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Feeding of Greenland Halibut (*Reinhardtius hippoglossoides*) in the Northwest Atlantic

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Abstract

The seasonal feeding of Greenland halibut in the shelf and slope areas of the Northwest Atlantic from Davis Strait to eastern Newfoundland was studied from the field analysis of 76,700 stomachs during surveys in 1969-81. Roundnose grenadier, beaked redfish, Atlantic cod, young Greenland halibut, capelin, sand lance, squid and various crustaceans were important components of the diet of Greenland halibut. Consumption of the various food organisms seems to be closely associated with their distribution and the bathypelagic way of life of Greenland halibut. In the northern part of the survey area (Subareas 0, 1 and 2), where Greenland halibut were generally large, beaked redfish and roundnose grenadier were the major prey. In the southern part of the region off Newfoundland, where Greenland halibut were smaller in size, small food organisms (capelin, sand lance, young cod and crustaceans) were prevalent in the diet. The daily food requirements of both male and female Greenland halibut were estimated to range from 1.2% of body weight at age 5 to 0.5% at ages 14-17 years. Quantitatively, females need more food than males of the same age. Use of minimum estimates of stock size from a bottom-trawl survey of the region implies that the population consumes more than 750,000 tons of food annually.

Introduction

Greenland halibut (*Reinhardtius hippoglossoides*) is a significant component of the deepwater fishes in the Northwest Atlantic and has yielded catches in the range of 30,000-63,000 (metric) tons (average 46,000 tons annually) during 1970-82 (NAFO, 1984). The development of an otter-trawl fishery for Greenland halibut along the slopes of the continental shelves in the late 1960's and 1970's provided the opportunity to study various aspects of the biology of the species. Significant contributions were those by Templeman (1973) and Chumakov (1975) on distribution and abundance, Bowering (1978) on age and growth, Zubchenko (1980) on parasites, and Bowering (1984) on migrations.

Although there are detailed accounts of the food of Greenland halibut in the Barents Sea (Nizovtsev, 1977) and in the fjords of West Greenland (Jensen, 1935; Smidt, 1969), similar data for the Northwest Atlantic have been published only sporadically, and the information is generally sparse (Chumakov, 1969; Podrazhanskaya, 1969, 1977, 1982; Konstantinov and Podrazhanskaya, 1972). Greenland halibut belongs to the bathypelagic complex of fishes, and feeding is the least developed aspect of their biology. The aim of this paper is to examine the feeding spectrum of Greenland halibut in various areas of the Northwest Atlantic and attempt to estimate the daily food requirements of the population.

Materials and Methods

Samples of Greenland halibut were collected during 1969-81 from trawl catches of USSR research and exploratory vessels off Baffin Island, West Greenland, Labrador and eastern Newfoundland, which correspond to NAFO Subareas 0, 1, 2 and 3 respectively (Fig. 1). The field analysis aboard fishing vessels involved examination of 15,769 Greenland halibut stomachs from Subarea 0, 34,498 stomachs from Subarea 1, 14,276 stomachs from Subarea 2, and 12,150 stomachs from Divisions 3K and 3L of Subarea 3. Relatively small numbers of stomachs (82 from Labrador and 43 from eastern Newfoundland) were subjected to detailed weight analysis of food components in the laboratory.

Specimens in the field analysis ranged in length from 21 to 99 cm and in age from 2 to 20 years. The length, weight, sex, maturity stage and occurrence of different food items in the stomach were recorded for each fish. Some of the stomach contents (mostly fish) were identified to the level of genera or species, but, in many cases, identification to taxonomic levels lower than Class or Order was not possible. The degree of stomach fullness was visually estimated by the 5-point

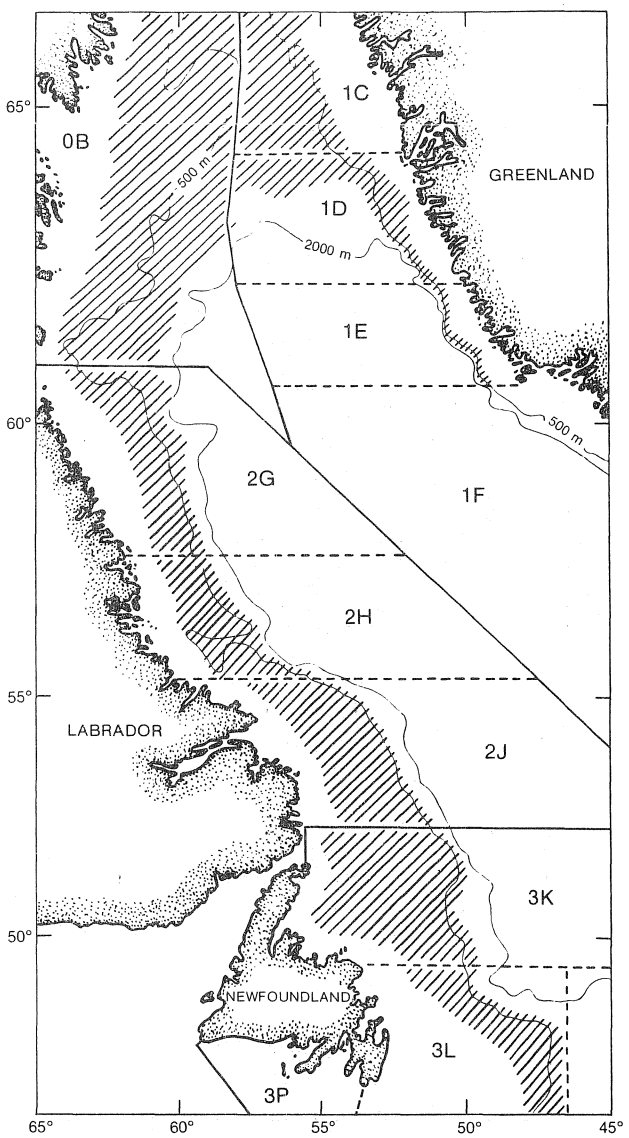

Fig. 1. Areas of the Northwest Atlantic where Greenland halibut were sampled (shaded).

scale: 0 = empty; 1 = one or a few food items with the stomach usually less than 1/4 full; 2 = stomach from about 1/4 to 3/4 full; 3 = stomach full or nearly full with some wrinkles in its wall; and 4 = stomach stretched by its food content with no wrinkles.

Analysis of the data involved expressing the occurrence of the different food items as percentages of the total number of stomachs examined from each area regardless of the presence or absence of food (Shorygin, 1952). For the few stomachs that were analyzed in the laboratory, the food components were weighed and expressed as percentages of the total weight of the stomach contents, and the total index of stomach fullness was determined from the formula

$$SF = (w/W) \times 10{,}000$$

where w is the total weight of stomach contents and W is the total weight of the fish.

An attempt was made to estimate the daily food requirements (R) of Greenland halibut by age-group and sex by the equation (Vinberg, 1956)

$$R = 1.25(I + 2E)$$

where I and 2E represent the food requirements for growth and basic metabolism respectively, and 1.25 is the coefficient of food digestion.

Results and Discussion

Peculiarities of Greenland halibut feeding

The food composition of the diet was quite variable, with nearly 40 representatives of different systematic groups in the Greenland halibut stomachs from the Northwest Atlantic as a whole (Table 1). In the four subareas, the numbers of empty stomachs were quite high (63–82%), thus accounting for the relatively low incidence of the various organisms. Nevertheless, fish was the dominant food type in the four areas, the percentage occurrence increasing from 15–17% in the Baffin Island–West Greenland region to 20–22% in the Labrador–Newfoundland region. The occurrence of crustaceans and molluscs was quite low (1.4–3.9%) in the three northern areas but was considerably higher (13.4 and 5.6%) off eastern Newfoundland.

Apart from the occasional incidence of echinoderms, worms, sponges and crabs, which represent the bottom fauna, most of the food organisms were typical pelagic or bathypelagic types. This is indicative of the bathypelagic way of life rather than a bottom-related one. Other features, which support the view that Greenland halibut is a bathypelagic predator, include the typical long body of a fast swimmer, protective coloring on both sides of the body, and the position of an eye on the top of the head providing two-sided range of peripheral vision, unlike other flatfishes, including Atlantic halibut (*Hippoglossus hippoglossus*) which has the two eyes on one side of the body (DeGroot, 1970; Konstantinov and Podrazhanskaya, 1972).

Studies of the morphological and ecological peculiarities of Greenland halibut in the continental shelf and slope areas from Baffin Island to eastern Newfoundland support the hypothesis of a single population in the region (Chumakov, 1975; Chumakov and Serebryakov, MS 1982). This region contains a system of water circulation which extends from near-polar to temperate latitudes. Connected with the variable conditions throughout this large region are real differences in the food of Greenland halibut. In the northern areas (Subareas 0 and 1) where Greenland halibut are mainly large and mature, beaked redfish (*Sebastes mentella*) (5.4–7.3%) and roundnose grenadier (*Coryphaenoides rupestris*) (3.4–5.0%) prevailed in the diet. Off Labrador (Subarea 2), the prevailing fish food consisted of lanternfishes (Myctophidae) (3.5%), round-

TABLE 1. Frequency of occurrence (%) of food organisms in the stomachs of Greenland halibut from the Northwest Atlantic by NAFO subareas, 1969-81.

Food organisms	Percent occurrence by subarea			
	0	1	2	3
Alepocephalus sp.	—	—	—	+
Ammodytes sp.	+	0.4	+	2.5
Anarhichas sp.	—	+	+	—
Antimora rostrata	+	—	+	+
Boreogadus saida	0.4	—	0.2	—
Coryphaenoides rupestris	3.4	5.0	2.8	0.6
Cottidae	+	+	—	—
Cyclopterus sp.	—	+	+	+
Gadus morhua	—	—	1.3	0.3
Hippogloissoides platessoides	+	+	0.1	0.8
Leptogonus decagonus	+	—	—	—
Liparis sp.	0.4	0.2	—	—
Lumpenus sp.	0.1	+	+	—
Lycodes pallidus	+	+	+	+
Mallotus villosus	—	—	2.6	9.9
Myctophidae	0.4	+	3.5	0.3
Paralepis rissoi krøyeri	0.5	0.4	0.9	+
Raja sp.	+	—	—	+
Reinhardtius hippoglossoides	0.3	0.2	0.2	0.3
Sebastes mentella	5.4	7.3	0.9	0.2
Triglops sp.	—	—	—	+
Unidentified fish	4.1	3.2	6.6	7.4
Total fish	15.2	17.2	19.7	21.9
Amphipoda (*Parathemisto* sp.)	—	—	—	0.7
Copepoda	0.1	+	+	+
Decapoda (*Hyas* sp.)	+	—	—	—
Decapoda (*Pandalus borealis*)	1.0	3.8	2.1	7.4
Euphausiacea	0.1	+	0.4	1.5
Mysidacea	—	+	+	0.1
Unidentified crustaceans	—	—	—	3.7
Total crustaceans	1.4	3.9	2.6	13.4
Bivalvia	+	—	+	—
Gastropoda	+	+	0.1	0.2
Decapoda (*Gonatus*, *Oegopsida*)	1.3	1.5	0.3	1.5
Octopoda (*Sepioides* sp.)	0.7	0.5	0.8	0.2
Unidentified molluscs	0.8	0.9	0.3	3.7
Total molluscs	2.4	2.9	1.5	5.6
Ctenaphora	—	—	+	—
Echinodermata	0.1	—	0.1	0.1
Hexacorallia	+	—	—	—
Holothuridea (*Ophiura* sp.)	—	—	+	—
Polychaeta	—	—	0.1	+
Scyphomedusae	+	—	0.1	—
Spongia (*Calcarea* sp.)	0.1	—	+	+
Total other invertebrates	0.2	—	0.3	0.1
Digested food	1.3	0.1	0.4	—
Total number of stomachs	15,769	34,498	14,276	12,150
Percent empty stomachs	82.3	76.7	76.2	63.2

nose grenadier (2.8%) and capelin (*Mallotus villosus*) (2.6%). Off eastern Newfoundland, Greenland halibut were generally smaller in size and fed mainly on such schooling fish as capelin (9.9%) and sand lance (*Ammodytes* sp.) (2.5%), as well as on crustaceans (13.4%), primarily *Pandalus borealis*.

The composition and amount of food in the diet of Greenland halibut varied greatly with depth, as illustrated by the stomach contents of specimens from the shelf (<500 m) and slope (>500 m) areas of the Labrador-Newfoundland region (Table 2). Although fish was the major prey in both depths, the species

TABLE 2. Food composition of Greenland halibut in the shelf and slope areas of the Labrador-Newfoundland region (Subareas 2 and 3).

Food organisms	Percent by weight: Shelf (≤500 m)	Slope (>500 m)
Parathemisto sp.	0.2	0.1
Northern shrimp	5.7	—
Unidentified shrimp	10.7	0.1
Squids	0.8	2.1
Total invertebrates	17.4	2.3
Beaked redfish	—	62.5
Eelpouts	8.2	—
Greenland halibut (young)	11.6	—
Grenadiers	—	0.9
Polar cod	23.1	2.3
Digested fish	39.7	30.8
Total fish	82.6	96.5
Digested food	—	1.2
Total number of stomachs	58	67
Percent empty stomachs	12.1	4.4
Stomach fullness index	151.5	319.9

composition (by weight) differed greatly, with polar cod (*Boreogadus saida*) (23.1%), young Greenland halibut (11.6%) and eelpouts (*Lycodes* sp.) (8.2%) being the most important types on the shelf, and beaked redfish being the major prey in deep water of the slope. Shrimp was quite important (16.4%) as food on the shelf but not on the slope. The increase with depth in the amount of squid as prey is consistent with data reported by Nesis (1971) on the existence of squids in the bathyal and bathypelagial of the Arctic and North Atlantic waters. It is well known that the densest concentrations of Greenland halibut in the Northwest Atlantic occur at depths of 700–1,100 m (Chumakov, MS 1981). According to Podrazhanskaya (1982), the feeding intensity of Greenland halibut increases with depth and attains its maximum at depths of 600–700 m. The increase in feeding intensity with depth is clearly evident in Table 2 by the large increase in the total index of stomach fullness from 152 on the shelf to 320 on the slope. Variation in feeding intensity of Greenland halibut with depth was also observed in the Barents Sea, but the trend was opposite, with the index of stomach fullness being highest in depths of 100–400 m (Nizovtsev, 1977).

Analysis of the field data on feeding of Greenland halibut by month (Table 3) indicated increased feeding activity during the summer and autumn months and a sharp decline to very low levels during winter and spring. This pattern of increasing stomach fullness in summer-autumn for Greenland halibut is also typical of other species which live in the shelf and slope areas of the Northwest Atlantic, namely haddock (*Melanogrammus aeglefinus*) (Podrazhanskaya and Shestov, 1980), Atlantic cod (Turuk, 1968), beaked redfish (Konchina, 1970), and roundnose grenadier (Podrazhanskaya, 1969).

TABLE 3. Monthly feeding characteristics of Greenland halibut in the Northwest Atlantic by subareas. (See Table 1 for total numbers of specimens examined.)

Month	Number of feeding fish (% of monthly total): 0	1	2	3	Average degree of stomach fullness: 0	1	2	3
Jan	5.0	7.6	11.7	20.0	0.1	0.2	0.2	0.5
Feb		7.1	18.6	17.0		0.2	0.6	0.4
Mar			17.5	11.7			0.4	0.3
Apr			4.0	16.7			0.1	0.4
May			2.9	36.0			0.1	0.9
Jun			12.7	45.0			0.2	1.0
Jul	11.0	14.7	12.5	38.1	0.2	0.1	0.2	0.9
Aug	13.7	23.1	25.8	62.4	0.4	0.4	0.4	1.4
Sep	25.2	20.0	38.6	67.6	1.1	0.4	0.9	2.0
Oct	37.3	41.2	54.6	51.0	1.0	1.0	1.5	1.5
Nov	10.8	15.3	27.8	28.3	0.3	0.5	0.8	0.8
Dec	8.6	10.7	16.4	21.4	0.1	0.5	0.4	0.5

Daily food requirements

Use of the Vinberg (1956) equation to estimate the daily food requirements of Greenland halibut involves determining the energy requirements of the fish for growth (I) and basal metabolism (2E). Because of sexual differences in growth and the broad size-range of fish in the population, the calculations were performed for males and females separately and by age-groups, for which average fish weights were available.

Evidently, Greenland halibut feed mainly during the second half of the year (Table 3). Thus, growth was considered to occur over a 6-month period (180 days), and the mean daily growth increment (expressed as % of body weight) was calculated from the formula

$$\triangle I = \frac{2(W_n - W_o)}{n(W_n + W_o)} \times 100\%$$

where W_o and W_n are weights of fish at the beginning and end of the growth period, and n = 180 days. The weight-at-age data in Table 4 were used to calculate the mean daily growth increments, which decreased from 0.31 to 0.03% of body weight for males aged 4–16 years and from 0.33 to 0.04% for females aged 4–20 years. For each age-group and sex, the daily energy requirements for growth (I), expressed in calories, was determined by the formula

$$I = W \times \triangle I \times 1{,}960$$

where the caloricity of Greenland halibut flesh was assumed to be 1,960 cal/g (Anon., 1976).

In the absence of data on the energy metabolism (2E) for Greenland halibut, the experimental data of Chekunova (1972) on oxygen consumption by Atlantic

TABLE 4. Estimated daily energy requirements of Greenland halibut in the Northwest Atlantic for growth (I) by sex and age-group.

Age (yr)	Mean weight W(g)		Daily growth increments ΔI (%)		Energy needs for growth (I, cal/day)	
	Male	Female	Male	Female	Male	Female
4	300	300				
5	530	550	0.308	0.327	3,200	3,525
6	810	850	0.232	0.238	3,683	3,965
7	1,140	1,220	0.188	0.199	4,201	4,758
8	1,520	1,670	0.159	0.173	4,737	5,663
9	1,940	2,180	0.135	0.147	5,133	6,281
10	2,400	2,750	0.118	0.129	5,551	6,953
11	2,880	3,390	0.101	0.116	5,701	7,707
12	3,360	4,090	0.086	0.104	5,664	8,337
13	3,820	4,840	0.071	0.093	5,316	8,822
14	4,260	5,640	0.060	0.085	5,010	9,396
15	4,630	6,480	0.046	0.077	4,174	9,780
16	4,880	7,360	0.029	0.071	2,774	10,242
17	—	8,280	—	0.065	—	10,549
18	—	9,220	—	0.060	—	10,843
19	—	10,150	—	0.053	—	10,544
20	—	11,050	—	0.042	—	9,996

cod, at temperatures similar to those which are experienced by Greenland halibut (3° to 5° C), were used to obtain the relationship

$$O_2 = 0.267\ W^{0.723}$$

where W is fish weight (g) from Table 3, and O_2 is oxygen consumption (ml/hr). With an oxycaloricity coefficient of 4.86 cal/ml O_2 (Ivlev, 1934), the hourly O_2 values were used in the formula

$$E = O_2 \times 24 \times 4.86$$

to obtain values of basal energy metabolism, expressed as calories per day (Table 5).

Use of the calculated energy requirements for growth (I) and basal metabolism (E) from Tables 4 and 5 in the equation

$$R = 1.25(I + 2E)$$

yields the estimated daily food requirements (R, expressed in calories). Conversion of these values to weights of consumed food requires information on the average caloricity of the food species which make up the diet. In the absence of information on caloricity of the food components of Greenland halibut, data on the caloricity of representative species from different sources were used: 2,000 cal for fish, represented by *Electrons japonica* (Kleymenov, 1971); 850 cal for shrimp, represented by *Pandalus latirostris* (Vinogradova, 1962); and 890 cal for cephalopods, represented by *Todarodes pacificus* (Ertel, 1970). If the diet of Greenland halibut is assumed to consist of approximately 80% fish, 10% shrimp and 10% cephalopods, the average caloricity of 1 g of food would be 1,774 cal. Thus, the equation

$$R' = R/1{,}774$$

TABLE 5. Estimated daily energy requirements of Greenland halibut for basal metabolism (E) by sex and age-group.

Age (yr)	O_2 consumption (ml/hr)		Basal metabolism (E, cal/day)	
	Male	Female	Male	Female
4	16.6	16.6	1,939	1,936
5	25.1	25.8	2,925	3,006
6	34.1	35.3	3,976	4,117
7	43.6	45.8	5,090	5,346
8	53.7	57.5	6,267	6,708
9	64.1	69.7	7,477	8,134
10	78.8	82.5	8,720	9,622
11	85.3	96.0	9,948	11,193
12	95.3	109.9	11,120	12,820
13	104.6	124.1	12,202	14,480
14	113.2	138.7	13,202	16,172
15	120.2	153.3	14,022	17,880
16	124.9	168.1	14,566	19,605
17	—	183.0	—	21,347
18	—	197.8	—	23,073
19	—	212.0	—	24,784
20	—	225.5	—	26,300

TABLE 6. Mean daily food requirements (R) of Greenland halibut, expressed as weight (g) and as percent of body weight.

Age (yr)	Mean daily food requirements (R')			
	Weight (g)		% body weight	
	Male	Female	Male	Female
5	6.38	6.72	1.20	1.22
6	8.20	8.60	1.01	1.01
7	10.13	10.89	0.89	0.89
8	12.17	13.44	0.80	0.81
9	14.15	15.89	0.73	0.73
10	16.20	18.46	0.68	0.67
11	18.04	21.20	0.63	0.63
12	19.66	23.94	0.59	0.59
13	20.94	26.62	0.55	0.55
14	22.13	29.41	0.52	0.52
15	22.70	32.09	0.49	0.50
16	22.48	34.84	0.46	0.47
17	—	37.52	—	0.45
18	—	40.16	—	0.43
19	—	42.36	—	0.41
20	—	43.47	—	0.39

was used to obtain estimates of the daily food requirements (R') expressed in grams (Table 6). Due to their larger size, females require more food than males of the same age. Relative to body weight, the estimated daily food requirements, being essentially the same for males and females of the same age-groups, decline gradually from 1.2% at age 5 to about 0.5% at ages 14–17 years.

Knowledge of the total abundance of Greenland halibut by sex and age-group, used in conjunction with the daily estimates of food consumption in Table 6, should provide a general indication of the total quantity of food that would be consumed by age 5 and older fish during the 6-month growing period. Use of estimates of the total abundance of male and female Greenland halibut (by sex and age) in the region from

Baffin Island (Subarea 0) southward to northeastern Newfoundland (Div. 3K), based on the results of a trawl survey in November 1980–January 1981 (Chumakov, 1982; Chumakov and Serebryakov, MS 1982), indicates that the population consumes more than 750,000 tons of food annually.

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