Abstract—It is evident from several field experiments with vertical long-lines and archival tags, as well as concurrent studies of predator-prey relationships, that adult specimens of the deep-water flatfish Greenland halibut (*Reinhardtius hippoglossoides*) make regular excursions several hundred meters through the water column. The distribution of longline catches within the water column is confined to a well-defined depth layer overlapping with the distribution of blue whiting (*Micromesistius poutassou*), an important prey species, and depth recordings from archival tags overlap with Atlantic herring (*Clupea harengus*), the other major fish prey. The degree of pelagic use varies with fish size as well as seasons. Smaller individuals are found further off the bottom, and pelagic activity is greatest during early autumn. Interaction with pelagic prey species can influence results from bottom trawl surveys.

Manuscript submitted 19 February 2008.
Manuscript accepted 1 July 2008.
Fish. Bull. 106:457–470 (2008).

Pelagic behavior of adult Greenland halibut (*Reinhardtius hippoglossoides*)

Tone Vollen (contact author)[1,2]

Ole T. Albert (equal authorship)[1]

Email address for T. Vollen: tone.vollen@imr.no

[1] Institute of Marine Research
Sykehusveien 23,
N-9019 Tromsø, Norway
Present address: Institute of Marine Research
Sykehusveien 23, N-9019
Tromsø, Norway

[2] Department of Aquatic Biosciences
Norwegian College of Fishery Science
University of Tromsø
N-9037 Tromsø, Norway

Greenland halibut (*Reinhardtius hippoglossoides* (Walbaum)) is a deep-water flatfish of high commercial value in the northernmost parts of the Atlantic and Pacific oceans. The absence of a swim bladder renders the species virtually invisible to echo sounders; therefore data from scientific and commercial fishing operations conducted close to the seabed with trawls, long-lines, and gill nets are used for stock assessments (Bowering and Nedreaas, 2000). This practice may be surprising, given the general perception of Greenland halibut as a more free-swimming species than other flatfishes (Merrett and Haedrich, 1997). If indeed the use of the pelagic zone by this species is extensive or frequent, results from bottom trawl surveys may be biased and less informative for use in assessments. This problem increases if the pelagic behavior varies over time or is unevenly distributed among sizes, the sexes, and maturity groups.

The perception that Greenland halibut may be a pelagically distributed species has primarily been based on assumptions, anecdotical information, and circumstantial evidence. Morphological characters such as a streamlined body shape, pigmentation of the blind side, and positioning of the left eye on the dorsal ridge of the head led de Groot (1970) to suggest that Greenland halibut behaves more like a roundfish. This has been supported by historical reports of specimens of Greenland halibut being caught in pelagic waters with hand lines and salmon drift nets (Christensen and Lear, 1977; Merret and Haedrich, 1997). More recent documentation of pelagic use is scarce, particularly for adult specimens.

Jørgensen (1997) reported that one-year-old Greenland halibut were commonly found in pelagic trawls in West Greenland waters, and two-year-olds appeared much less frequently. Older individuals were virtually absent from pelagic trawls, even when they were captured in high abundance in bottom trawls. The author concluded, however, that these results may have been influenced by differences in the selectivity patterns of bottom and pelagic trawls.

Although records are scarce, a significant portion of the diet of adult Greenland halibut consists of bathy- and mesopelagic fish, mollusks, and crustaceans such as redfish (*Sebastes* spp.), blue whiting (*Micromesistius poutassou*), cephalopods, shrimps, and euphausiids, as well as epipelagic species such as Atlantic herring (*Clupea harengus*) and capelin (*Mallotus villosus*) (Bowering and Lilly, 1992; Dawe et al., 1998; Michalsen and Nedreaas, 1998; Hovde et al., 2002; Solmundsson, 2007). We therefore used the assumed feeding modus of pelagic

Greenland halibut to study their pelagic distribution. A series of experiments with vertical longlines were designed to catch the species in the pelagic zone, and information on individual depth trajectories were obtained from archival tags for comparisons with the vertical distribution of longline catches. In addition, stomach contents from concurrent bottom trawl hauls provided information on diet of Greenland halibut, length compositions were obtained from demersal longlines and bottom trawl, and acoustic surveys gave insight into the pelagic distribution of some of the prey species. The study aims at describing the use of the pelagic zone by adult Greenland halibut in the Northeast Arctic, both in terms of temporal variability and through parameters such as size, sex, and maturity.

Materials and methods

Data were mainly collected from dedicated surveys with hired commercial longline vessels within a limited area of the continental slope between northern Norway and Bear Island (the central study area, Fig. 1). The longline vessels were used for pelagic fishing with vertical longlines, fishing with demersal longlines, and release of fish tagged with archival tags. Data were also collected from a number of additional surveys in the same or nearby areas and time periods. These additional surveys included bottom-trawl surveys for stomach contents analyses and length-frequency distributions, and trawl acoustic surveys for acoustic profiles. The additional surveys were not originally designed for this study, and data from these investigations were extracted for the extended survey area (Fig. 1).

Vertical longlines

Vertical longline experiments were conducted within the central study area during seven surveys in March, August, and November from 2003 through 2005 (Fig. 1). The main survey, with 73% of all the vertical longline settings, took place in August 2005. During the first six surveys the experiments were only a minor part of the total mission. These six were made partly to gather experience, and partly to establish a time series to be compared with the main survey.

The vertical longline gear consisted of an anchor (25 kg minimum), a rope, a hooked longline, another rope and, finally, a buoy at the surface. A Mustad autoline system was used on all vessels. The hooked longline was 9 mm thick and had hooks of type Mustad EZ 12.0, ganglion length was approximately 50 cm, and the spacing between hooks was 1.5 meters. To record the position and action of the vertical longline, archival tags (DST-milli, Star Oddi, Reykjavik, Iceland) were attached to the top and bottom of the hooked section, as well as over the anchor. Bait was a 1:1 ration of Atlantic mackerel (*Scomber scombrus*) and flying squid (*Todarodes sagittatus*)—the most common bait types used to target catch of Greenland halibut (Bjordal and Løkkeborg, 1996). Bait size was approximately 2.5 cm × 5 cm.

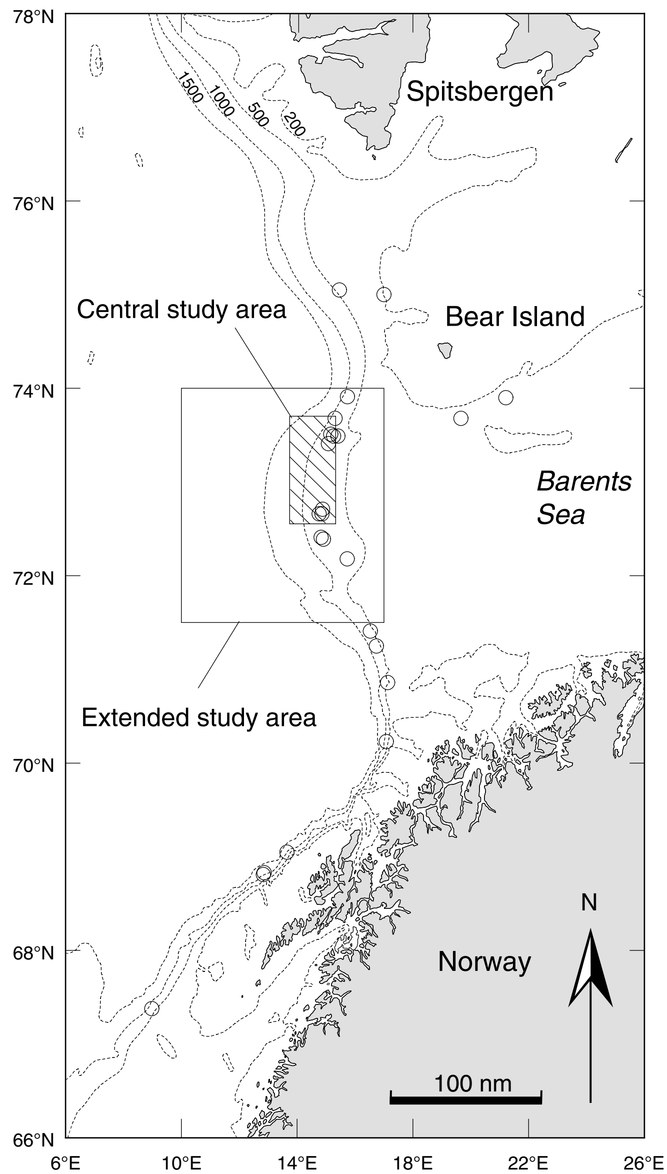

Figure 1

Bathymetric map of both the central and expanded study area situated along the continental slope between Norway and Spitsbergen. Depths are in meters. The longline experiments, as well as release of Greenland halibut (*Reinhardtius hippoglossoides*) tagged with archival tags, were made within the central study area, whereas data from the acoustic surveys and bottom trawl surveys were gathered from the extended study area. Recapture positions of individuals with archival tags are marked with open circles.

The hooked section of the longline covered most of the water column, from 45 m below the surface to 20–150 m over the bottom. Longlines were rigged to ensure that the hooks did not touch the bottom, and the position of the anchor and the highest and lowest hooks were monitored by using archival tags. At bottom depths greater than 1000 m, a drifting vertical longline with no anchor was used. Soak time ranged from 3 to 33 hours. During the main survey in August 2005 mean soak time was 12.6 (±6.1 standard deviation [SD]) hours.

The vertical longlines were rigged to optimize the vertical stability. During the main survey in August 2005 the anchor settled on the seafloor within 10–15 minutes, and the vertical longline settled at the proper depth after about 30 minutes. Once settled, depth of the lowest hook typically had a 2SD of 15–45 m. Stability increased for hooks higher up in the water column (Fig. 2). With the exception of the few deepest hooks, which at some settings may have been close to the seabed for a few minutes, hooks were at a pelagic depth throughout the soak time. During earlier cruises the vertical stability was more variable, with 2SD ranging from 2 to 150 m. The hauling process was completed in approximately 30 minutes in all experimental periods.

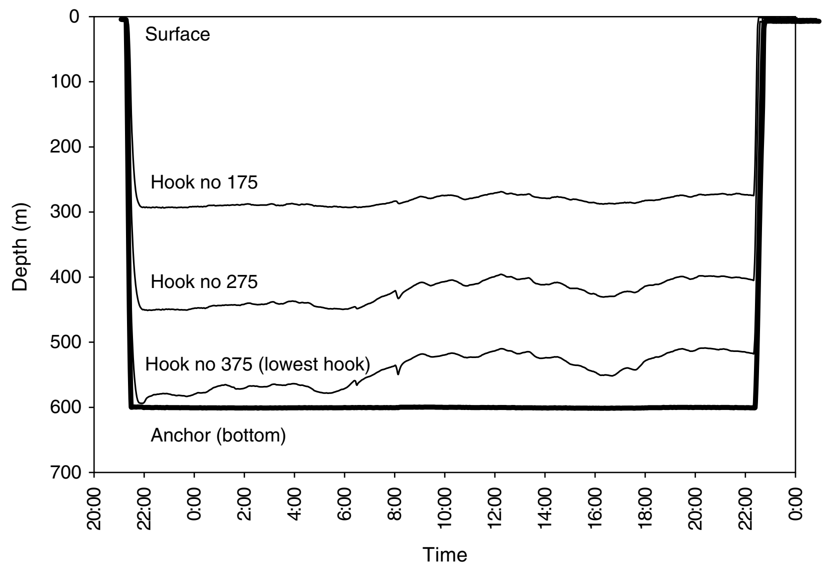

Figure 2

Depth profile of a vertical longline from August 2005. One archival tag was attached to the anchor and another three to the vertical longline at different intervals. Depths were recorded every 3 minutes from time of setting to hauling. Vertical movements of this longline were larger than those for most longlines from August 2005 (2 standard deviations of mean depth for the lowest hook=51 m, versus 15–45 m for most August 2005 longlines).

All fish caught on vertical longlines were classified to species, and the catch depth D_c was calculated as follows:

$$D_c = D_h + (D_l - D_h)H_c/H_{max},$$

where D_h and D_l = the mean depths of the highest and lowest hook as measured by archival tags;
H_c = the hook number of the catch; and
H_{max} = the total number of hooks on the hooked section.

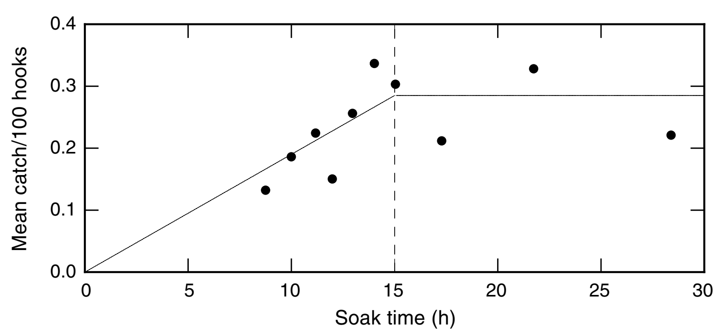

Figure 3

Observed relationship between mean catch (in number) of Greenland halibut (*Reinhardtius hippoglossoides*) and soak time (1-hour groups) for vertical longlines. n=221. The solid line represents the saturation model used. All means were based on groups of nine or more vertical longlines from August 2005.

For all Greenland halibut a standard biological sampling was performed (length, weight, sex, maturity, and stomach fullness). Stomachs with contents were frozen and analyzed in the laboratory. Prey items were counted, weighed, and determined to the lowest possible taxonomic level. The digestion status was noted according to a five-point scale: 1) fresh, 2) digestion just started, 3) moderately digested, 4) highly digested, and 5) digestion almost complete. Longline bait was easily recognized and excluded from the analysis.

According to data from August 2005, the catch rate of vertical longlines increased with soak time until saturation was reached after approximately 15 hours (Fig. 3). Fishing effort, E_{ijk}, generated by a single vertical longline k during setting time T_k within a given combination of fishing depth interval i and bottom depth interval j was thus defined as

$$E_{ijk} = T'_k \times H_{ijk}/100,$$

where $T'_k = T_k$ if $T_k < 15$ hours;
T'_k = 15 hours if $T_k \geq 15$ hours; and
H_{ijk} = the number of hooks.

Table 1

Overview of recaptured (Rec.) archival tags from Greenland halibut (*Reinhardtius hippoglossoides*). Fish total length (TL, cm) measured during tagging. F=female; M=male.

Rec. no.	Interval between recording (min)	Release date	No. of days recording	Fish TL	Fish sex
1	60	30.11.02	687	67	—
2	60	08.12.02	334	64	F
3	60	08.12.02	24	68	—
4	60	08.12.02	188	61	—
5	60	08.12.02	12	54	M
6	60	12.12.02	18	67	F
7	60	13.12.02	16	67	F
8	60	13.12.02	70	74	F
9	10	12.08.03	151	57	—
10	10	14.08.03	149	57	—
11	15	14.08.05	306	76	F
12	15	14.08.05	120	63	F
13	15	15.08.05	54	66	F
14	15	15.08.05	67	77	F
15	15	15.08.05	296	74	F
16	15	15.08.05	10	57	—
17	15	15.08.05	8	73	F
18	15	15.08.05	51	55	F
19	15	16.08.05	54	63	F
20	15	16.08.05	61	75	F
21	15	16.08.05	177	77	—
22	15	16.05.06	261	67	—
23	15	16.05.06	261	47	F
24	15	16.05.06	99	68	F
25	15	17.05.06	196	65	—

Total effort within *ij* was the sum of E_{ijk} for k=(1 to N_{ij}), where N_{ij} is the number of vertical longlines in *ij*.

Demersal longlines

Length-frequency distribution data of Greenland halibut on the bottom (separated by sex) were collected by using demersal longlines. In August 2005 the demersal longlines were 3.5 km long and were deployed in an east-west direction perpendicular to the continental slope. Fishing depth ranged from 450 to 950 m (mean of 655 [±155] m). Soak time ranged from 3 to 22 hours (mean of 10.7 [±5.2] hours). The hooked section on demersal longlines was identical to that of vertical longlines.

Archival tags

On four occasions (November 2002, August 2003, August 2005, and May 2006) a total of 503 Greenland halibut were tagged with archival tags (DST milli or DST Pitch and Roll, Star-Oddi, Reykjavik, Iceland). All individuals were tagged from demersal longlines within the central study area. The longlines were carefully hauled and only individual fish in apparently good shape were tagged and then immediately released. Recaptures were made with bottom trawls, mainly along the continental slope (Fig. 1). The tags were programmed to record time and ambient depth (pressure) every 10, 15, or 60 minutes, and the depth trajectories were recovered after recapture. Up to October 2007, a total of 38 (7.6%) of the released tags were recaptured. Of the recaptured tags, 13 had been destroyed and there was no possibility of data extraction. Of the 25 tags containing data, three tags had stopped recording after being exposed to depths greater than 1000 m, and six tags had stopped recording because the memory was full. For the remaining 16 tags, data were recovered for the whole period from release to recapture. Table 1 shows recording sequence, number of data sampled, as well as sex and length of the tagged individual for all 25 tags used in the analysis. These tagging experiments will form the basis for more detailed future publications; here we restrict ourselves to consider the vertical activity and compare it with the results from the vertical longline experiments.

The tags, by design, conveyed no direct information on bottom depth or the distance from the bottom. However, it was assumed that readings of constant ambient depth can only occur when the fish are on the bottom, whereas data showing frequent changes in vertical position may indicate pelagic swimming behavior. The vertical activity was analyzed in two ways: standardized vertical distance and vertical swimming activity. Standardized vertical distance (*VD*) between succeeding observations of ambient depths (*D*) were standardized to equal time intervals:

$$VD_i = 3600 \times \text{abs}(D_i - D_{i-1})/s,$$

where s = the time step (in seconds) between observation i–1 and i.

For each individual fish and day, the extent of vertical swimming activity (*VA*) was estimated as

$$VA = \Sigma(D_{max,i} - D_{min,i})/12,$$

Where $D_{max,i}$ and $D_{min,i}$ represents the maximum and minimum depths recorded within a two-hour time interval i, and the summation is across the twelve two-hour time intervals within each day.

Thus *VA* is not only dependent on the vertical range traveled during a day, but also on the frequency of vertical excursions throughout the day. Whereas *VD* measures the speed during a depth change, *VA* is a measure of activity through the day.

Additional surveys

Trawl acoustic surveys were conducted in the Barents Sea and Norwegian Sea in August 2003–2005, as part of a regular monitoring program of pelagic fish stocks in these areas. In the present study, data from these investigations were extracted for the extended survey area. The surveys were conducted with a Simrad EK 60 echosounder, frequency 38 kHz (Kongsberg Maritime AS, Horten, Norway). The acoustic recordings were scrutinized each day by using the Bergen Echo Integrator, and allocation of S_A (nautical area scattering coefficient) values on species was made by trained personnel using standard procedures (Korneliussen, 2004).

Bathymetric distributions of selected species of fish in bottom trawls were used for comparisons with the pelagic records. Data were gathered from the annual Norwegian Greenland halibut surveys in August 2003–2005, within the extended study area. In these surveys an Alfredo-5 commercial bottom trawl with rockhopper ground gear (Engås and Godø, 1989) and a measured mean vertical opening of 3.8–4 m was used at towing speeds of 3.5–4.0 knots. Mesh size in the codend was 60 mm.

Stomach-contents data were collected from the same surveys, as well as on similar surveys in November 2003 and March 2004. A standard biological sampling (length, weight, sex, maturity, and stomach fullness) was performed for two individuals in every 5-cm length group. Individuals sampled were chosen randomly, except in August 2005 when only individuals with stomachs containing food were sampled. These stomachs were frozen and analyzed in the laboratory. Methods were the same as those used for stomachs sampled from vertical longline catches.

Results

Pelagic catches of Greenland halibut

Greenland halibut were caught on vertical longlines in most parts of the water column, but despite high effort, the species was rarely recorded in the upper few hundred meters of the water column. Throughout the experimental period a total of 283 individuals were caught, and the species was recorded during all surveys but one. Catch depth ranged from 208 to 934 m (Fig. 4). Seventy percent of all catches were from the main survey in August 2005, when 93% of the individuals were caught between 400 m and 800 m depth. There seemed to be an upper catch limit which was relatively stable across bottom depths. In August 2005 this limit was 300 m at 600–700 m bottom depth, 400 m at 800–1000 m bottom depth, and 500 m at 1200 m bottom depth. The westward distribution boundary could not be identified because of inadequate coverage of large depths.

Greenland halibut was caught at shallower depths in November than in either March or August. For March and August surveys, mean catch depth above 400–700 m bottom depth ranged from 484 m to 554 m. For the two November surveys, the corresponding numbers were 378 m and 363 m, respectively, differing significantly from all individual March and August surveys (*t*-tests, $P<0.001$). The two November surveys were also the only surveys where fish were captured in the region above 300 m catch depth (Fig. 4).

There were no clear or significant changes in length composition with catch depth, but rather with bottom depth and with distance from the bottom (data from August 2005, Fig. 5). This was partly due to males, which are smaller than females, being distributed higher up in the water column (*t*-tests, $P<0.001$) and partly to a significant decrease of female length (linear regression, $P<0.05$). Below 100 m from the bottom, approximately 50% of the catches were males, whereas above 300 m, 75% were males.

The length range of individuals caught on vertical longlines was broad (41–85 cm), but the length and sex composition seemed to have more in common with bottom trawl catches than bottom longline catches (Fig.6). Bottom longlines caught few fish smaller than 50 cm, which were primarily males. Bottom trawls, on the other hand, caught fish as small as 30 cm length, indicating that both sexes were available at the bottom in approximately equal shares.

During individual surveys in March and August, the proportion of females in the pelagic longline catches varied from 8% to 48% (mean of 35%). In November no females were caught—a finding that differed significantly from all March and August surveys (χ^2, df=1,

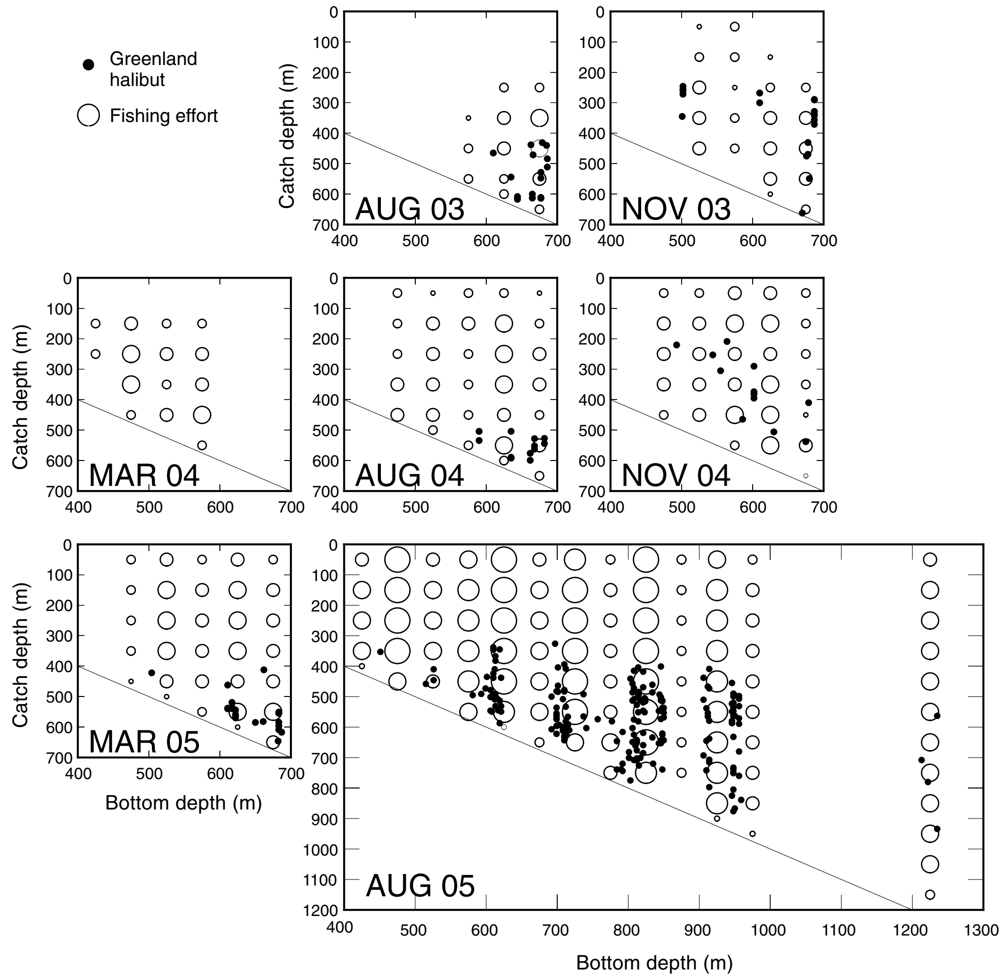

Figure 4

Pelagic catches (noted as individuals) of Greenland halibut (*Reinhardtius hippoglossoides*) on vertical longlines. Individual catches are shown by bottom depth (m) and catch depth (m). Fishing effort is shown for each 100-m catch depth interval and 50-m bottom depth interval. The area of the fishing effort symbol is proportional to fishing effort (hooks × hours/100). The straight diagonal line represents the bottom.

$P<0.01$). In November all Greenland halibut caught were classified as late maturing or ripe, whereas in catches from March and August all but three individuals were immature or early maturing.

Individual depth trajectories

Of the 25 recaptured fish with intact archival tags, the time recorded varied from a few weeks up to two years, yielding a total of 296,000 depth recordings. All tags were both released and recaptured at or close to the continental slope (Fig. 1). For all recordings combined, the 25th, 50th, and 75th percentiles of depth were 454, 522, and 617 m, respectively. Six percent of all recordings were from depths above 300 m, from 11 recaptures. For individual tags this percentage ranged from zero to 20%, with a mean of 2.8%. One individual was regularly recorded above 100 m depth, and seven individuals were recorded below 1000 m. Only one of the 16 individuals, for which sex was determined, was male.

Most of the recaptured tags revealed alternating periods of distinctly different vertical activity by Greenland halibut. Such periods were apparent on both small (hours-days) and large (days-months) scales. Diurnal variation was most apparent at depths above 300 m (Fig. 7). Here the occurrence of large standardized vertical distance (*VD*) between successive records was three times higher at night (21h–03h) than during the midday (09h–15h), and records of vertical inactivity ($VD<0.5$ m per hour) were twice as numerous during daytime (Fig. 7). Above 300 m, the total number of observations was 19% higher at night

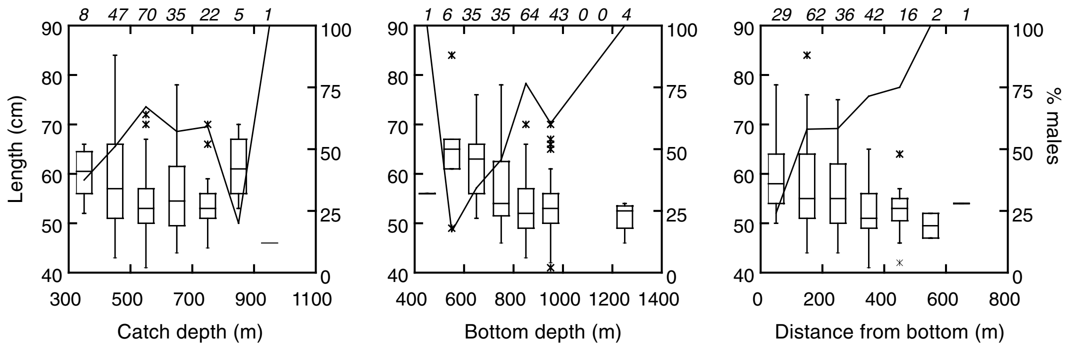

Figure 5

Line plot of sex composition and box plot of length of Greenland halibut (*Reinhardtius hippoglossoides*) caught on vertical longlines, by catch depth, bottom depth, and catch depth in distance from the bottom (all in 100-m intervals). Data are from August 2005. The number of individuals is given above plots. The plots show median, inter quartile range, upper and lower fence, and outliers as defined in SYSTAT 11 (SYSTAT Software Inc., San Jose, CA). Note that % males and % females add up to 100%.

time than during the day, indicating that many of the Greenland halibut in the upper 300 m during night may migrate to deeper waters during the day. The higher number of observations early in the day in the 300–500 m depth zone, and later in the day at depths below 500 m support this (Fig. 7). The vertical activity increased and the diurnal signal weakened with increasing depth. The number of recaptures was not considered high enough to warrant analyses of individual and seasonal differences in the diurnal activity pattern.

The larger-scale time-variability is illustrated in Figure 8, which shows the depth trajectory of five tagged fish, together representing the typical pattern seen in all tags. In most cases periods of high vertical activity began with a sudden descent to much deeper depths than those occupied at any time during the periods of low vertical activity. This pattern is clearly apparent from examples A1, A2, and C1 in Figure 8, where periods of low vertical activity at depth less than 500 m suddenly changed to periods of high-frequency changes in depth between 500 and 800 m. Example A3 shows a trajectory from a tag that stopped recording after a sudden descent to depths greater than 1000 m, which is the depth limit of the tag. This cessation in recording happened to three of the 25 recovered time series.

The degree of high vertical swimming activity (*VA*) varied throughout the year (Fig. 9). The proportion of days with high vertical activity was greatest during August–October and least in January and February.

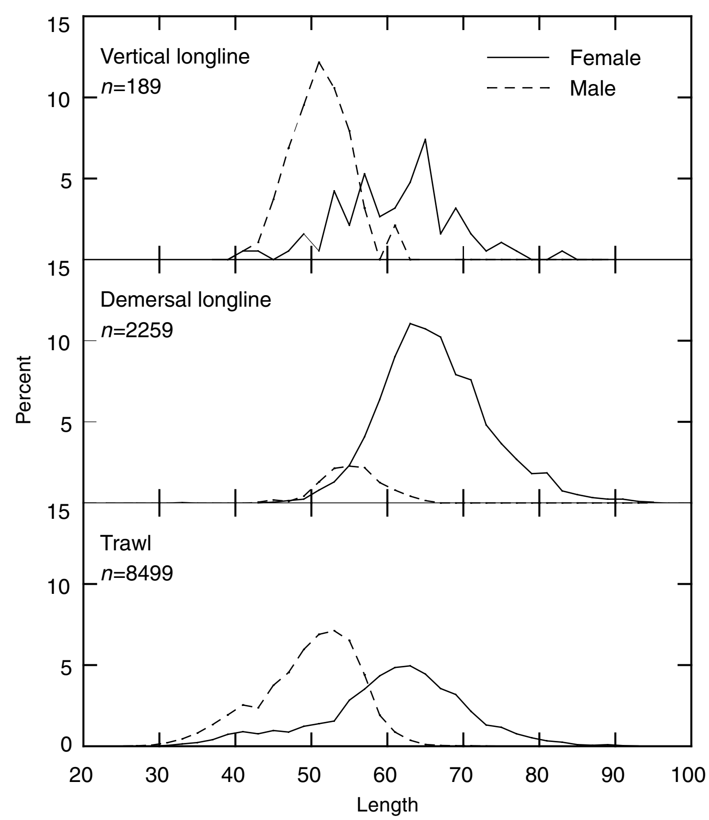

Figure 6

Length-frequency distribution (2-cm length groups) of female and male Greenland halibut (*Reinhardtius hippoglossoides*) caught by vertical longlines, conventional demersal longlines, and demersal trawl. Data are from August 2005. Bottom depths covered were 451–1235 m for vertical longlines, 349–932 m for demersal longlines, and 433–1325 m for trawl.

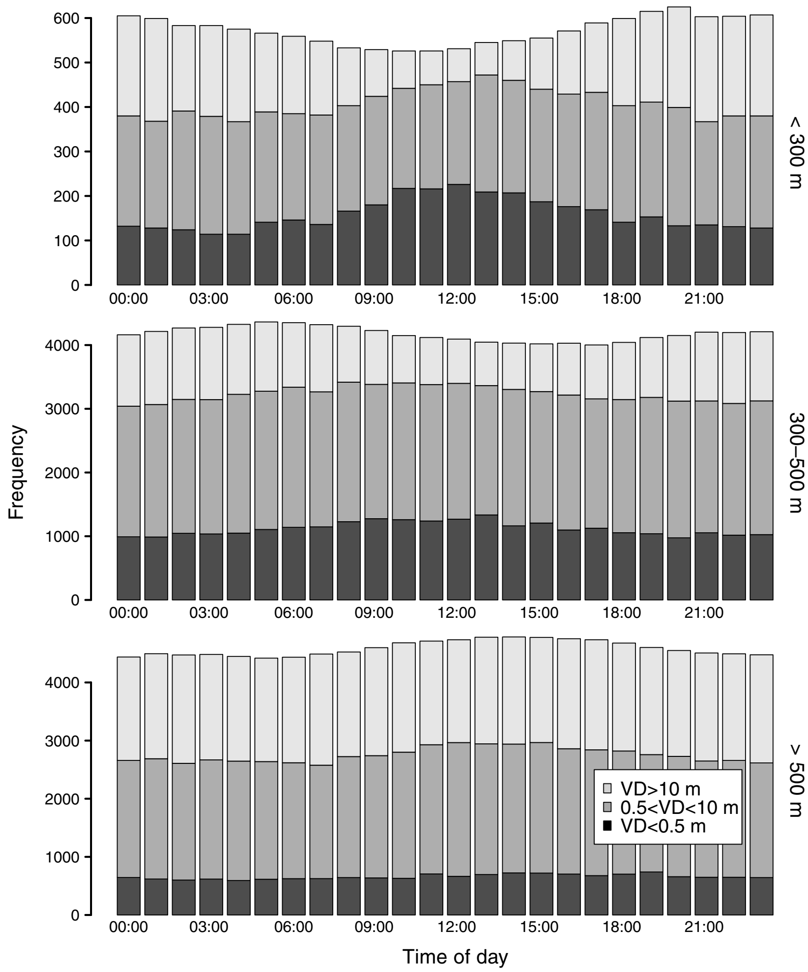

Figure 7

Diurnal variations in standardized vertical distance (*VD,* in meters) traveled by Greenland halibut (*Reinhardtius hippoglossoides*) tagged with archival tags, within each of three depth intervals. The different shaded bars represent frequencies of high (>10 m), medium (0.5–10 m), and low (<0.5 m) *VD,* respectively.

Prey composition

The main prey categories found in Greenland halibut stomachs were crustaceans, cephalopods, and fish. These species all occurred in 35–47% of stomachs with contents (all trawl surveys combined, Table 2). Crustaceans were mainly shrimps (primarily *Pasiphaea* spp. and *Pandalus borealis*) and gammarid amphipods, whereas *Gonatus fabricii* was the predominant cephalopod. Herring and blue whiting were the most common fish prey. One stomach contained a fish tag that one month earlier had been attached to a 19-cm salmon (*Salmo salar*), but whether this tag represents a direct or indirect foraging link between salmon and Greenland halibut, remains unknown (Rikardsen et al., 2008).

Of the three main categories of prey, Crustacea were a relatively stable contributor, whereas frequency of occurrence of cephalopods and fish varied between surveys (χ^2, df=4, P<0.01). This temporal variability was mainly due to three species or species groups. *Gonatus fabricii* was recorded more frequently in August than in March and November, whereas herring was most frequent in August 2003 and March 2004, and blue whiting in August 2003 and 2004.

Figure 10 shows how the diet changed with the size of the predator. In terms of weight, the contribution of cephalopods, shrimps, and most other crustaceans decreased with increasing length of Greenland halibut. On the other hand, the contribution of herring and most other fish increased with increasing predator length. Eelpouts and flatfish were found only in Greenland halibut specimens larger than 65 cm, and redfish were eaten only by individuals larger than 75 cm.

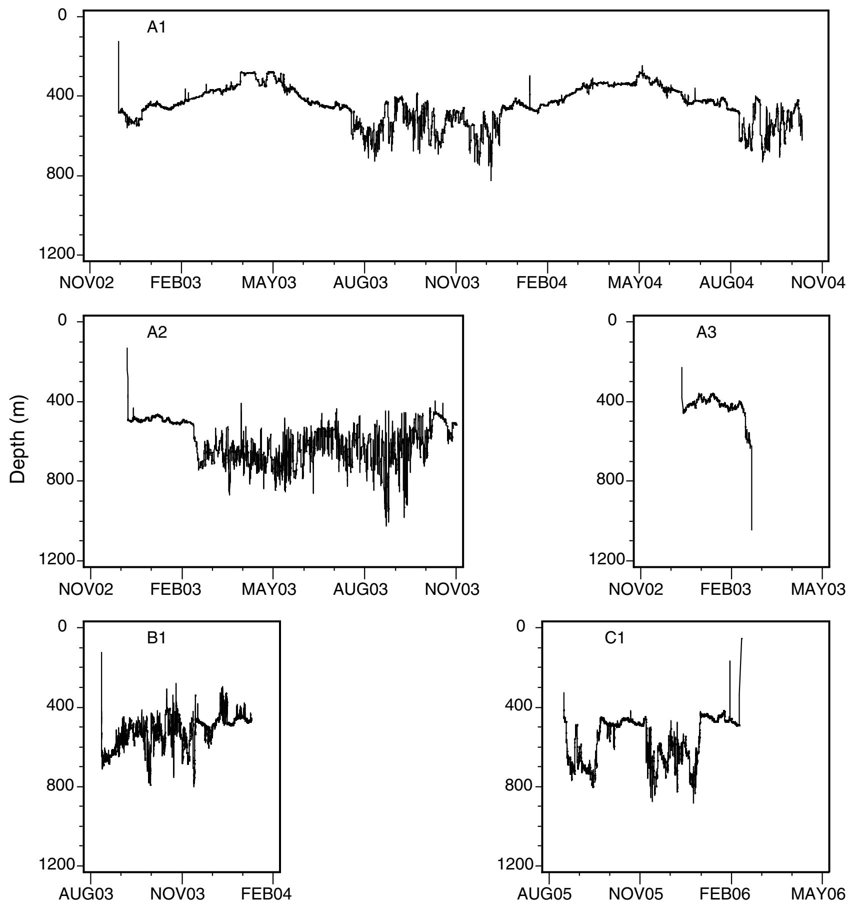

Figure 8

Examples of individual depth trajectories determined from archival tags on recaptured Greenland halibut (*Reinhardtius hippoglossoides*). Examples A1–A3 from release in November 2002, example B1 from release in August 2003, and example C1 from release in August 2005. For A3 the recordings stopped before recapture, probably because the fish descended beyond the depth limit that the tag was designed to withstand.

Of all Greenland halibut caught on vertical longlines in August 2005, only 27 individuals, or 14%, had recently been feeding, as evidenced by the presence of prey in the stomachs. This percentage ranged from 14% to 40% for fish caught in bottom trawls (Table 2). Stomachs from specimens caught on vertical longlines contained food from all major prey groups that were also found in stomachs of trawl-caught fish. Of these specimens, 33% contained fresh prey, i.e. prey without signs of digestion. For trawl-caught fish during the same period this percentage was significantly lower; only 7% contained fresh prey (χ^2, df=1, P<0.01). In terms of percentage by number, 17% of the prey items from vertical longlines and 5% from bottom trawl catches were classified as fresh (χ^2, df=1, P <0.01). The fresh prey of Greenland halibut caught by vertical longlines were *G. fabricii* and the hyperiid amphipod *Parathemisto abyssorum*. The Greenland halibut were all captured in waters above an 800–900 m bottom depth, and 70% of them were caught more than 300 m above the bottom. The fresh contents from trawl catches consisted of hyperiid amphipods, *G. fabricii*, and *Pasiphaea* sp., as well as one case of offal. These individuals were caught at 600–1200 m depth.

Pelagic distribution of potential prey

The acoustic profiles from the extended study area in August 2003–05 were all quite similar, with an acoustic layer in the upper 50 m and another around 300 m depth (Fig. 11). Data from 2005 showed that this pattern continued out to the deeper part of the slope. That year the echo sounder was regrettably set to record only down to 500 m depths, but data from 2003 and 2004 strongly indicated that very little backscatter should be expected below 500–600 m.

Table 2

Percent frequency of occurrence of prey categories determined from stomach contents of Greenland halibut (*Reinhardtius hippoglossoides*) caught on five individual bottom trawl surveys in August 2003–05, November 2003, and March 2004, and on the vertical longline survey in August 2005, and for all bottom trawls combined.

	Aug 2003 bottom trawl	Nov 2003 bottom trawl	Mar 2004 bottom trawl	Aug 2004 bottom trawl	Aug 2005 bottom trawl	Aug 2005 vertical longline	Combined bottom trawl
Crustaceans							
Amphipods	4.5	5.4	6.7	7.1	14.7	22.2	7.8
Euphausiids	0.0	5.4	0.7	2.4	0.0	0.0	1.1
Shrimps	28.8	35.1	15.3	21.4	36.0	48.1	24.6
Undetermined	3.0	8.1	24.7	7.1	13.3	3.7	14.9
Cephalopods							
Gonatus fabricii	37.9	10.8	20.0	35.7	58.7	40.7	34.6
Rossia spp.	0.0	0.0	1.3	2.4	1.3	3.7	1.1
Undetermined	1.5	0.0	4.7	2.4	4.0	0.0	3.5
Fish							
Salmon [1]	0.0	0.0	0.0	0.0	1.3	0.0	0.3
Herring	18.2	8.1	36.0	2.4	5.3	0.0	20.0
Blue whiting	9.1	5.4	2.7	14.3	2.7	0.0	5.4
Sebastes spp.	3.0	0.0	0.7	0.0	0.0	0.0	0.8
Other fish	0.0	5.4	1.3	4.8	2.7	0.0	2.2
Undetermined	21.2	32.4	31.3	14.3	12.0	3.7	23.8
Offal	3.0	0.0	0.0	4.8	4.0	0.0	1.9
Other	3.0	2.7	1.3	11.9	1.3	0.0	1.8
Number of stomachs examined	327	98	378	298	—	—	198
Stomachs with contents	66	37	150	42	75	370	27
Empty stomachs	80%	62%	60%	86%	—	—	86%

[1] A Carlin dangler tag from a tagged salmon was found in one Greenland halibut stomach.

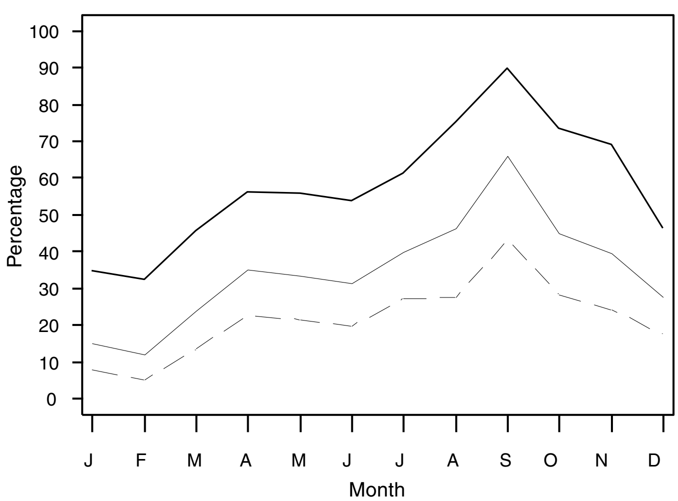

Figure 9

Seasonal variation in mean vertical activity (*VA*) for Greenland halibut (*Reinhardtius hippoglossoides*) tagged with archival tags. For each month, the number of days of individual archival tag recordings where *VA* was greater than 5 (bold), 10 (regular), and 15 m (dotted line) respectively, is given as a percentage of the total number of days recorded by all tags combined.

During these acoustic surveys, most of the total backscatter was allocated to herring in the upper layer and blue whiting in the lower layer. As usual with these types of surveys, the allocation was based on visual recognition of typical patterns, guided by data on target strength of individual echoes and catch composition from sporadic pelagic trawl hauls (mostly outside our extended survey area). Figure 11 shows how catches of redfish and gadoids on vertical longlines compare with the results from the acoustic surveys. The gadoids Atlantic cod (*Gadus morhua*), saithe (*Pollachius virens*), and blue whiting were generally caught within the depth range of the lower acoustic layer, i.e. from 200 to 500 m. The low-target-strength species, the deepwater redfish (*Sebastes mentella*), was caught in the lower part of this layer and below, mostly from 400 to 600 m depth. The bathymetric distribution of Greenland halibut catches from pelagic longlines overlapped to a large extent with the distribution of the prey species redfish and blue whiting, much less with other gadoids, and not with herring.

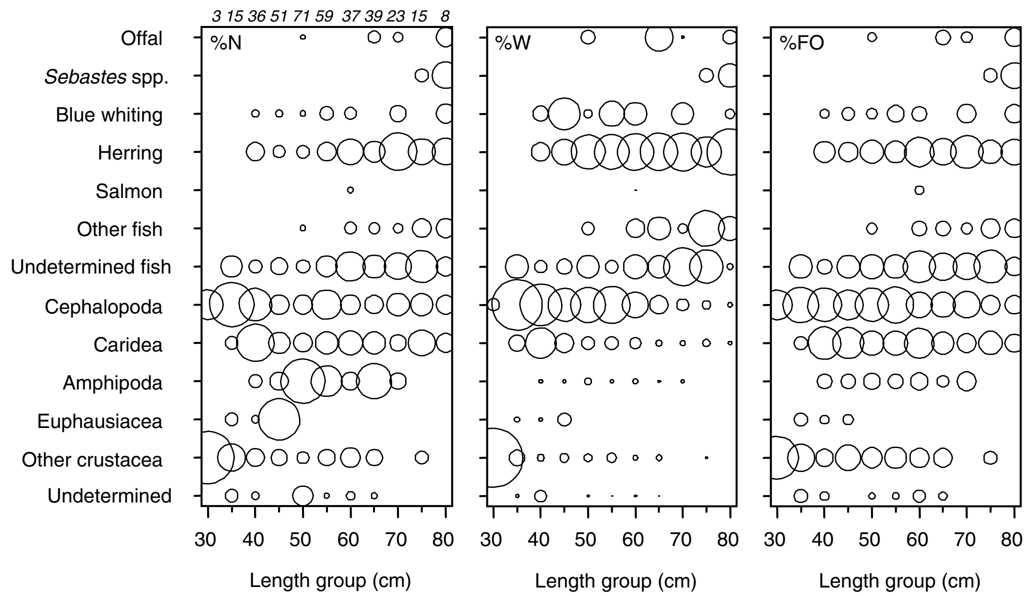

Figure 10

Prey composition by 5-cm length groups of Greenland halibut (*Reinhardtius hippoglossoides*) from bottom trawl, all periods combined. Bubble size is proportional to percentage composition by numbers (%N), weight (%W), and frequency of occurrence (%FO). Number of stomachs with contents is given above left panel.

The abundance of Greenland halibut in bottom trawl was highest between 500 and 800 m, and the species was virtually absent below 1000 m. Figure 11 also shows that the backscatter from the 10-m high bottom-zone almost disappeared below 500 m depth, when Greenland halibut, which does not have a swim-bladder and thus a very low target-strength, dominated almost completely over all other fish species. Above 500 m, blue whiting and several demersal species were numerous, whereas Greenland halibut catches were near zero.

Discussion

Greenland halibut caught in pelagic waters ranged in length from 41 to 84 cm, which is within the same range as that found for those caught on the bottom. This is in contrast to a study by Jørgensen (1997), who found that although one- and two-year-old Greenland halibut from West Greenland nursery areas were found in high abundance in pelagic waters, larger fish (>52 cm) were not found in the pelagic zone of the area inhabited by adult fish. However, Jørgensen commented that the pelagic occurrence of larger specimens may have been underestimated if these fish were able to avoid the pelagic trawl. Support for the ability of large individuals to avoid bottom trawls has subsequently been noted (Albert et al., 2003).

The influence of gear selectivity processes was apparent in length-frequency distributions of catches from demersal longlines and bottom trawls—distributions that closely resembled those found by Huse et al. (1999). The results from trawl catches indicated that small individuals were present on the bottom even though these fish were not caught by demersal longlines. The reason for this could be that the commercial longlines used in the experiment targeted large individuals by factors such as hook- and bait-size, which are important in the size-selectivity of longlines (Bjordal and Løkkeborg, 1996). Also, differences in swimming speed and in the competitive ability between small and large fish may impart a selection bias, bringing a relatively high proportion of large individuals into contact with the gear (Bjordal and Løkkeborg, 1996). Therefore, because small fish were common in pelagic longline catches, this may imply that these fish were more abundant than catch rates indicated.

The depth recordings from archival tags supported the findings from vertical longline results. The recordings showed periods of distinctly different vertical activity, both on a small scale (diurnal) and large scale (typically several weeks). Although the depth-recordings bore no information about the distance from the sea floor, it seems reasonable to assume that the high vertical activity periods were associated, at least partly, with pelagic distribution. The diurnal signal was most apparent at shallower depths, but could also be interpreted as an increase in migration to lower depths during daytime. Depth recordings from the

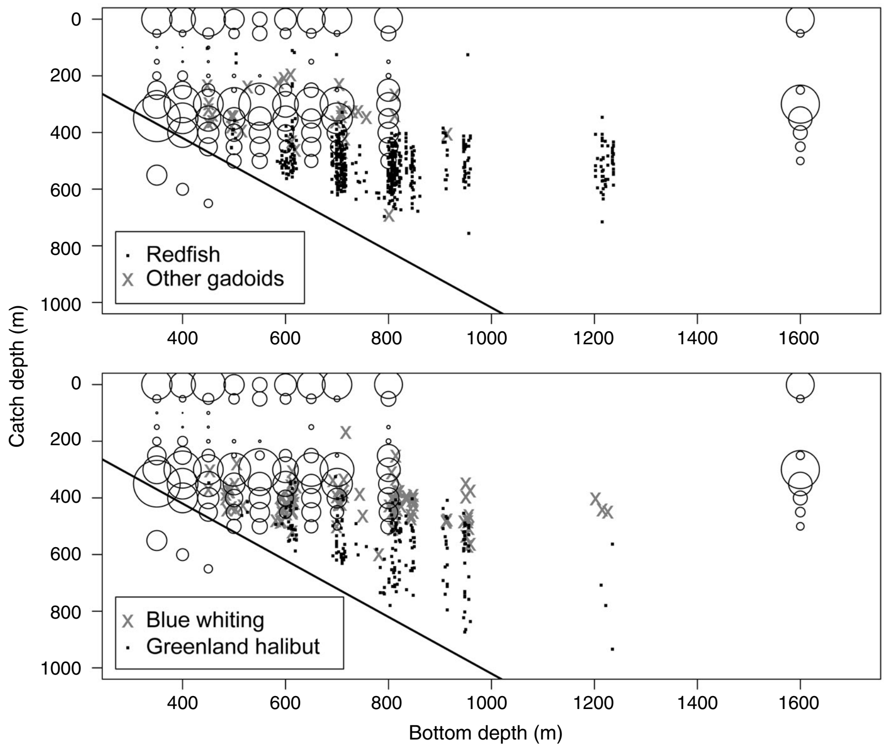

Figure 11

Total acoustic backscatter (bubbles) and catch (noted as individuals) on vertical longlines. **Upper panel** shows total backscatter together with longline catches of redfish (*Sebastes mentella*) (■) and gadoides (X); **lower panel** shows total backscatter and longline catches of blue whiting (*Micromesistius poutassou*) (X) and Greenland halibut (*Reinhardtius hippoglossoides*) (■)). Data from August 2005. Diagonal line represents the bottom, and bubbles beneath this line are acoustic recordings from the bottom channel, i.e., from the water column from the bottom up to 10 m off the bottom.

high vertical activity periods were comparable to depth distribution of vertical longline catches.

Individual and seasonal differences in diurnal activity patterns could not be investigated further due to the low number of recaptures, and due to the unbalanced sex distribution of recaptured fish. However, diurnal variability in bottom trawl catches associated with small individuals migrating into the water column at night time has already been reported off the coast of Labrador during summer (Bowering and Parsons, 1986). Such behavior is probably related to foraging, and should be expected to vary according to prey availability. This may explain why diurnal variability was not previously observed in bottom trawl catches of Greenland halibut from West Greenland waters (Jørgensen, 1997).

The predominant prey species or prey groups in stomachs of Greenland halibut captured with bottom trawl were herring, blue whiting, shrimps, amphipods, and the cephalopod *G. fabricii*. This finding is in agreement with that of previous studies from the Barents Sea-Norwegian Sea continental slope (Michalsen and Nedreaas, 1998; Bjelland et al., 2000; Hovde et al., 2002). The acoustic surveys demonstrated that the vertical distribution of blue whiting overlapped with the distribution of Greenland halibut as determined from vertical longlines. For herring, which were the most important fish prey, no overlapping distributions were evident. Herring were not recorded below 200 m depth during the trawl acoustic surveys—a depth that is shallower than any recording of Greenland halibut from vertical longlines, but archival tag recordings showed that Greenland halibut may be found higher up in the water column, up to above 100 m depth.

A broad overlap could be seen between the vertical distributions of redfish and Greenland halibut. Despite this overlap, redfish occurred only in stomachs of fish larger than 75 cm. This finding may be due to the size selectivity of prey as seen in West Greenland waters, where Greenland halibut up to 64 cm total length fed only on redfish smaller than 15 cm, even though larger specimens were present (Pedersen and Riget, 1993). In our area, redfish smaller than 15 cm have been virtually absent because recruitment has been very low since 1990.

The cephalopod *G. fabricii* and the shrimps *Pasiphaea* spp. and *P. borealis*, all important prey species, may also have been encountered in the pelagic zone. *Gonatus fabricii* juveniles are distributed in the surface layers, living gradually deeper as they become older. As adults, *G. fabricii* are largely benthic at depths of 200–3000 m, performing upwards migrations at night (Kristensen, 1983; Bjørke, 2001). The mesopelagic shrimp *Pasiphaea* spp. is widely distributed in the Norwegian Sea and have the highest biomasses around 200–600 m depth (Dalpadado et al., 1998), whereas the shrimp *P. borealis* is known to perform diurnal vertical migrations, ascending in the water column in the evening and returning to the sea bottom in the morning (see Garcia, 2007).

In our study, Greenland halibut larger than 65 cm were the only ones feeding on demersal species such as eelpouts and other flatfish, but they also fed on epipelagic species such as herring. This finding differs from that of previous studies where the diet of large Greenland halibut was dominated by large groundfish, even when smaller size individuals fed heavily on smaller pelagic fish such as capelin (Yang and Livingston, 1988; Bowering and Lilly, 1992; Solmundsson, 2007).

Because their pelagic distribution is supposed to be linked to foraging activity, the presence of suitable pelagic prey should be expected to influence the pelagic behavior of Greenland halibut. Important prey species such as cephalopods, capelin, and herring have strong seasonal migration patterns, and the abundance of these within any given geographic area is prone to seasonal and annual variations. One example would be herring, which was found to be prominent as prey on the continental slope in October 1997, whereas in January 1998 it was not identified as prey at all (Hovde, 2002). Heavy feeding on capelin, another migratory small pelagic species, has also been observed for Greenland halibut (Smidt, 1969; Bowering and Lilly, 1992).

The vertical activity level of individual Greenland halibut showed a clear seasonal pattern, being highest in August–October. This is the period preceding the main spawning season, when mature Greenland halibut gather in the slope area (Albert et al., 2001). It is also the period when annual surveys are made for population monitoring of the Northeast Arctic stock.

Concluding remarks

This is the first published account of adult Greenland halibut being caught in pelagic waters in considerable quantities in any part of its distribution area. In the present study, adult individuals were found to be widely distributed in the water column. Pelagic activity was related to fish size and dial and seasonal cycles and was influenced by variability in the distribution of prey species. Variations in availability to the survey trawl could be biasing the length- and sex-distribution of these catches as well as obscuring trends in population abundance and structure as derived from stock assessment. The methods used in our study are not suitable for quantifying pelagic behavior, but both diet composition and vertical activity from archival tags indicate that use of the pelagic zone may be significant. In order to improve abundance estimates, and thereby the basis for management decisions, it is important to develop methods to estimate the availability of adult Greenland halibut to bottom sampling trawl.

Acknowledgments

Four anonymous reviewers and the journal editor are thanked for valuable comments and suggestions on an earlier version of the manuscript.

Literature cited

Albert, O. T., A. Harbitz, and Å. S. Høines.
2003. Greenland halibut observed by video in front of survey trawl: behaviour, escapement, and spatial pattern. J. Sea Res. 50:117–127.

Albert, O. T., E. M. Nilssen, A. Stene, A. C. Gundersen, and K. H. Nedreaas.
2001. Maturity classes and spawning behaviour of Greenland halibut (*Reinhardtius hippoglossoides*). Fish. Res. 51:217–228.

Bjelland, O., O. A. Bergstad, J. E. Skjæraasen, and K. Meland.
2000. Trophic ecology of deep-water fishes associated with the continental slope of the eastern Norwegian Sea. Sarsia 85(2):101–117.

Bjordal, Å., and S. Løkkeborg.
1996. Longlining, 156 p. Fishing News Books, Oxford.

Bjørke, H.
2001. Predators of the squid *Gonatus fabricii* (Lichtenstein) in the Norwegian Sea. Fish. Res. 52(1–2):113–120.

Bowering, W. R., and G. R. Lilly.
1992. Greenland halibut (*Reinhardtius hippoglossoides*) off southern Labrador and northeastern Newfoundland (Northwest Atlantic) feed primarily on capelin (*Mallotus villosus*). Neth. J. Sea Res. 29:211–222.

Bowering, W. R., and K. H. Nedreaas.
2000. A comparison of Greenland halibut (*Reinhardtius hippoglossoides* (Walbaum)) fisheries and distribution in the Northwest and Northeast Atlantic. Sarsia 85:61–76.

Bowering, W. R., and D. G. Parsons.
1986. Diel variability in trawl catches of Greenland halibut from the channels off coastal Labrador and implications for resource assessment. N. Am. J. Fish. Manag. 6(2):149–155.

Christensen, O., and W. H. Lear.
1977. Bycatches in salmon drift-nets at West Greenland in 1972. Meddelelser om Grønland. 205(5):1–38.

Dalpadado, P., B. Eilertsen, W. Melle, and H. R. Skjoldal.
1998. Summer distribution patterns and biomass estimates of macrozooplankton and micronekton in the Nordic Seas. Sarsia 83(2):103–116.

Dawe, E. G., W. R. Bowering, and J. B. Joy.
1998. Predominance of squid (*Gonatus* spp.) in the diet of Greenland halibut (*Reinhardtius hippoglossoides*) on the deep slope of the northeast Newfoundland continental shelf. Fish. Res. 36:267–273.

de Groot, S. J.
1970. Some notes on an ambivalent behaviour of Greenland halibut *Reinhardtius hippoglossoides* (Walb.). Pisces: Pleuronectiformes. J. Fish Biol. 2:275–279.

Engås A., and O. R. Godø.
1989. Escape of fish under the fishing line of a Norwegian sampling trawl and its influence on survey results. ICES J. Mar. Sci. 45(3):269–276.

Garcia, E. G.
2007. The northern shrimp (*Pandalus borealis*) offshore fishery in the Northeast Atlantic. Adv. Mar. Biol. 52:147–266.

Hovde, S. C., O. T. Albert, and E. M. Nilssen.
2002. Spatial, seasonal and ontogenetic variation in diet of Northeast Arctic Greenland halibut (*Reinhardtius hippoglossoides*). ICES J. Mar. Sci. 59:421–437.

Huse, I., A. C. Gundersen, and K. H. Nedreaas.
1999. Relative selectivity of Greenland halibut (*Reinhardtius hippoglossoides*, Walbaum) by trawls, longlines and gillnets. Fish. Res. 44:75–93.

Jørgensen, O. A.
1997. Pelagic occurrence of Greenland halibut, *Reinhardtius hippoglossoides* (Walbaum), in West Greenland waters. J. Northwest Atl. Fish. Sci. 21:39–50.

Korneliussen, R. J.
2004. The Bergen echo integrator post-processing system, with focus on recent improvements. Fish. Res. 21(1–3):159–169.

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

Merrett, N. R., and R. L. Haedrich.
1997. Deep-sea demersal fish and fisheries, 282 p. Chapman and Hall, London.

Michalsen, K., and K. H. Nedreaas.
1998. Food and feeding of Greenland halibut (*Reinhardtius hippoglossoides*, Walbaum) in the Barents Sea and East Greenland waters. Sarsia 83:401–407.

Pedersen, S. A., and F. Riget.
1993. Feeding-habits of redfish (*Sebastes* spp.) and Greenland halibut (*Reinhardtius hipploglossoides*) in West Greenland waters. ICES J. Mar. Sci. 50(4):445–459.

Rikardsen, A. H., L. P. Hansen, A. J. Jensen, T. Vollen, and B. Finstad.
2008. Do Norwegian Atlantic salmon feed in the northern Barents Sea? Tag recoveries from 70 to 78°N. J. Fish Biol. 72:1792–1798.

Smidt, E. L. B.
1969. The Greenland halibut, *Reinhardtius hippoglossoides* (Walb.), biology and exploitation in Greenland waters. Medd. Danm. Fisk. Havunders., N.S. 6(4):79–148.

Solmundsson, J.
2007. Trophic ecology of Greenland halibut (*Reinhardtius hippoglossoides*) on the Icelandic continental shelf and slope. Mar. Biol. Res. 3:231–242.

Yang, M. S., and P. A. Livingston.
1988. Food-habits and daily ration of Greenland halibut, *Reinhardtius hippoglossoides*, in the Eastern Bering Sea. Fish. Bull. 84:675–690.