during the period 1990-1994 were recorded to be between 368 and 3238 seals annually. These were mainly adult females performing feeding migrations to the eastern coast of Finnmark county in the period between breeding and moult (March-April) (see NILSEN & al. 1995a). In the period 1 January to 14 May 1995, a total of 10 616 seals were recorded as by-catches in coastal fisheries, mainly in North Norway, but also further to the south along the coast to Møre og Romsdal county. Harp seals dominated, but individuals of other seal species (e.g., grey seals *Halichoerus grypus* (FABRICIUS) and ringed seals *Phoca hispida* (SCHREBER)) were also observed. During the winter of 1995, harp seals were observed as far south as the southern parts of the North Sea (Peter J.H. van Bree, Institute of Taxonomic Zoology, University of Amsterdam, pers. commn).

Recaptures of tagged seals

In the period 17 December 1994 to 30 March 1995, 39 harp seals tagged in the White Sea were recaptured in gill net fisheries along the Norwegian coast, ranging from the western part of Finnmark county and southwest to Sogn og Fjordane county (Fig. 1). Most recaptures were from coastal areas in Finnmark, Troms and Nordland counties. These seals had all been tagged as pups during the breeding season (February-March), 36 in 1994, 2 in 1993 and 1 in 1992.

During the Norwegian commercial sealing operations in the East Ice in 1995, recaptures of 11 harp seals tagged in 1990-1993 and 3 harp seal pups tagged during the breeding season in 1995 in the White Sea were recorded.

Age and sex composition

Coast of North Norway. Of 87 by-caught harp seals examined at the coast of Troms in 1995, 42 were males and 45 were females. Age data are available from 79 of these seals. All of them were immature animals;

Table 1. Comparison of body condition, expressed as the condition index C (see text for definition) and the dorsal blubber thickness d, of harp seals sampled during the same periods (February and April) in 1995 and in years without extensive seal invasions to the Norwegian coast (1992 and 1993). One year old animals and adult females (standard body length more than 150 cm) were considered.

Period	Year	Body condition (mean \pm SD)	
		C	d
One year old animals			
February	1993	72.4 \pm 9.4	42.3 \pm 6.3
	1995	29.6 \pm 9.8	15.9 \pm 6.0
Adult females			
April	1992	53.1 \pm 9.4	39.7 \pm 8.1
	1995	33.3 \pm 5.5	25.1 \pm 4.6

88.6 % were approximately 11 months old, 7.6 % were two years old and 2.5 % were three years old. The oldest seal was a twelve year old (immature) female. All 27 seals collected in Tana in April 1995 were mature females ranging from 8 to 21 years old.

East Ice. The age-composition of 1189 male and 508 female harp seals taken by Norwegian sealers in the East Ice moulting areas during the period 4 April to 1 May 1995 showed a very low representation of one and two years old animals (Fig. 2). The year classes born during the late 1980s were also very scarce, in particular the 1987 and 1988 year classes.

Body condition

Both the mean body condition index and the mean dorsal blubber thickness of approximately one year old seals sampled in Troms in February 1995, were significantly lower ($n = 124$, $p < 0.0001$) than the corresponding body condition measurements for similarly aged seals sampled in the southeastern Barents Sea in February 1993 (Table 1). Also the mean body condition index and the mean dorsal blubber thickness of mature females with standard body length more than 150 cm collected in April 1995, were significantly lower ($n = 101$, $p < 0.0001$) than the similar parameters observed for mature females collected at the eastern coastal areas of Finnmark and in the southeastern Barents Sea in April 1992.

Diets in coastal waters of North Norway

On the coast of Troms 11 of 83 (13.3 %) of the collected stomachs were empty, while all stomachs collected in Tana had contents. The contents varied from 'fresh' to well digested specimens, where only otoliths, bones or remains from crustaceans were recovered. Twenty-one different prey species were identified in the two areas, and unidentified cephalopod remains, and otoliths from the cottidae and stichaeidae families were also found (Table 2). Remains from birds, algae and the stones (Table 2) recovered in seal stomachs were not included in the numerical or biomass estimates.

In Troms in January-February 1995, gadoids occurred in most stomachs (Table 2). Analyses of the relative numerical frequencies in the seal diet revealed an apparent dominance of various crustaceans, saithe *Pollachius virens* (L.) and other gadoids in this area (Fig. 3). Gadoids, in particular saithe, and to a lesser extent cod *Gadus morhua* (L.), contributed most to the calculated biomass in the stomachs, while the contribution from crustaceans was low (Fig. 3). Eleven fish-tags from cod tagged in Ullsfjord, Troms in 1992-1994 (Torstein Pedersen, Norwegian College of Fisheries Science, University of Tromsø, pers. commn) were found in three harp seal stomachs collected in this area.

Table 2. Frequencies of empty stomachs and identified species of prey in stomachs of harp seals captured in two coastal areas of North Norway in 1995. Other remains include feathers, algae and stones; feathers from little auk *Alle alle* were found in two stomachs from Troms and in one from Tana. Algae remains were found in nine stomachs collected in Troms and in two from Tana. One stomach from Troms also contained a number of stones (see NORDØY 1995). N = number of stomachs examined.

Prey item	Percentage occurrence	
	Troms N = 83	Tana N = 27
Empty	13.3	0
Crustacea		
Mollusca		
Unident. cephalopod remains	4.8	
Euphausiacea		
<i>Thysanoessa</i> sp.	1.2	3.7
Decapoda		
<i>Pandalus borealis</i> (KRØYER)	1.2	48.1
<i>Pandalus</i> sp.	10.8	3.7
<i>Crangon</i> sp.	1.2	
<i>Sabinea septemcarinatus</i> (SABINE)		3.7
Unident. brachiopod remains	14.5	3.7
Unident. crustacea remains	2.4	
Pisces		
Clupeidae		
<i>Clupea harengus</i> (L.)	18.1	40.7
Argentinidae		
<i>Argentina silus</i> (ASCANIUS)	2.4	
Osmeridae		
<i>Mallotus villosus</i> (MÜLLER)	3.6	55.6
Gadidae		
<i>Gadus morhua</i> (L.)	22.9	74.1
<i>Melanogrammus aeglefinus</i> (L.)	31.3	74.1
<i>Pollachius virens</i> (L.)	56.6	22.2
<i>Trisopterus esmarkii</i> (NILSSON)	8.4	22.2
<i>Micromesistius poutassou</i> (RISSE)	1.2	3.7
<i>Rhinonemus cimbrius</i> (L.)		7.4
<i>Gadiculus argenteus thori</i> (J. SCHMIDT)		7.4
Unident. gadoid remains	53.0	70.4
Scorpenidae		
<i>Sebastes</i> sp.	1.2	48.2
Zoarcidae		
<i>Lycodes</i> sp.		18.5
Ammodytidae		
<i>Ammodytes</i> sp.	2.4	44.4
Cottidae		
Unident. cottid remains	2.4	
Stichaeidae		
Unident. stichaeid remains		25.9
Pleuronectidae		
<i>Hippoglossoides platessoides</i> (FABRICIUS)		29.6
<i>Glyptocephalus cynglossus</i> (L.)		7.4
<i>Microstomus kitt</i> (WALBAUM)		25.9
Unident. pleuronectid remains	3.6	48.2
Unident. fish remains	31.3	85.2
Other remains	13.3	7.4

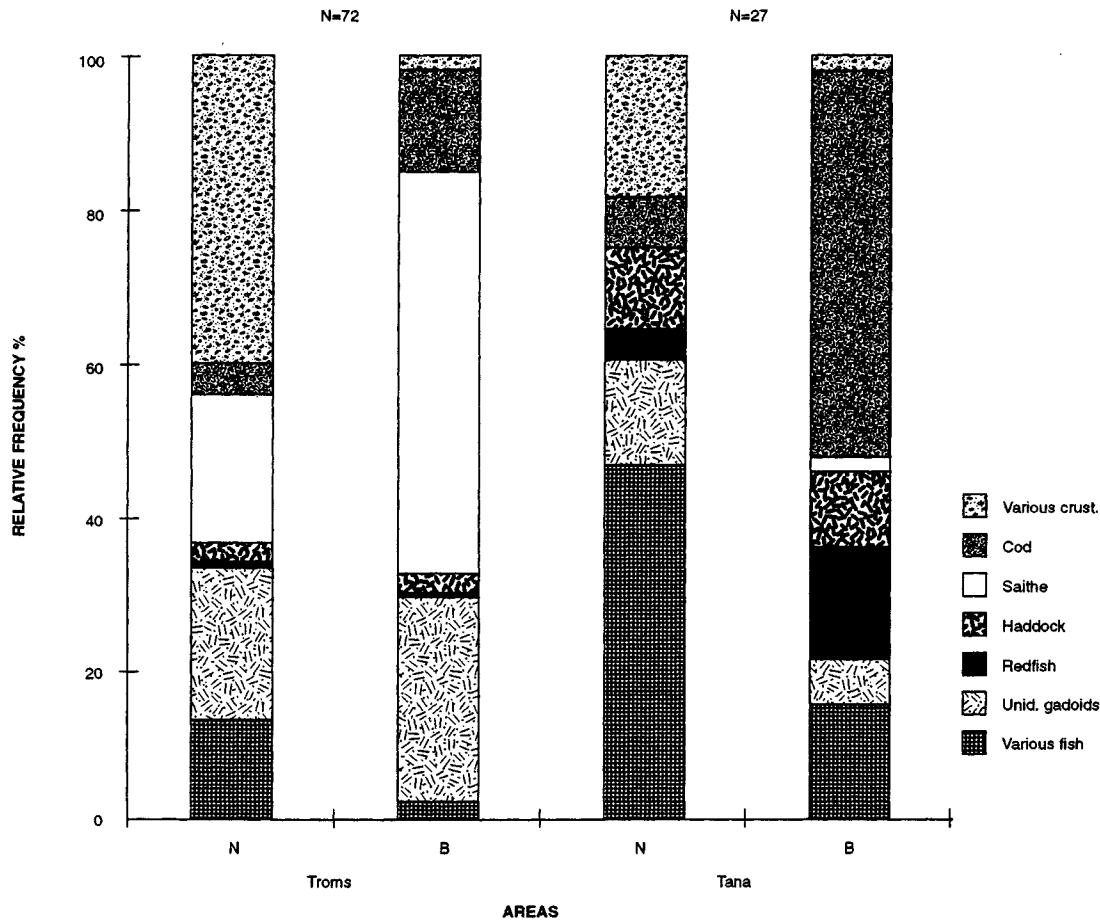


Fig. 3. Relative occurrence in terms of numerical frequency (N) and calculated biomass (B) of prey species in stomach contents of harp seals collected in coastal areas of Troms county in January-February and in Tana, Finnmark county in early April 1995.

Gadoids were most frequent in the seal stomachs also in Tana in April 1995, but herring, capelin, redfish *Sebastes* sp., sandeels *Ammodytes* sp. and shrimp *Pandalus borealis* (KRÖYER) occurred in more than 40 % of the collected stomachs (Table 2). Cod, haddock *Melanogrammus aeglefinus* (L.), redfish, other fish species such as Norway pout *Trisopterus esmarkii* (NILSSON), blue whiting *Micromesistius poutassou* (Risso), herring, capelin, Atlantic argentine *Argentina silus* (ASCANIUS) sandeels and pleuronectidae characterized the numerical estimates which also comprised crustaceans (Fig. 3). In terms of calculated fresh weight the contribution of crustaceans were, however, small in this area. Cod dominated in the stomach contents biomass, but also haddock and redfish contributed considerably (Fig. 3). The contribution of capelin to the biomass in Tana was approximately 6 %.

DISCUSSION

Harp seals occurred in coastal areas of Norway during the winter in 1994/1995 in two apparently separate invasions: Immature seals (mainly from the 1994-cohort) were distributed along the coast of North Norway and also further south along the Norwegian coast in the period from early December 1994 and through mid-winter 1995. In the second half of March and until mid-April 1995, mature females invaded the eastern coast of Finnmark county. This latter early spring invasion appeared to be similar to previous observations in eastern Finnmark in the 1990s, when adult females were seen to perform annual feeding migrations in March-April, i.e. the period between lactation and moult (HAUG & al. 1994; NILSEN & al. 1995a). The invasion of immature seals earlier in the winter is, however, a new migration pattern, not seen in the area after 1988. This invasion of

immature seals is comparable to the extensive seal invasions in 1986-1988, although the 1986-1988 invasions spanned a longer period (January-August), included larger numbers and comprised a mixture of immature and adult seals (HAUG & al. 1991). The presence of both young and adult invading seals was confirmed also before 1986 (BJØRGE & al. 1981; WIIG 1988).

The number of by-caught seals in different areas and periods will depend on the effort in coastal gill net fisheries. An adequate index of the fishing effort is lacking. However, according to data provided from Norges Råfisklag, the numbers of gill net vessels that took part in the winter cod-fisheries in North Norwegian coastal waters were relatively constant during the period 1992-1995, ranging between 3166-3360 vessels. More than 10 000 seals caught in gill nets in northern Norway in 1995 is, however, a substantial increase in the magnitude of the harp seal invasions compared to the period 1989-1994 when only mature females were taken as by-catches during early spring in the eastern parts of Finnmark county.

Recaptures during the early winter invasion of harp seals tagged (mainly in 1994) in the White Sea indicate that some of the invading seals belonged to the East Ice stock. The number of 39 recaptures from the 1992-1994 cohorts along the Norwegian coast, compared with only 11 recaptures from the 1990-1993 year-classes during the commercial seal hunt of in total 6582 seals (1+) in the East Ice (ØRITSLAND 1996), suggests that considerable numbers of immature seals from the Barents Sea stock were abundant in Norwegian coastal waters during the winter of 1995. Certainly, the invasion may also have included seals from the West Ice stock where, except from fourteen pups in 1994, no harp seal pups have been tagged since 1991 (ØIEN & ØRITSLAND 1995; ØRITSLAND 1995). Results from earlier tagging experiments (ØIEN & ØRITSLAND 1995) suggest a certain mixing of immature animals between these two stocks.

The very low representation of year-classes born in the late 1980s, in particular the 1987 and 1988 year-classes, in the age-composition data from the East Ice moulting patches in 1995 (Fig. 2) supports previously reported recruitment failure to the Barents Sea harp seal stock in this period (KJELLQWIST & al. 1995; ØRITSLAND 1995, 1996). The abundance of the youngest age-groups in the commercial sealing were high in the periods 1978-1985 and 1992-1993 (see KJELLQWIST & al. 1995). The recruitment to the stock seemed again to be lower in 1994 (see ØRITSLAND 1995). The low representation of the 1993 year-class and, more pronounced, the 1994 year-class in this study suggests a possible poor survival also of these two cohorts and a decreased recruitment to the stock in these two years. The invasion of young animals to the Norwegian coast during early winter in 1994/1995 may

have contributed to this. Certainly, the age- and sex-composition of harp seals observed in commercial catches in the moulting patches will depend on when the catch is carried out. Adult males followed by immatures of both sexes are the first to haul out on the ice to moult, while adult females gradually join these groups later in the season (NAZARENKO & TIMOSHENKO 1974; SERGEANT 1991). Preference for particular age- and sex-groups of seals by the sealers (e.g., adult males which are more valuable) may also complicate the sampling of representative age- and sex-composition data. In 1995, the catch was carried out during the periods 4-13 April and 27 April to 1 May, which is assumed to give a representative picture of the age-composition. All age-groups are normally present in the moulting areas during these periods, but the more valuable adult males may have biased the sex-composition.

Changes in harp seal migrations that have resulted in invasions of seals to coastal areas of northern Norway have been recorded on several previous occasions, e.g. at the beginning of this century in the periods 1901-1903 and 1916-1919, and the reason for the invasions is by no means fully understood (see HAUG & NILSSEN 1995). In 1987 and 1988 the invading harp seals, particularly the subadults, were said to be thin and in very poor condition (WIIG 1988; ØRITSLAND 1990). Also adult harp seals inhabiting the White Sea during winter and spring in 1987 and 1988 were unusually thin (TIMOSHENKO 1995). Adult seals taken in gill nets in North Norway in February 1988 were in poor condition, and significantly thinner than animals taken in the East Ice in February 1993 (NILSSEN & al., 1997). Food shortage, possibly resulting from the 1985/1986 collapse of the capelin stock, may have forced large numbers of harp seals to leave their traditional wintering areas in the southeastern Barents Sea in favour of the coast of North Norway in 1986-1988 (HAUG & NILSSEN 1995). The observation that both the one-year old seals and the mature females taken in the coastal areas of North Norway in 1995 were in significantly poorer condition than comparable age-groups in similar periods in 1992 and 1993 (Table 1), suggests that the seals may have faced a food shortage also during winter in 1995.

In 1989 the spawning of the Barents Sea capelin was successful, and there was some recovery of the stock, but there was a further decline in stock size between 1992 and 1993 (ANON. 1994). However, substantial increases in the abundance of immature Norwegian spring spawning herring in the southeastern Barents Sea may have resulted in the establishment of a suitable alternative winter food resource for the harp seals, thereby contributing to reduce the magnitude of the seal invasions in the period 1989-1994. Immature herring was observed to be the dominant prey species for harp seals in the south-

eastern Barents Sea during early winter in 1993 (NILSSEN & al. 1994). The abundance of immature herring in this area in the period 1992-1994 comprised strong year-classes in 1991 and 1992 and weak 1993 and 1994 cohorts. The strong year-classes started to migrate out of the Barents Sea in 1994, which led to a decrease in the abundance of immature herring in the southern Barents Sea in 1994/1995 (ANON. 1996a, b) and a more westerly distribution of the 0-group and immatures in autumn 1994 compared to 1993 (ANON. 1994, 1996a). This may have forced harp seals to migrate westwards to feed in coastal waters of Norway during early winter in 1995.

Capelin was observed to be the most important harp seal prey during the seal invasions to the eastern parts of Finnmark county in the early 1980s (BJØRGE & al. 1981; WIIG 1988) and in 1991 and 1992 (NILSSEN & al. 1995a). Capelin is also known to be important harp seal prey during late autumn in central parts of the Barents Sea (NILSSEN & al. 1995b). The collapse of the Barents Sea capelin stock the mid-1980s and again in 1992/1993 has contributed to a reduced abundance of capelin in Norwegian coastal waters with subsequent reduction in importance of this species as a prey for the invading harp seals. This is supported by the dominance of gadoids on the diet of the seals sampled at the coast of Troms and Finnmark counties in 1995, a situation similar to the seal diet observed during the large invasions in 1986-1988 (see HAUG & al. 1991; NILSSEN & al. 1992). The results

from the stomach contents analyses may have been biased to some extent due to erosion of otoliths in the digestive system (MURIE & LAVIGNE 1985). However, the diets comprised mainly gadoids, which are known to be more resistant to gastric acid compared with otoliths from e.g. herring and capelin (JOBLING & BREIBY 1986).

Harp seals are known to feed also on polar cod *Boreogadus saida* (LEPECHIN) during late autumn and winter (CHAPSKII 1961; NILSSEN & al. 1995b). The stock size of polar cod in the Barents Sea has increased after 1991 and was estimated at nearly one million tons in 1992 and 1993 (GJØSÆTER 1995; ANON. 1996a). This may have contributed to restrict the harp seal invasions to northern Norway in early winter 1995 to include only immature animals.

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