FOOD AND FEEDING OF GREENLAND HALIBUT (*REINHARDTIUS HIPPOGLOSSOIDES*, WALBAUM) IN THE BARENTS SEA AND EAST GREENLAND WATERS

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MICHALSEN, KATHRINE & KJELL H. NEDREAAS 1998 11 30. Food and feeding of Greenland halibut (*Reinhardtius hippoglossoides*, Walbaum) in the Barents Sea and East Greenland waters. – *Sarsia* 83:401-407. Bergen. ISSN 0036-4827.

This report describes the diet of Greenland halibut (*Reinhardtius hippoglossoides*, Walbaum) on the continental slope in the western Barents Sea (1992-1994) and on the shelf outside East Greenland (1991). The proportion of empty stomachs was high: for many predator length groups more than 80 %. There was a decreasing percentage of empty stomachs with increasing predator length. Cephalopods, and especially *Gonatus fabricii*, was the most important prey category for Greenland halibut at East Greenland in 1991 as well as in the Barents Sea in 1992 and 1994. In the Barents Sea in 1993, however, indeterminable fish remains and herring were the most important prey categories. Herring and blue whiting were the most important species of fish prey in the Barents Sea. It was impossible to identify the fish remains at East Greenland. The potential of stomach data in further ecological investigations and management of Greenland halibut is discussed.

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KEYWORDS: Greenland halibut; food; feeding; Barents Sea; East Greenland.

INTRODUCTION

Greenland halibut is an arctic-boreal fish, distributed in both the North Atlantic and in the North Pacific (ALTON & al. 1988; GODØ & HAUG 1989; BOWERING & BRODIE 1995; HJØRLEIFSSON 1997).

In the Northeast Arctic the main spawning areas of the Greenland halibut are thought to be located at depths between 400 and 800 m along the continental slope between Bear Island and Norway (HOGNESTAD 1969; NIZOVTSEV 1969; GODØ & HAUG 1989). Spawning may, however, occur north to Southwest of Spitsbergen (approx. 76°30'N). Females with running roe have been taken west of Træna Bank (approx. 66°N) indicating that spawning also takes place further south (BREIBY & ELIASSEN 1984).

For a long time the Northeast Arctic Greenland halibut stock was only moderately exploited by longlines. In 1965 a commercial trawl fishery started and the total catches reached a peak of about 90 000 tonnes in 1970 (ANON. 1997). The catches then declined and for a long period (1978-1990) approximately 20 000 tonnes were caught annually. As a consequence of lower cod quotas, the Greenland halibut catches again peaked in 1991 at more than 32 000 tonnes. Due to reduced stock size and recruitment failure strong regulations were introduced the year after, in 1992.

Even though the commercial importance of Greenland halibut has increased in recent years, the role of this species in the marine ecosystem is not well documented. However, a review of the biology, distribution, fisheries and management of this species in the eastern Norwegian and Barents Seas (i.e., the Northeast Arctic stock) is given by GODØ & HAUG (1989).

Previous studies of the food and feeding of Greenland halibut off Greenland (SMIDT 1969; DEGROOT 1970; PEDERSEN & RIGET 1993), outside Canada (CHUMAKOV & PODRAZHANSKAYA 1986; BOWERING & LILLY 1992; ORR & BOWERING 1997; RODRIGUEZ-MARIN & al. 1997; DAVE & al. 1998), and in the Bering Sea (ALTON & al. 1988; YANG & LIVINGSTON 1988) have shown that this species feeds predominantly on plankton and cephalopods when it is small and shifts towards less cephalopods and more fish as it gets larger. In the Northeast Atlantic, it has been reported that both adult and juvenile Greenland halibut have a varied fish diet (NIZOVTSEV 1969; HAUG & GULLIKSEN 1982). The present investigation expands upon these earlier studies by analysing stomach data from the main fishing areas. These data were collected over a four-year period and represent a larger size range of Greenland halibut than the previous studies.

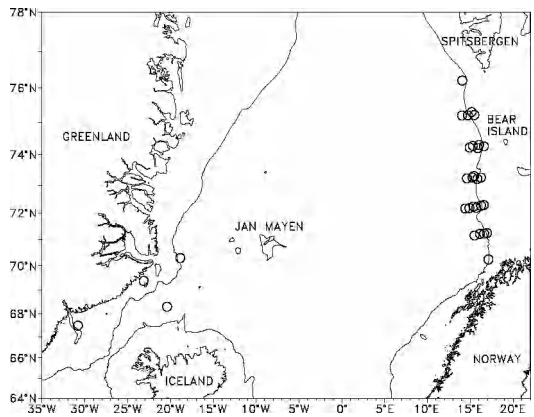

Fig. 1. Map of study area including 500 m depth contour. Sampling stations are indicated by open circles.

MATERIAL AND METHODS

Study area and sampling stations

In 1991 on the shelf outside East Greenland, 153 stomachs were collected from 7 stations located at depths between 488 and 1200 meters (Fig. 1, Table 1). Hence the number of samples is rather limited. The sampling was conducted onboard the longliner M/V *Stålodd* during 31 Aug.-10 Sept. Both mackerel (1/3) and squid (2/3) were used as bait.

From 1992 to 1994 stomachs were collected from the main fishing area along the continental slope in the western part of the Barents Sea at depths between 560 and 810 meters (Fig. 1). Sampling was conducted by F/T *Kongsfjord* and F/T *Varegg* using a commercial cod trawl (Alfredo no. 5 with 135 mm mesh size in the codend). Each trawl haul lasted for about 3 hours. A total of 454, 1100 and 2650 stomachs were collected in 1992, 1993 and 1994, respectively (Table 1). Sampling in 1992-1993 was conducted in autumn (mid-October), whereas, the stomachs in 1994 were sampled in spring (last half of May).

Data collection and stomach examination

Fish from the whole catch or from a representative sub-sample were length measured to the nearest centimetre below. At East Greenland in 1991 and in the Barents Sea in 1992 length-stratified stomach sampling (5 fish per 5 cm length group) was conducted at each station. During the sampling in 1993 and 1994, samples of 50 or 100 fish per station were sampled. Stomachs were frozen and brought to the laboratory on land for further analyses.

In the laboratory the stomach contents were identified to the lowest possible taxon. Bones, otoliths or other hard parts were also used for this purpose. Each food category was counted, and when possible, the length of the prey was measured. Excess liquid was removed by filter paper before each prey category was weighted. In order to study diurnal feeding rhythms the degree of digestion of the prey items was evaluated using a qualitative scale. However, no back calculations of prey biomass were performed.

Empty stomachs, both with and without heavily contracted musculature were noticed. Those without were often filled with sea water. If these stomachs in reality were regurgitated during the fishing operation there may have been an overestimation of empty stomachs.

Predator size distribution

The total length distribution of the Greenland halibut from the Barents Sea caught by trawl for stomach analyses was consistent from year to year, ranging from 30-89 cm with a peak at 45-50 cm fish (Fig. 2). The longline samples at East Greenland, however, were taken from a greater depth range. No clear trend in fish length by depth was observed.

RESULTS

Stomach fullness

The proportion of empty stomachs within the 10 cm fish length groups varied from 45 % to 8 2% in the East Greenland area and from 25 % to 77 % in the Barents Sea in 1992 (Table 2). The proportions of empty stomachs from the Greenland halibut caught in the Barents Sea were higher in 1993 and 1994 were higher, in most cases above 80 %. There seems to be a decrease in the percentage of empty stomachs with increasing length, although a small number of stomachs from fish above 80 cm (13 specimens) showed a high percentage of emptiness.

Table 1. Stations where stomachs of Greenland halibut were collected during surveys in 1991 (East Greenland) and in 1992, 1993 and 1994 (Barents Sea).

Fishing gear	Date	Sampling area	Stations (N)	Stomachs (N)	Total catch (N)	Bottom depth (m)
Long line (East Greenland)	31.08-10.09 1991	67°30'N-70°30'N 18°30'W-31°00'W	7	153	1 765	488-1200
Bottom Trawl (Barents Sea)	07.10-20.10 1992	72°00'N-76°00'N 14°00'E-16°30'E	13	454	41 641	560-715
	16.10-23.10 1993	71°30'N-76°00'N 13°30'E-16°30'E	20	1100	28 780	554-680
	17.05-01.06 1994	70°30'N-76°00'N 14°00'E-17°30'E	27	2650	137 070	680-815

Diet composition

East Greenland. The stomach contents of the Greenland halibut caught at East Greenland comprised 12 different prey categories (Table 3). When the stomach contents were aggregated into more general prey categories and presented as weight percentages (Table 4), the diet of Greenland halibut at East Greenland fell into two main prey groups: cephalopods and indeterminable fish remains (Teleostei indet.). It was impossible to identify these fish remains. None of the prey categories occurred in a great number of stomachs (Table 5). Cephalopods and indeterminable fish were the most frequently occurring prey and were observed in about 13 % and 10 % of the stomachs, respectively.

Norwegian and Barents Seas. In the 1992 autumn investigation of the Barents Sea, blue whiting and the squid *Gonatus fabricii* were the prey items resulting in highest mean weight per predator. In addition, indeterminable fish, herring and Greenland halibut were of major importance (Table 3). A total of 31 different taxonomic categories were found in the stomachs.

In the autumn of 1993, the stomach contents of the Greenland halibut were composed of some of the same prey categories, but with indeterminable fish and herring as the dominant components in weight, while *Gonatus fabricii* and blue whiting were consumed in a lesser extent than the year before. A total of 18 different taxonomic categories were observed.

Also in 1994 *Gonatus fabricii* was the most important prey item. The weight contribution of Greenland halibut as prey (i.e. cannibalism) was slightly higher compared with the two previous years while the amount of herring and blue whiting were much lower. Shrimps were the third most important prey. A total of 23 different taxonomic categories were found.

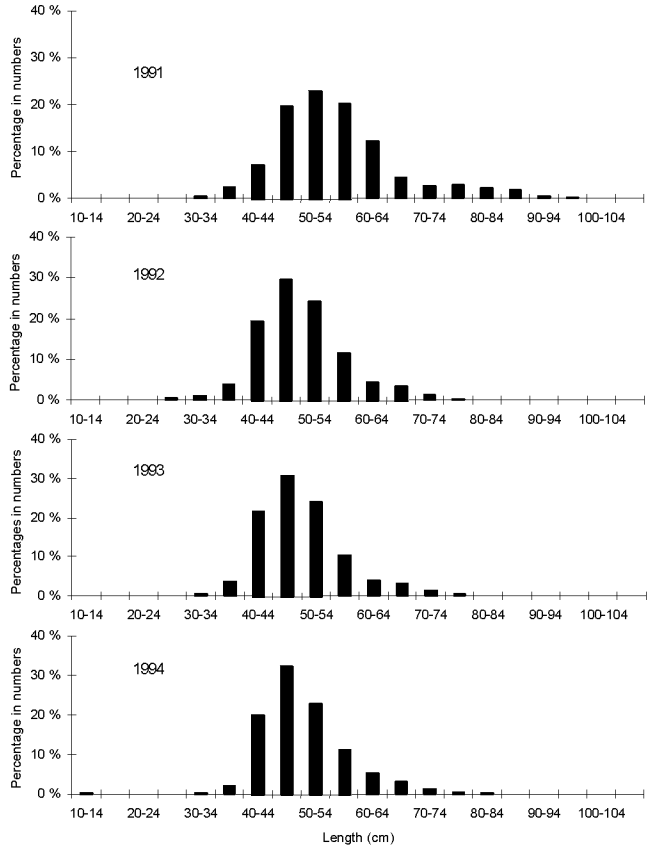

Fig. 2. Length distribution of Greenland halibut caught by longline (1991) off East Greenland and trawl (1992-1994) in the Barents Sea. Percentage in numbers per 5 cm length group is given.

Table 2. Length distribution and stomach fullness of Greenland halibut in the East Greenland area (1991) and in the Barents Sea 1992, 1993 and 1994.

	East Greenland		Barents Sea					
	1991		1992		1993		1994	
Length group (cm)	Total number (n=153)	Empty stomachs (%)	Total number (n=454)	Empty stomachs (%)	Total number (n=1100)	Empty stomachs (%)	Total number (n=2650)	Empty stomachs (%)
30-39	8	75.00	57	77.19	68	89.71	49	95.92
40-49	49	65.31	122	56.56	488	89.75	1241	90.73
50-59	48	75.00	124	62.10	350	84.24	1018	88.73
60-69	17	82.35	108	63.89	141	73.76	277	85.92
70-79	20	45.00	39	46.15	46	67.39	59	88.14
80-89	11	63.64	4	25.00	7	100.0	5	100.0
> 90	-	-	-	-	-	-	1	100.0

When the stomach contents were pooled into more general prey categories and presented as weight percentages (Table 4), the diet of Greenland halibut caught in the Barents Sea in 1992-1993, fell into the same five main prey groups in both years. In 1994 heads of Greenland halibut as offal from the fisheries were also registered. In the same year herring and blue whiting were replaced by shrimps and cod-remains (possibly offal) in importance. This may be a result of changing the timing of the 1994 sampling season, to spring, compared to the autumn sampling in 1992-1993.

In the Barents Sea material all of the prey categories (non-aggregated) were found in less than 10 % of the stomachs (Table 5).

Table 3. Prey items from stomachs of Greenland halibut caught in the Barents Sea and in the East Greenland area. '$\overline{w}$' shows the mean weight (in grams) of the prey item per predator with stomach content '-' indicates absence of this prey and '+' indicates prey weight less than 0.01g.

	East Greenland	Barents Sea		
	1991	1992	1993	1994
Species	$\overline{w}$	$\overline{w}$	$\overline{w}$	$\overline{w}$
Polychaeta, indet.	-	+	-	-
Mya arenaria	-	+	-	-
Cephalopoda, indet.	1.41	0.78	0.59	0.86
Gonatidae, indet.	0.84	0.44	0.40	0.14
Gonatus fabricii	1.45	6.49	3.32	6.16
Octpodida, indet.	0.89	-	-	0.33
Octopus vulgaris	-	0.67	-	-
Crustacea, indet.	-	0.02	-	0.02
Amphipoda	-	-	0.01	+
Gammaridea, indet.	-	0.04	0.02	-
Anonyx nugax	-	0.02	-	+
Tmetomyx , sp.	-	+	+	0.04
Hyperiidea, indet.	-	+	-	-
Paratemisto, sp.	0.03	+	+	-
Parathemisto libellula	0.18	-	+	-
Lycaeidae, sp.	-	-	+	-
Euphausiidae, indet.	-	0.02	0.02	-
Meganyctiphanes norvegica	-	0.01	-	-
Sergestres arcticus	-	0.23	-	-
Caridea, indet.	0.27	0.19	0.12	0.94
Pasiphaeidae, indet.	-	0.80	0.41	1.36
Pasiphaea tarda	-	0.06	-	0.08
Pasiphaea multidentata	-	0.02	-	-
Pandalus borealis	-	0.11	0.08	0.06
Crangonidae, indet.	-	0.01	-	-
Pontophilus norvegicus	0.06	-	-	-
Asteriodea, indet.	+	-	-	-
Ophiura texturata	0.21	-	-	-
Teleostei, indet.	3.09	4.02	6.71	1.28
Clupea harengus	-	4.80	6.43	0.80
Gadidae, indet.	0.11	0.08	-	0.20
Gadus morhua	-	-	-	1.55
Micromesistius poutassou	-	7.06	3.99	0.02
Onogadus argentatus	-	0.22	-	-
Zoarcidae, indet.	-	0.51	-	1.16
Sebastes, sp.	-	1.05	0.66	0.22
Sebastes mentella	-	0.28	-	-
Cottunculus microps	-	-	-	0.48
Ammodytes marinus	-	-	-	0.11
Reinhardtius hippoglossoides	-	3.76	1.90	2.49
Indeterminate	-	0.01	-	0.07

DISCUSSION

Predator size distribution

Fairly constant bottom depths for the trawl samples each year in this study (560-810 meters) showed small variations in length distribution within as well as between the three years of study. Others have shown that large Greenland halibut generally are distributed at greater depths than the small ones (Smidt 1969; Templeman 1973; Bowering & Chumakov 1989; Gil & al. 1997a).

Stomach fullness

The observed decreasing percentage of empty stomachs with increasing length is in accordance with the finding by e.g., Rodriguez-Marin & al. (1997) outside Canada. However, a small number of stomachs from fish longer than 80 cm in 1993 and 1994 in the present material showed a high percentage of emptiness.

Diet composition

There is little information on food and feeding of adult Greenland halibut from the Norwegian and Barents Seas. Nizovtsev (1969) reports that the diet during spawning in the Barents Sea was mainly comprised of cephalopods and fish such as blue whiting (*Micromesistius poutassou*) and herring (*Clupea harengus*). Along the coast of Spitsbergen the polar cod (*Boreogadus saida*) was the most important food item for the juvenile Greenland halibut analysed by Haug & Gulliksen (1982).

Cephalopods were the most important prey category for Greenland halibut both at East Greenland in 1991 and in the Barents Sea in 1992 and 1994. In the Barents Sea in 1993, however, indeterminable fish remains and herring were more important. Regarding only the fish prey, herring and blue whiting were the most important species in the Barents Sea. The present results from the Barents Sea is in accordance with the diet observed by Nizovtsev (1969), mentioned above. The importance of *Gonatus fabricii* as food for Greenland halibut has recently also been documented from the deep slope

areas outside Newfoundland (Dave & al. 1998). In addition *Gonatus* sp. is one of the preferable preys for the northern bottlenose whale (*Hyperoodon ampullatus*, Clark & Kristensen 1980). Fishermen have, due to these species' common preference for *Gonatus* as prey, therefore used aggregations of the whales to localise fishable aggregations of Greenland halibut (pers. commn).

Since Greenland halibut was found as prey in the stomachs of fish analysed from the Barents Sea, it can be concluded that cannibalism occurs. This is consistent with investigations from the Labrador coast and West Greenland waters (Bowering & Lilly 1992; Pedersen & Riget 1992) as well as outside Newfoundland (Rodriguez-Marin & al. 1997). Nevertheless, the magnitude of cannibalism could be difficult to quantify because the predator might be attracted to the offal of Greenland halibut from the fishing vessel, especially when this offal is well digested.

General comments and some remarks for future investigations

From the stomach analyses we can conclude that Greenland halibut is a highly predatory fish which leaves the bottom to feed on pelagic prey in the water column (very few strictly bottom living organisms were found in the stomachs). The near absence of capelin in the Barents Sea in 1992-1997 may have led Greenland halibut to prey on less preferable prey since capelin has been reported to be an important prey in other areas (e.g. Bowering & Lilly 1992). The presence of herring in the diet is also believed to vary according to the migrations of herring into the Greenland halibut areas. In September 1995-1997, herring were frequently found in Greenland halibut stomachs during scientific experimental gillnet fisheries in the same areas.

Since Greenland halibut is probably dependent on visual stimuli to be able to catch prey items there is reason to believe that food consumption may be diurnal which, in turn, will lead to a diurnal vertical migration. Clear diurnal feeding trends have seldom been reported. This may be due to long trawling time and large variations in day length. Some studies have shown that Greenland halibut feed continuously during day and night (Yang & Livingston 1988). By comparing day and night catches, Chumakov (1969) concluded that Greenland halibut make daily vertical migrations. However, he did not correlate this behaviour with diurnal feeding. Investigations of possible diurnal variations in trawl catch rates in the Spanish fishery outside Newfoundland did not reveal any day-night differences (Gil & al. 1997b). By examining the proportion of empty stomachs Junquera (1993) concluded that diurnal feeding activity does take place. For cod it has been documented that it takes at least a week to digest and empty the stomach (dos Santos 1990) and it is therefore doubtful whether the diurnal cycles observed in the percentage empty stomachs can reflect a diurnal feeding activity. The sampling design of the present study, with long trawl duration and few samples within a day, did not provide enough information to study any diurnal cycle.

All diet studies of Greenland halibut show high proportions of empty stomachs. Whether this should be taken as a confirmation of low feeding rates or as an artefact caused by the sampling is unknown. The possibility of overestimating empty stomachs due to regurgitating when trawling and hauling in the trawl or longline should be investigated more closely. The long duration of a trawl haul may cause stress which may increase the proportion of empty stomachs. There could also be a higher probability for hungry fish with empty stomachs to be caught by longlines.

The literature show that the feeding of Greenland halibut depends on many different factors. Chumakov & Podrazhanskaya (1986) report that the mean daily food requirements expressed as percent of body weight are the same for males and females of the same age-group but decline gradually with predator age. Both quantitatively and qualitatively, the diet changes with the geographical distribution, depth, time of year and length of

Table 4. Weight-percent (W %) of prey groups from stomachs of Greenland halibut caught in the Barents Sea and in the East Greenland areas. '-' indicates absence of these prey group.

	East Greenland	Barents Sea		
Prey categories	1991	1992	1993	1994
Cephalopoda	53.81	27.06	17.45	39.38
Amphipods	2.44	0.22	0.17	0.27
Krill	-	0.08	0.08	-
Shrimps	3.77	2.29	2.47	12.92
Brittle stars	2.49	-	-	-
Fish indet.	37.47	18.26	27.21	6.73
Clupea harengus	-	15.48	26.07	4.35
Gadidae	-	-	-	1.06
Gadus morhua	-	-	-	8.16
Micromesistius poutassou	-	22.77	16.17	0.10
Ciliata septentrionalis	-	0.70	-	-
Zoarcidae	-	-	-	6.11
Sebastes sp.	-	0.89	2.66	1.16
Cottunculus microps	-	-	-	2.50
Ammodytes marinus	-	-	-	0.54
Reinhardtius hippoglossoides	-	12.13	7.72	13.09
Offal (heads of *R. hippoglossoides*)	-	-	-	3.14
Other	-	0.11	-	0.48

the Greenland halibut itself (Haug & Gulliksen 1982; Chumakov & Podrazhanskaya 1986; Yang & Livingston 1988; Bowering & Lilly 1992; Junquera 1993).

Better knowledge about the vertical distribution of the Greenland halibut in the water column and seasonal variation in the diet composition are necessary for describing the annual food consumption and the ecological role of this species. The present study could not quantify predator size differences in the diet. For such an analysis, an increased number of stomachs within each length group would be necessary, especially when the diet is composed of a wide range of taxonomic groups in addition to a high proportion of empty stomachs.

Table 5. Frequency of occurrence (%) of prey groups from stomachs of Greenland halibut caught in the Barents Sea and in the East Greenland areas.'-' indicates absence of these prey group.

	East Greenland	Barents Sea		
Species	1991	1992	1993	1994
Polychaeta, indet.	-	0.20	-	-
Mya arenaria	-	0.20	-	-
Cephalopoda, indet.	13.10	9.90	2.46	1.70
Gonatidae, indet.	1.30	0.20	0.72	0.04
Gonatus fabricii	1.30	7.50	1.82	1.54
Octpodida, indet.	2.00	-	-	0.15
Octopus vulgaris	-	0.20	-	-
Crustacea, indet.	-	7.50	-	0.12
Amphipoda	-	-	0.18	0.04
Gammaridea, indet.	-	0.90	0.37	-
Anonyx nugax	-	0.90	-	0.04
Tmetomyx , sp.	-	0.70	0.08	0.07
Hyperiidea, indet.	-	0.20	-	-
Paratemisto, sp.	0.70	0.20	0.18	-
Parathemisto libellula	6.50	-	0.08	-
Lycaeidae, sp.	-	-	0.08	-
Euphausiidae, indet.	-	0.90	0.37	-
Meganyctiphanes norvegica	-	0.40	-	-
Sergestres arcticus	-	2.60	-	-
Caridea, indet.	4.60	4.40	0.72	2.64
Pasiphaeidae, indet.	-	0.40	1.00	2.15
Pasiphaea tarda	-	0.40	-	0.15
Pasiphaea multidentata	-	0.20	-	-
Pandalus borealis	-	0.70	0.18	0.15
Crangonidae, indet.	-	0.20	-	-
Pontophilus norvegicus	0.70	-	-	-
Asteriodea, indet.	+	-	-	-
Ophiura texturata	0.70	-	-	-
Teleostei, indet.	10.50	8.20	5.55	1.39
Clupea harengus	-	2.00	2.73	0.34
Gadidae, indet.	0.11	0.70	-	0.04
Gadus morhua	-	-	-	0.12
Micromesistius poutassou	-	3.80	0.90	0.04
Onogadus argentatus	-	0.20	-	-
Zoarcidae, indet.	-	0.20	-	0.27
Sebastes, sp.	-	1.10	0.45	0.04
Sebastes mentella	-	0.70	-	-
Cottunculus microps	-	-	-	0.04
Ammodytes marinus	-	-	-	0.07
Reinhardtius hippoglossoides	-	0.90	0.45	0.34
Indeterminate	-	0.20	-	0.04

ACKNOWLEDGEMENTS

We are grateful for help and co-operation received from technical personnel and crew on board M/V *Stålodd*, F/T *Kongsfjord* and F/T *Varegg*. We also wish to thank Lisbet Solbakken for help with the figures, Ole Thomas Albert for critical comments to the manuscript and C. Tara Marshall for correcting the English.

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Accepted 19 May 1998
Editorial responsibility: Ulf Båmstedt