Abstract-A total of 7244 Greenland halibut (Reinhardtius hippoglossoides, Walbaum) were tagged in Greenland waters between 1986 and 1998 to increase information on stock delineations, to clarify migration routes, and to describe the seasonal movements of fiord populations. At present 517 recaptured Greenland halibut have been recorded. For Greenland halibut released in Davis Strait, Baffin Bay, and the fjords of southwestern and eastern Greenland, a substantial portion of recovered fish demonstrated migratory behavior, up to 2500 km, primarily to Denmark Strait between Greenland and Iceland. The recaptured fish provided evidence of intermingling between the population in Denmark Strait and the populations in Davis Strait and the southwest Greenland fjords. These observations support those of other studies that indicate that Greenland halibut inhabiting Davis Strait and the fjords of southwestern and eastern Greenland originate in the spawning grounds west of Iceland. The high mobility of offshore Greenland halibut within Baffin Bay and Davis Strait suggests that Greenland halibut migrate extensively between feeding and spawning areas. Greenland halibut in the fjords of northwestern Greenland appear to be resident in behavior and do not intermingle with offshore or more southerly inshore populations. A seasonal pattern in the recovery of these fish indicates that Greenland halibut aggregate in the inner part of fjords during the second half of the year (when inshore waters are not covered with ice).

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Intermingling and seasonal migrations of Greenland halibut (*Reinhardtius hippoglossoides*) populations determined from tagging studies

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Greenland halibut, Reinhardtius hippoglossoides (Walbaum), are widely distributed in the Northwest Atlantic. Their range covers a geographical area from Smith Sound, between Greenland and Canada, southward throughout Baffin Bay and Davis Strait to the northeastern coast of the United States and eastward along eastern Greenland to Iceland (Smidt, 1969; Bowering and Brodie, 1995). The spawning grounds of Greenland halibut are believed to be located southwest of Iceland (Sigurdsson¹) and cover an extended area from Davis Strait, south of 67°N (Jensen, 1935; Smidt, 1969) to south of Flemish Pass off Newfoundland (Junguera and Zamarro, 1994) between 800 and 2000 m depths. The Greenland halibut populations off the eastern coast of Canada, in Davis Strait, in the fjords of western Greenland, in the Denmark Strait, and in Icelandic waters are believed to be recruited from these spawning grounds (Templeman, 1973; Sigurdsson¹). Anumber of scientists have examined interactions among different local populations of Greenland halibut in the Northwest Atlantic. They have considered and, in some cases, attempted to quantify meristic characteristics (Templeman, 1970; Misra and Bowering, 1984; Riget et al., 1992; Rasmussen et al., 1999), genetic variability (Fairbairn, 1981; Riget et al., 1992; Vis et al., 1997), the occurrence of parasites as natural tags (Khan et al., 1982; Boje et al., 1997), and tagging data (Smidt, 1969; Bowering, 1984; Riget and Boje, 1989; Boje²). The results of these investigations suggest that the entire Greenland halibut population between

Greenland and Canada must be considered a single stock unit. There is some evidence that the populations between Greenland and Iceland originate from a spawning stock situated along the continental slopes west of Iceland. A number of Greenland halibut populations seem to maintain a degree of isolation without any prespawning migration to their original spawning areas; this is characteristic of the Greenland halibut population in the Gulf of St. Lawrence (Khan et al., 1982) as well as for populations in the fjords of northwestern Greenland (Riget and Boje, 1989). Spawning has been observed in the Gulf of St. Lawrence (Bowering, 1980), but only a few ripe females have been sighted in the fjords of western Greenland (Riget and Boje, 1989).

Previous tagging experiments in the fjords of western Greenland (Smidt, 1969; Riget and Boje, 1989; Boje²) suggest that Greenland halibut stocks in the southernmost fjords may be recruited from Icelandic spawning grounds. The Irminger Current and the East Greenland Polar Current carry eggs and larvae from these spawning

¹ Sigurdsson, A. 1979. The Greenland halibut (*Reinhardtius hippoglossoides* (Walbaum)) at Iceland. Hafrannsóknir, 16, Marine Research Institute, Reykjavik, Iceland.

² Boje, J. 1993. Migrations of Greenland halibut in the Northwest Atlantic from tagging experiments in West Greenland 1986– 89. ICES (International Council for the Exploration of the Sea) C. M. Doc. 1993/ G:65, 14 p. ICES, Palægade 2-4, DK-1261 Copenhagen K, Denmark.

grounds to eastern Greenland and probably as far as southwestern Greenland (Sigurdsson¹; Boje³). In 1959, Smidt (1969) observed the recapture west of Iceland of Greenland halibut that had been tagged in Licthenau Fjord in southwestern Greenland in 1954. Riget and Boje (1989) noted the recapture west of Iceland in 1980 of Greenland halibut that had been tagged in Godthaab Fjord in 1964.

In the present study, tagging experiments in the fjords of eastern and western Greenland from 1986 to 1998 are evaluated to determine the stock discreteness of Greenland halibut populations in the Northwest Atlantic and to describe seasonal migrations of Greenland halibut within inshore areas.

Materials and methods

Greenland halibut from four areas around Greenland were tagged between 1986 and 1998. The tagging was carried out in the fjords of eastern Greenland at Ammassalik in September 1990, in the fjords of southwestern Greenland from Cape Farewell to Godthaab Fjord in January 1987–88, in the fjords of northwestern Greenland from Disko Bay to Upernavik during July–August 1986–98, and off western Greenland from Davis Strait to Baffin Bay during May–August 1991–93 (Table 1, Fig. 1). Samples were collected with longlines (Mustad Autoline Systems) from research vessels fishing at depths between 400 and 900 m—a range that is standard for the

commercial fishery (Boje⁴). Fishing time for each set was approximately six hours.

A landing net was placed under each fish from the time it left the water until the fish was landed onboard the ship to avoid damage from the hook (i.e. the gravitational drag of the hook while the specimen was removed from the water). The hook was removed with care and only fish hooked in the mouth region were selected for tagging because these injuries were generally not fatal. Condition of the fish was judged visually, mainly by examining the color of the gills and by assessing internal hooking injuries. Length of the fish was measured to the nearest full centimeter (total length) and fish larger than 35 cm were selected to increase the possibility of immediate recapture in the fishery. Each fish was tagged in the musculature with



Map of release sites (shaded areas). NAFO (Northwest Atlantic Fisheries Organization) (0–2) and ICES (International Council for the Exploration of the Sea) (V–XIV) divisions are indicated.

a yellow T-bar tag (Floy T-bar anchor tags, FD-68B yellow) just below the dorsal fin ray near the head. Immediately after having been tagged, the fish was released.

For an evaluation of migratory routes, the numbers of recaptured fish were adjusted for fishing activities (annual landings) in recapture area (i.e. NAFO/ICES division) for the year of recapture and these numbers were expressed as the number of halibut per 100 metric tons of annual landings in the recapture division. Landing statistics were obtained from Greenland Statistical Office, NAFO Statistical Bulletin 1986–93, NAFO STATLANT 21A data and ICES Cooperative Research Reports of the ACFM 1986–98.

To analyze seasonal movements among "resident" Greenland halibut (i.e. fish caught less than 100 km from the release site) of northwestern Greenland, the fjords were stratified into five rectangles of equal area, and positioned in an east-west direction. A random-walk model (Skellam, 1951) was applied to the distribution of all releases (n=4319) pooled for the entire period, 1986–98, for all five areas, assuming equal probability that the fish would migrate either east or west or remain in the area (P=0.33). The model operated on a time unit of three months, thereby allowing each fish to move from only one rectangle to the next rectangle within a quarter of a year.

³ Boje, J. 1997. Larval growth and spawning of Greenland halibut in West Greenland waters and the possible influences by hydrographic conditions. ICES (International Council for the Exploration of the Sea) international symposium on "Recruitment dynamics of exploited marine populations: physical-biological interactions," Baltimore 22–24 Sept. 1997. ICES, Palægade 2-4, DK-1261 Copenhagen K, Denmark.

⁴ Boje, J. 1989. The fishery for Greenland halibut in Subarea 1. NAFO (Northwest Atlantic Fisheries Organization) SCR Doc. 89/27, ser. N1603, 8 p.

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	East Greenland fjords	1990	September	Ammassalik	XIVb	40-74	183		9	ۍ ا		6					23	12.6
	Southwest Greenland	1988	January	Cape Farewell	1F	35 - 91	120	4	1	5	1			-			6	7.5
	fjords	1987	January	Godthaab Fjord	1D	34 - 110	839	$14 \ 2$	0	6	1		П	1			46	5.5
	Northwest Greenland	1986	August	Ilulissat	1A	33–95	43		1	1		1					က	7.0
	fjords	1987	August	Ilulissat	1A	30 - 90	154	1	0	4	5	2		1			15	9.7
		1993	August	Ilulissat	1A	26 - 96	34										0	
		1994	August	Ilulissat	1A	34 - 68	71	4	7	1							7	9.9
		1986	August	$\operatorname{Torsukkattak}$	1A	31 - 85	272	1	9	5		ະ ຕ	2		1		18	6.6
		1987	August	Torsukkattak	1A	38 - 100	384	8	1	8	0	2				က	52	13.5
		1993	August	$\operatorname{Torsukkattak}$	1A	48 - 82	88	7 1	0	7							24	27.3
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		1996	August	Torsukkattak	1A	49 - 76	31	1	1								2	6.1
		1997	July	Torsukkattak	1A	44 - 93	264	3 1	5								18	6.8
		1987	August	Uummannaq	1A	36-98	244	0	7	3 S	8	 ന		1			27	11.1
		1993	August	Uummannaq	1A	39-87	136	3 1	5	9	1	2					24	17.6
		1994	August	Uummannaq	1A	42 - 84	49	1	2	Ч	1						5	10.2
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		1989	August	Upernavik	1A	35 - 107	634	2	<u>1</u>	5	4	6	00	2			77	12.1
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Totals $26-110$ 7244 88 212 101 51 34 18 3 6 1 3 517		1993	August	Baffin Bay	1A	43 - 92	716		1			-	2				4	0.6
	Totals					26 - 110	7244	88 21	2 10	-	51 3	4 13	00	9 6	1	က	517	7.1

The model run covered a total of eight years, which was the maximum time recorded for time at liberty of tagged Greenland halibut at sea. The random walk distribution was compared with the true recapture distribution by means of a chi-square test. The true recapture distribution was corrected for fishing effort by using the frequency of recaptured halibut per unit landing in a statistical square (smallest statistical unit to assign landings), where landings were monthly averages for the period 1993–97. By pooling landings monthly for this 5-year period there were no zero values in the data set. Effort data were not available for the inshore fishery; therefore landings data were used instead. Previously landings data for these inshore areas were found to correlate well with fishing effort (Anonymous, 1998).

Migration distances are given in kilometers (1 km=0.540 nautical mile). For all analyses, SAS statistical (SAS, 1988) and Statistica (StatSoft, Inc., 2000) software were used.

Results

A total of 7244 Greenland halibut were tagged from 1986 to 1998. By the end of 1998, 517 recaptured Greenland halibut (7.1% of halibut released during the entire period) were recovered (Table 1). The majority of recaptured fish were reported within two years after tagging, but some were reported as late as eight years after tagging. In general, Greenland halibut tagged in the fjords of northwestern Greenland (Ilulissat, Torsukkattak, Uummannaq, and Upernavik) tended to remain resident, whereas some Greenland halibut from the three other tagging sites (East Greenland fjords, Southwest Greenland fjords, and West Greenland offshore) displayed migratory behavior.

Prevailing migratory patterns

An overview of the numbers of recaptured Greenland halibut (adjusted for fishing activity for each release site versus recapture area) is presented in Table 2. Most recaptured Greenland halibut were found at their release locality (especially at Ammassalik in East Greenland, in the fjords of Cape Farewell, in Godthaab Fjord, Uummannaq, and Upernavik in West Greenland), and 99% of the recaptured halibut were taken within the release area. For releases in the two neighboring fjords in northwestern Greenland, Ilulissat, and Torsukkattak, 10-14% of recaptured Greenland halibut showed intermingling between the two fjords. Limited intermingling was also noted between Ilulissat and Uummannag (<1-3%). Of the 21 recaptured Greenland halibut from Davis Strait and Baffin Bay, 96% and 77%, respectively, were caught in the release area (values adjusted for fishing effort). Of 23 recaptured Greenland halibut in Ammassalik in East Greenland, the vast majority (99%) were recaptured near the tagging site; whereas single specimens (less than 1%) were recaptured in Denmark Strait and north of the



Figure 2

Migration pattern for long-distance migrants only. Numbers indicate percentage of recaptured fish from different tagging sites in Greenland that were caught at fishing grounds shown by the arrows (northwestern Greenland Fjord Torsukkattak, off Newfoundland, west of Iceland, and north of the Faroe Islands).

Faroe Islands. Greenland halibut recovered from releases in the fjords of southwestern Greenland (Cape Farewell and Godthaab Fjord,) were mostly recaptured at the release site (99%), whereas the remaining were captured in Denmark Strait, except for a single specimen captured off Newfoundland. The majority of released halibut from the most comprehensive tagging effort in the fjords of northwestern Greenland were recaptured at their tagging site (approximately 90%). This observed fidelity to tagging site was most pronounced in the northern areas of the fjord systems at Uummannaq and Upernavik. No released fish from the fjords of northwestern Greenland were recaptured outside the area. Of the halibut released in the offshore areas of western Greenland, i.e. Davis Strait and Baffin Bay, most were recovered at their release sites, but a few specimens were also recovered as far as Denmark Strait and Newfoundland. Although only four Greenland halibut were recaptured from Baffin Bay, two of them were captured in the fjord of northwestern Greenland (Torsukkattak). Adjusted for fishing effort, they accounted for 17% of recaptured Greenland halibut from Baffin Bay.

Long-distance migrants

Twenty-three specimens were recovered at substantial distances from their release sites (Fig. 2). Greenland halibut tagged in Godthaab Fjord and recaptured in Denmark Strait (6 specimens) migrated an average of approximately

						Recap	ture area					
elease location	Faroe Islands	Denmark Strait	Ammassalik	Cape Farewell	Godthaab Fjord	Newfoundland	Davis Strait	 Ilulissat 7	forsukkattak	Upernavik	Uummannaq	Total recaptured halibut (not adjusted
mmassalik	2	2	23000									60
ape Farewell	(1)	1	(66)	569								67
odthaab Fjord				(88)	1459	1						46
avis Strait		с С С			(66)	(1))	34					17
affin Bay) – ((2)	(96) 17		4			4
ılissat		(c)						98	16 16		က်	26
orsukkattak								(83) 67	(14) 614 (00)		(9) (3)	113
ummannaq								() (T)	(06)		313	153
pernavik								(1>)	3 (<1)	523 (99)	(99) 4 (<1)	108
otal recaptures (not adjusted)	1	17	16	7	39	ç	14	42	100	105	155	499^{1}

1100 km: whereas fish released in Godthaab Fjord and Davis Strait and recaptured off Newfoundland (1 and 2, respectively) migrated an average of 1800 km. A single fish recaptured north of the Faroe Islands was released at Ammassalik in eastern Greenland. All recaptured Greenland halibut in Denmark Strait had been released at inshore areas of eastern and southern Greenland or from offshore areas of western Greenland. From the latter area, one fish tagged in Baffin Bay had thus migrated about 2500 km. Recaptured Greenland halibut off Newfoundland were tagged in Davis Strait and Godthaab Fjord. Two fish released from Baffin Bay were recaptured in the northern fjord of Disko Bay (Torsukkattak).

A cumulative distribution of estimated migration distance for each main release site (Fig. 3) revealed that Greenland halibut from the offshore area of western Greenland were the more frequent longdistance migrants, and only about 50% were resident. About 70% of recaptured Greenland halibut from East Greenland fjords migrated 400 km or less. Approximately 80% of Greenland halibut from the fjords of southwestern Greenland were resident, whereas the remaining 20% undertook migrations of 1000-1200 km. Nearly all Greenland halibut in the northwestern fjords were resident and migrated less than 100 km.

Inshore seasonal migration

Recapture data from the fjords of northwestern Greenland were examined to determine whether recapture location varied seasonally, i.e. whether seasonal migrations occurred. The inshore fishery is carried out in all seasons mainly with longlines. Catches tend to peak during the warmer period in July-August, when water is free from ice in the inner part of the fjords, but substantial numbers are also caught from January to June, when waters are covered by ice, in a fishery distributed throughout



the fjord (Simonsen and Boje⁵). The catch-adjusted recapture data were categorized by stratifying the fjords into five rectangles of equal area, ranging from the mouth of the fjord to the inner part of the fjord. A chi-square test on the real recapture distribution compared with a randomwalk distribution based on pooled release data, proved significant (P < 0.0001), indicating that Greenland halibut do not migrate randomly in the fjord system, but tend to aggregate at specific localities at certain times of the year. Pooling the data by ice-cover period (1st and 2nd quarters) and open-water period (3rd and 4th quarters) and weighing the distribution within each quarter equally also resulted in significantly different distributions between the real data and the random-walk data. The real pooled data, shown by quarters (Fig. 4), demonstrated that Greenland halibut display a dispersed distribution during the icecover period (1st and 2nd quarters) but concentrate in the inner parts of the fjords during the open-water period (3rd and 4th quarters). The steep gradient from the 4th to the 1st quarter may be due to the fishing practices of the commercial fisheries, which are virtually dormant between November and February. Thus fish recaptured from the fishery for the two quarters mainly represent only the months of October and March, respectively.

Discussion

Sampling by hook-and-line gear does not reflect the true abundance of Greenland halibut in prespawning and spawning conditions. But, because the majority of the tagging took place outside the spawning period (winter and early spring), the sampling gear should not have biased any recovery patterns. Tagging in the southwest Greenland fjords took place in January, but the recovery pattern for those areas was confirmed by tagging data from other seasons of the year (Riget and Boje, 1989). Therefore, I assumed that any tagged specimens represent feeding fish, not spawning groups of the population.

Although Greenland halibut demonstrated long-distance displacements of about 2500 km in a two-year period, most recoveries indicated rather limited movement. The majority of tagged and recaptured Greenland halibut in this study support the current understanding of stock relationships among Greenland halibut populations (Bowering and Brodie, 1995; Boje et al., 1997; Vis et al., 1997). However, several cases of single recoveries suggest links between halibut populations not considered before. One fish recorded off Newfoundland had been released in Godthaab Fjord two years earlier, yet currently it is believed that Greenland halibut from Godthaab Fjord and other fjords of southwestern Greenland originate from the Icelandic spawning stock (Smidt, 1969; Riget et al., 1989; Boje, 1993). Released Greenland halibut from Baffin Bay yielded single recoveries in the northwestern Greenland fjord of Torsukkattak and in Denmark Strait. The latter is a migration distance of about 2500 km. Also, one Greenland halibut released in eastern Greenland at

⁵ Simonsen, C. S., and J. Boje. 2000. An assessment of the Greenland halibut stock component in NAFO Division 1A inshore. NAFO (Northwest Atlantic Fisheries Organziaton) SCR Doc. 00/47, ser. N4278, 37 p. NAFO Secretariat, 2 Morris Drive, P. O. Box 638, P. O. Box 638, Dartmouth, Nova Scotia, Canada B2Y 3Y9.



Ammassalik was recaptured north of the Faroe Islands four years after release, which indicates a link between the Greenland halibut populations in the Northwest Atlantic and those in the Northeast Atlantic and suggests some intermingling of halibut populations in the Atlantic Ocean. Studies on genetic differentiation have shown that Greenland halibut in the North Atlantic are genetically homogenous, indicating that populations do intermingle (Riget et al., 1992; Vis et al., 1997). Tagging experiments in Icelandic waters (Sigurdsson, 1981) included recoveries at long distances east of the release sites (Norway), even to the Barents Sea, also suggesting that there are interactions between the Northwest Atlantic and the Northeast Atlantic populations of Greenland halibut.

The 17 Greenland halibut recovered in Denmark Strait from tagging sites in West Greenland indicated a mix between West and East Greenland stocks, confirming previous work, especially tagging studies by Smidt (1969) and Boje² who documented recaptured Greenland halibut off western Iceland from releases in the Godthaab and Licthenau fjords of southern Greenland. Genetic studies and studies using parasites as natural tags (Riget et al., 1992; Boje et al., 1997) have shown that Greenland halibut in the fjords of southwestern Greenland differ considerably from offshore fish in Davis Strait. Riget and Boje (1988) hypothesized that young Greenland halibut in the southernmost coastal areas of western Greenland originate from different spawning grounds than those in the northern part of western Greenland. Larval distribution studies provide additional information on a link between the populations of southwestern Greenland and those of Denmark Strait. Magnusson's⁶ data and more recently data on Icelandic 0-group Greenland halibut, 1970–97 (Hjörleifsson⁷) have provided evidence of larvae in a continuous belt from the Icelandic spawning grounds westward along the continental slope of eastern Greenland and southward to Cape Farewell. From pelagic Greenland halibut eggs and larvae in the western and southeastern Greenland areas, Smidt (1969) distinguished two groups of larvae with different growth patterns and hypothesized the intermingling of larvae from two different spawning areas, namely the spawning complex in Davis Strait and the stock west of Iceland (Denmark Strait). These authors have suggested that Greenland halibut eggs and larvae are transported by the East Greenland Current from Denmark Strait to the southernmost areas of western Greenland, a route shown earlier for cod (Tåning, 1937; Buch et al., 1994).

The behavior of Greenland halibut tagged in the fjords of northwestern Greenland is guite remarkable. The majority have remained within 50 km of release sites, even up to eight years after release and very few fish have undergone large-scale migrations of 100 to 500 km. Greenland halibut released from the fjords of northwestern Greenland have never been reported outside the fjord areas, but apparent residency may also be the result of almost no fishing activity in Baffin Bay (area adjacent to Uummannag and Upernavik fjord). However, an assumed spawning migration to Davis Strait, is not plausible because a considerable fishery has developed in this area since the late 1980s (Anonymous, 1998). My data are consistent with the general assumption that Greenland halibut in the fjords of northwestern Greenland are recruited from the Davis Strait spawning stock (Smidt, 1969, 1998; Riget et al., 1989) and that adults thereafter remain resident in the fjords, i.e. do not undertake any significant spawning

⁶ Magnusson, J. 1977. Notes on eggs and larvae of Greenland halibut at Iceland. ICES (International Council for the Exploration of the Sea) C.M. 1977/F:47, 6 p. ICES, Palægade 2-4, DK-1261 Copenhagen K, Denmark.

⁷ Hjörleifsson, E. 1999. Personal commun. Marine Research Institute, P.O. Box 1390, Skúlagata 4, IS-l21 Reykjavík, Iceland.

migrations. Some spawning and spent specimens have been observed in the fjords (Smidt, 1969; Riget et al., 1989; Nielsen and Boje⁸) and therefore spawning may occur in the fjords, at least sporadically. However, low bottom temperatures in the fjords probably inhibit the maturation process (Jensen, 1935; Templeman, 1973).

The seasonality apparent in local migrations for fish in the fjords of northwestern Greenland (Fig. 4) is presumed to correlate with feeding behavior. Allthough information is not available on the seasonality of prey organisms for Greenland halibut in the fjords, seasonal patterns for primary production are expected to affect other trophic levels in the food chain. Seasonality is reflected in the practices of the fishery; it tends to be concentrated in the inner part of the fjords during summer and more dispersed during winter near cities and human settlements (Simonsen and Boje⁵).

Davis Strait tagging data demonstrated that Greenland halibut within this area migrate widely and show no distinct patterns in orientation of movement. Such movements could be associated with spawning as suggested by Bowering (1984), i.e. a northward migration of Greenland halibut tagged in Newfoundland and Labrador to a proposed spawning area in Davis Strait. Jørgensen (1997) also found indications of movements during six years of a survey series, which he interpreted as seasonal movements between feeding areas and spawning grounds in the eastern part of Davis Strait. The wide migrations of offshore Greenland halibut as observed in the present study, i.e. within Davis Strait and from Davis Strait and Godthaab Fjord to Newfoundland, lend support to a proposed relationship between adult movements and spawning behavior.

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