FOOD HABITS AND DAILY RATION OF GREENLAND HALIBUT, *REINHARDTIUS HIPPOGLOSSOIDES*, IN THE EASTERN BERING SEA

M. S. YANG AND P. A. LIVINGSTON[1]

ABSTRACT

This study shows that diet of Greenland halibut varies mainly by depth and size, and that size of prey fish increases as the Greenland halibut increases in size. A total of 1,333 Greenland halibut (or turbot), *Reinhardtius hippoglossoides*, stomachs were collected in the eastern Bering Sea from May 1983 to November 1985 and analyzed. Stomach content data were divided into four groups based on sample location (depth). Using length of the sample animals within each depth group, data were further divided into five size groups. Walleye pollock, *Theragra chalcogramma*, was the most important prey (58% by weight of the total stomach content). Squids (mainly *Berryteuthis* sp.) were the second most (20% by weight) important food of Greenland halibut. Zoarcids and some deep-water fishes (e.g., bathylagids, myctophids, macrourids) were also important food for Greenland halibut 30–69 cm long. Euphausiids were only important as food (64% by weight) of the fish <20 cm collected in the continental shelf <200 m deep. Fishes ≥70 cm fed almost exclusively on fish in all depth areas.

Variation in mean stomach content weight throughout the day was used to determine the diel feeding pattern; from this it appears that Greenland halibut is a continuous feeder. Daily rations (% of body weight per day) of Greenland halibut were calculated using an exponential gastric evacuation rate model. Fish ≥70 cm had a higher daily ration value (1.17% of body weight per day) than did those of the two smaller size groups (0.66 and 0.64% of body weight per day for 30–49 and 50–69 cm size groups, respectively).

Greenland halibut (or turbot), *Reinhardtius hippoglossoides*, is an amphiboreal fish, occurring in both the North Atlantic and the North Pacific, but not in the intervening Arctic Ocean (Hubbs and Wilimovsky 1964). Within this range, the species has been most extensively studied in the Atlantic Ocean. In the Pacific Ocean, Greenland halibut has been found from Baja California (Schmidt 1934), Oregon (Niska and Magill 1967), and Vancouver B.C. (Westrheim and Pletcher 1966), through the Bering and Okhotsk Seas (Shmidt 1950), to Honshu Island, Japan (Hart 1973), but the center of abundance is in the eastern Bering Sea area.

Data of the resource assessment surveys (from 1979 to 1985) in the eastern Bering Sea performed by the Northwest and Alaska Fisheries Center (NWAFC), National Marine Fisheries Service (NMFS), show that Greenland halibut ranked between 5th and 12th place in terms of relative abundance (kg/ha) among the groundfish species; however, it is the most abundant species in continental slope areas (Bakkala 1986[2]).

These assessments suggest that Greenland halibut is a key member of the eastern Bering Sea ecosystem. The importance of this species in predator-prey relationships of this ecosystem is poorly understood since little is known about its food habits and food consumption rate. Food habits of Greenland halibut in the North Atlantic have been studied by Bowering and Lilly (1985) and Haug and Gulliksen (1982). In the eastern Bering Sea, Mikawa (1963), Mito (1974), Smith et al. (1978), and Livingston et al. (1986) reported stomach contents analysis of the Greenland halibut, but the sample sizes in these studies were small and the analyses were limited. The objective of this study is to provide a description of the food habits of Greenland halibut in the eastern Bering Sea, including diel, spatial, and seasonal variations in stomach contents; influence of predator size; and daily ration.

[1]Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., BIN C15700, Building 4, Seattle, WA 98115.

[2]Bakkala, R. G. 1986. Greenland turbot—biological report. Unpubl. manuscr., 21 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115.

Manuscript accepted June 1988.
FISHERY BULLETIN: VOL. 86, NO. 4, 1988.

METHODS AND MATERIALS

Sample Collection and Stomach Content Analysis

Stomachs from 1,333 Greenland halibut were collected from May 1983 to November 1985 in the eastern Bering Sea area (Fig. 1) from NMFS research vessels and foreign commercial fishing vessels (through the U.S. Foreign Fisheries Observer Program). A bottom trawl was the only sampling gear used, and trawl samples were taken throughout the day and night. Due to the low abundance of Greenland halibut in the shelf area (<200 m), stomachs were taken from virtually all Greenland halibut encountered in trawl catches. Random size-stratified samples were obtained from the catches in the slope area. Captured fish were checked in the field for signs of regurgitation and were discarded when there was evidence of food items in the mouth or gill plates or of flaccid stomachs. Stomachs from the sampled fish were excised and put into cloth bags with a specimen label containing fork length, sex, and station information, and were preserved in 4% formaldehyde solution. Individual fish weights were not recorded at sea, but were estimated by using the weight-length equation,

$$W(g) = 0.0060717 \times L(\text{cm})^{3.08864}, \quad (1)$$

estimated from the Greenland halibut data base of the Resource Assessment and Conservation Engineering (RACE[3]) Division of the NWAFC.

[3]Northwest and Alaska Fisheries Center, National Marine Fisheries Service, 7600 Sand Point Way N.E., BIN C15700, Building 4, Seattle, WA 98115.

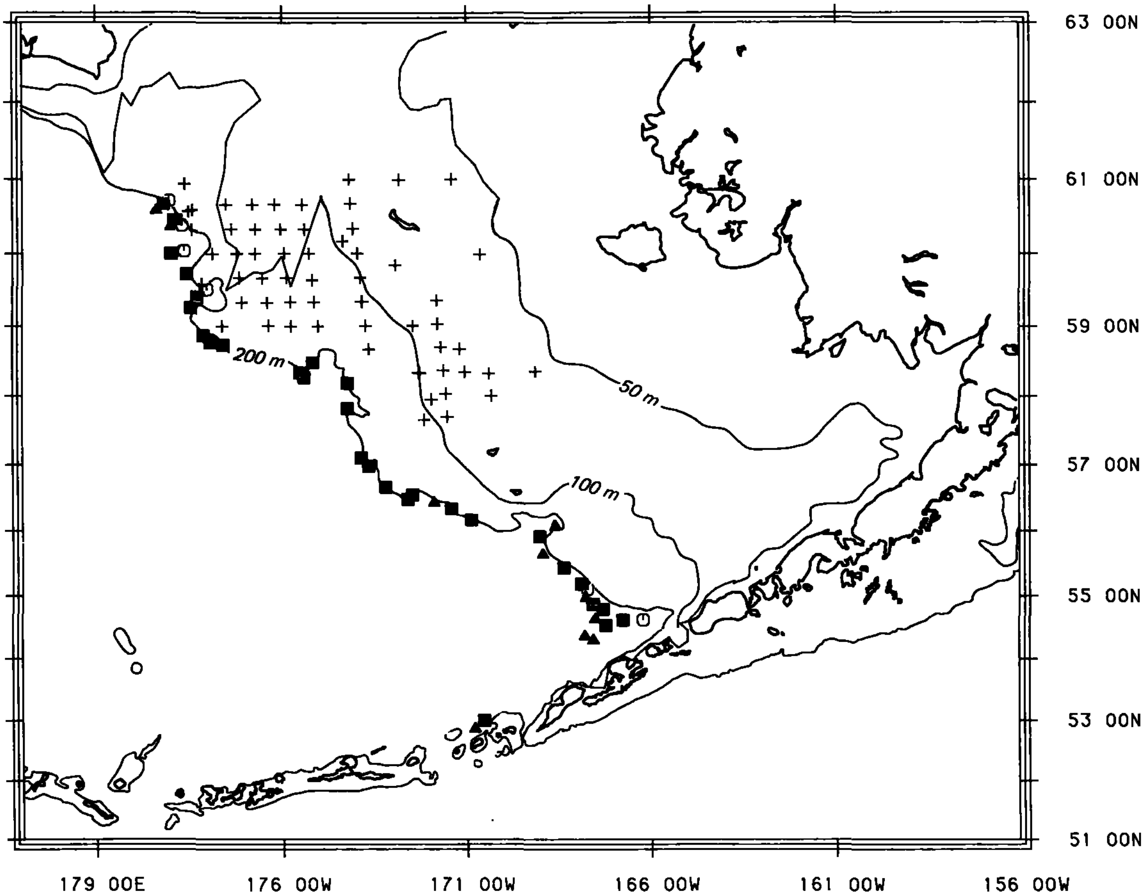

FIGURE 1.—Sampling locations for Greenland halibut in the eastern Bering Sea by four different depth strata, <200 m (+), 200–399 m (O), 400–599 m (■), and ≥600 m (▲).

Stomachs were analyzed individually in the laboratory. Prey items were identified to the lowest possible taxonomic level and counted. Wet weights of the prey items were recorded to the nearest milligram after blotting with paper towels. The fork lengths of prey fish were also measured.

Diet Description

Since the depth distribution of Greenland halibut in this study was broad (from 62 m to 891 m), stomach content data were first subjectively divided by 100 m depth groups. For each 100 m depth class, percent frequency of occurrence (%FO) of prey items, percentage of total stomach content weight (%W) by prey type, and the percentage of total prey number (%N) by prey type were calculated by using ECO/INDEX, a computer program for calculating feeding ecology indices (Vodopovich and Hoover 1981). Based on similarities of major prey items (using percent by weight), stomach content data were combined into four depth groups for analysis: Depth 1 (<200 m), Depth 2 (200–399 m), Depth 3 (400–599 m), and Depth 4 (≥600 m).

Within each of the four depth groups, data were subjectively divided by fish length into 10 cm size groups. By comparing percent by weight of the major prey categories (e.g., gadids, squids) for each size group, the fish within each of the four depth groups were finally lumped into five size groups: <20 cm, 20–29 cm, 30–49 cm, 50–69 cm, and ≥70 cm. Seasonal breakdowns of stomach contents by depth and predator size group could not be performed due to insufficient sample sizes.

Diel Feeding Pattern

Because of the small sample size of fish <30 cm long, only data from three size groups (30–49 cm, 50–69 cm, ≥70 cm) were used for diel feeding analysis. For each size group, the stomach content weights as percent of body weight were calculated for each 3-h period of the 24-h day. Any possible seasonal variations of the diel feeding pattern could not be analyzed because of insufficient seasonal samples.

Daily Ration

In this study, daily ration was calculated using Elliott and Persson's (1978) model. The basic assumption of this model are that the rate of gastric evacuation (R) is exponential and temperature dependent. If stomach samples are taken at fixed intervals of t hours, the mean stomach content weight as a percentage of fish weight (S_i) in each interval (i) is calculated for a total of m intervals over the 24-h period. According to Elliott and Persson (1978), the daily ration ($D.R.$) in terms of percentage of body weight is therefore given by

$$D.R. = \frac{Rt}{1 - \exp(-Rt)} \sum_{i=1}^{m} S_i \,(1 - \exp(-Rt))$$

$$= 24\,\bar{S}R \qquad (2)$$

where $\bar{S} = \sum S_i/m$. Elliott (1972) found the general relationship between R and temperature (T) was exponential:

$$R = ae^{bT}. \qquad (3)$$

Based on data presented in the literature for the normal temperature range of both freshwater and marine fishes, Durbin et al. (1983) concluded that the slope (b) is fairly constant for different prey types and fish species (mean = 0.115), while the intercept (a) changes with prey type and can be estimated from gastric evacuation rate experiments. Since there were no gastric evacuation rate data available for Greenland halibut, results of gastric evacuation experiments on walleye pollock, *Theragra chalcogramma*, feeding on juvenile pollock and squid were used (Dwyer et al. 1987). Although walleye pollock is taxonomically very different from Greenland halibut, these two species have some prey in common. In addition, both species are active, off-bottom feeders which could be expected to be more similar in terms of metabolic rates than benthic feeding, small mouth flounders whose food intake has been studied more extensively. The intercept "a" in Equation (2) was 0.0143 for juvenile walleye pollock and 0.0079 for squid. For this study, the intercept for walleye pollock prey was used to calculate daily ration when fish was the main prey (>70% of diet by weight), and the intercept for squid was used when squid was the main prey. If the diet was split evenly between fish and squid prey, daily ration was calculated using both intercept values to obtain a likely range of daily ration values.

Average bottom temperatures for the eastern Bering Sea for this study were estimated from oceanographic data on the Bering Sea (Ingraham

1983[4]). Because of the small differences in temperatures between different seasons (e.g., 2.90°C, 2.47°C, and 2.93°C were the average temperatures for spring, summer, and autumn at locations where fish 30–49 cm were collected), and the lack of samples for fish <30 cm, daily rations were calculated for three size groups (30–49 cm, 50–69 cm, and ≥70 cm) with all seasons combined. Temperatures used for each of the three size-groups were calculated by matching the haul locations of each size group in our study with the long-term monthly mean bottom temperature at those positions and calculating the average bottom temperature.

RESULTS

General Description of Diet

Stomachs from 1,333 Greenland halibut were analyzed; of these, 610 stomachs (46%) were empty. The size of the Greenland halibut ranged from 9 to 99 cm (fork length) with a mean of 56 cm. The sampling depth ranged from 62 to 891 m with most of the samples (55%) collected from the area 400–599 m deep.

Prey consumed included gastropods, cephalopods, crustaceans, ophiuroids, and fish (Table 1). Twelve families of fish and at least 14 different fish species were represented in the stomach contents. Fish dominated the contents in terms of frequency of occurrence, number, and weight; walleye pollock was the most important fish species consumed with respect to all three measures of prey importance. Three genera of squid were consumed (mainly *Berryteuthis* sp.) and were the second most important prey. The importance of the various prey species or groups (e.g., gadids, squids) changes with bottom depth and Greenland halibut size. Those changes will be discussed in the following sections.

Spatial and Size Differences

Depth 1 (<200 m)

Gadids constituted more than 87% by weight of the stomach contents of all but the smallest (<20 cm) size group (Fig. 2A). Euphausiids comprised 64% by weight (54% by number) of the diet of Greenland halibut <20 cm long. In size group 20–29 cm, the percentage by number of euphausiids was still high (52%), but the percentage by weight decreased dramatically to only 2%. Gadids were the dominant prey for size groups larger than 30 cm in Depth 1 in terms of percent of frequency of occurrence, percent of total stomach contents weight, and the percent of prey number. Cephalopods, clupeids, osmerids, stichaeids, myctophids, and macrourids were not important food items at this depth.

Depth 2 (200–399 m)

No Greenland halibut smaller than 30 cm were collected at this depth range. Cephalopods, in terms of the three diet measures shown in Figure 2B, were the dominant food items found in the size groups 30–49 cm and 50–69 cm. On the other hand, gadids were the dominant prey in size group ≥70 cm (Fig. 2B). When all sizes were combined, the cephalopods were more important than gadids (Fig. 2B, lower right); however, when the size groups were separated (Fig. 2B), the different contribution of gadids and cephalopods to different size groups is very clear (cephalopods are most important for fish <70 cm and gadids are important for fish ≥70 cm). Miscellaneous prey fishes found in the entire Depth 2 group included zoarcids, bathylagids, myctophids, and pleuronectids.

Depth 3 (400–599 m)

No stomachs of Greenland halibut smaller than 30 cm were collected in this depth range (Fig. 2C). For Greenland halibut 30–49 cm long, zoarcids (38.6%) were the most important prey item in terms of percentage by weight of the stomach contents, followed by cephalopods (30.7%) and gadids (17%). In terms of percent of prey number, cephalopods comprised 39% of the total prey in this size group, followed by gadids (22%), bathylagids (17.3%), and zoarcids (8.7%). For the size group 50–69 cm, cephalopods, gadids, and zoarcids comprised 61, 21, and 12% by weight of the stomach contents, respectively. Cephalopods also comprised the highest percentage (35%) by the number in this size group. Gadids were the dominant prey of large Greenland halibut (≥70 cm). They comprised 87% by weight, 69% by number, and 82% by frequency of occurrence of the stomach contents of this size group (Fig. 2C). Other prey fishes found in the Depth 3 group included stichaeids, myctophids, cottids, macrourids, cyclopterids, and pleuronectids. For the Depth 3 group (Fig. 2C, lower right), gadids were the domi-

[4]Ingraham, W. J. 1983. Temperature anomalies in the eastern Bering Sea 1953–82. NWAFC Processed Rep. 83-21, 348 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115.

TABLE 1.—Prey items found in the stomachs of Greenland halibut collected in the eastern Bering Sea during summer 1983 through fall 1985. %FO = percent frequency of occurrence, %*N* = percent by number, %W = percent by weight, t = <0.01% W.

Prey item	%FO	%*N*	%W
Gastropoda			
Buccinum sp.	0.4	0.34	0.14
Cephalopoda	31.9	22.67	20.28
Teuthoidea	30.8	21.98	19.65
Gonatidae	10.5	8.16	11.64
Gonatopsis sp.	1.9	1.20	2.97
Gonatus sp.	0.7	0.60	0.13
Gonatus magister	0.1	0.26	0.09
Berryteuthis sp.	6.4	4.81	6.69
Berryteuthis magister	0.3	0.26	1.03
Unidentified Gonatidae	1.4	1.03	0.73
Unidentified Teuthoidea	20.5	13.82	8.01
Octopoda	0.1	0.09	0.51
Unidentified Cephalopoda	1.0	0.60	0.12
Crustacea	7.8	12.39	0.41
Mysidacea	2.2	1.64	0.01
Gnathopausia gigas	0.7	0.52	t
Holmesiella anomala	1.0	0.77	t
Pseudomma truncatum	0.1	0.09	t
Unidentified Mysidacea	0.4	0.26	t
Cumacea	0.1	0.17	t
Amphipoda	1.2	1.54	t
Gammaridea	1.0	0.77	t
Hyperiidea			
Parathemisto libellula	0.3	0.77	t
Euphausiacea	1.8	4.90	t
Thysanoessa inermis	1.2	3.78	t
Unidentified Euphausiacea	0.6	1.12	t
Decapoda			
Caridea	2.4	3.79	0.15
Pasiphaeidae			
Pasiphaea pacifica	0.1	0.09	t
Hippolytidae	0.4	2.58	0.06
Eualus sp.	0.3	2.06	0.04
Eualus biunguis	0.3	0.52	0.02
Panadalidae	1.2	0.78	0.08
Pandalus sp.	0.8	0.52	0.04
Pandalopsis dispar	0.3	0.17	0.03
Unidentified Pandalidae	0.1	0.09	0.01
Crangonidae			
Crangon communis	0.3	0.17	0.01
Unidentified Caridea	0.3	0.17	t
Reptantia	0.4	0.27	0.25
Anomura			
Paralithodes sp.	0.1	. 0.09	0.14
Brachyura	0.3	0.18	0.11
Chionoecetes sp.	0.1	0.09	0.08
Chionoecetes opilio	0.1	0.09	0.03
Unidentified Crustacea	0.1	0.09	t
Ophiuroidea	1.1	1.81	t
Ophiurida	1.0	1.72	t
Unidentified Ophiuroidea	0.1	0.09	t
Larvacea Copelata	0.4	0.69	t
Teleostei	71.7	61.36	77.93
Clupeidae			
Clupea pallasii	0.3	0.17	0.74
Osmeridae	0.1	0.09	t
Bathylagidae	7.6	8.24	0.63
Leuroglossus stilbius	0.4	0.43	0.04
Unidentified Bathylagidae	7.2	7.81	0.59
Myctophidae	5.0	6.87	0.71
Stenobrachius leucopsarus	0.1	0.09	t
Unidentified Myctophidae	4.8	6.78	0.71
Gadidae	32.7	26.35	61.08
Theragra chalcogramma	28.2	23.35	58.39
Unidentified Gadidae	4.4	3.00	2.69
Zoarcidae	5.0	4.13	3.51
Lycodes sp.	4.1	3.52	2.95
Lycodes diapterus	0.1	0.09	0.05
Lycodes palearis	0.1	0.09	0.11
Unidentified Zoarcidae	0.6	0.43	0.40
Macrouridae	1.0	1.12	2.00
Coryphaenoides sp.	0.7	0.43	0.39
Coryphaenoides filifer	0.1	0.09	0.04
Unidentified Macrouridae	0.8	0.60	1.57
Icelidae			
Icelus spiniger	0.1	0.09	0.03
Cottidae	0.2	0.18	0.21
Dasycottus setiger	0.1	0.09	0.20
Hemitripterus boline	0.1	0.09	0.01
Cyclopteridae	0.6	0.35	1.73
Aptocyclus ventricosus	0.1	0.09	0.55
Careproctus cypselurus	0.1	0.09	0.82
Unidentified Cyclopteridae	0.3	0.17	0.36
Stichaeidae	0.7	0.43	0.09
Lumpenus maculatus	0.3	0.17	0.04
Unidentified Stichaeidae	0.4	0.26	0.05
Pleuronectidae			
Reinhardtius hippoglossoides	0.6	0.34	1.60
Unidentified Teleostei	20.6	12.88	5.02
Unidentified organic material	0.3	0.17	t
Total number of stomachs	1,333		
Total stomachs with food	723		
Total prey weight (g)	47,713.52		
Total prey number	1,165		

nant prey in the diet due to the consumption of walleye pollock by Greenland halibut ≥70 cm; however, cephalopods and other fishes were more important than gadids for the two smaller size groups.

Depth 4 (≥600 m)

No stomachs were collected for fish smaller than 30 cm in this depth group (Fig. 2D). For size groups 30–49 cm, cephalopods were the dominant prey (56%) of Greenland halibut in terms of percent by weight, followed by bathylagids at 29%. However, the percent of number and the percent of frequency of occurrence of bathylagids (FOG in Figure 2D, upper left) were higher than those of the cephalopods. The stomach contents (by weight) of Greenland halibut 50–69 cm long was composed of 57% cephalopods, 22% macrourids, 12% bathylagids, 4%

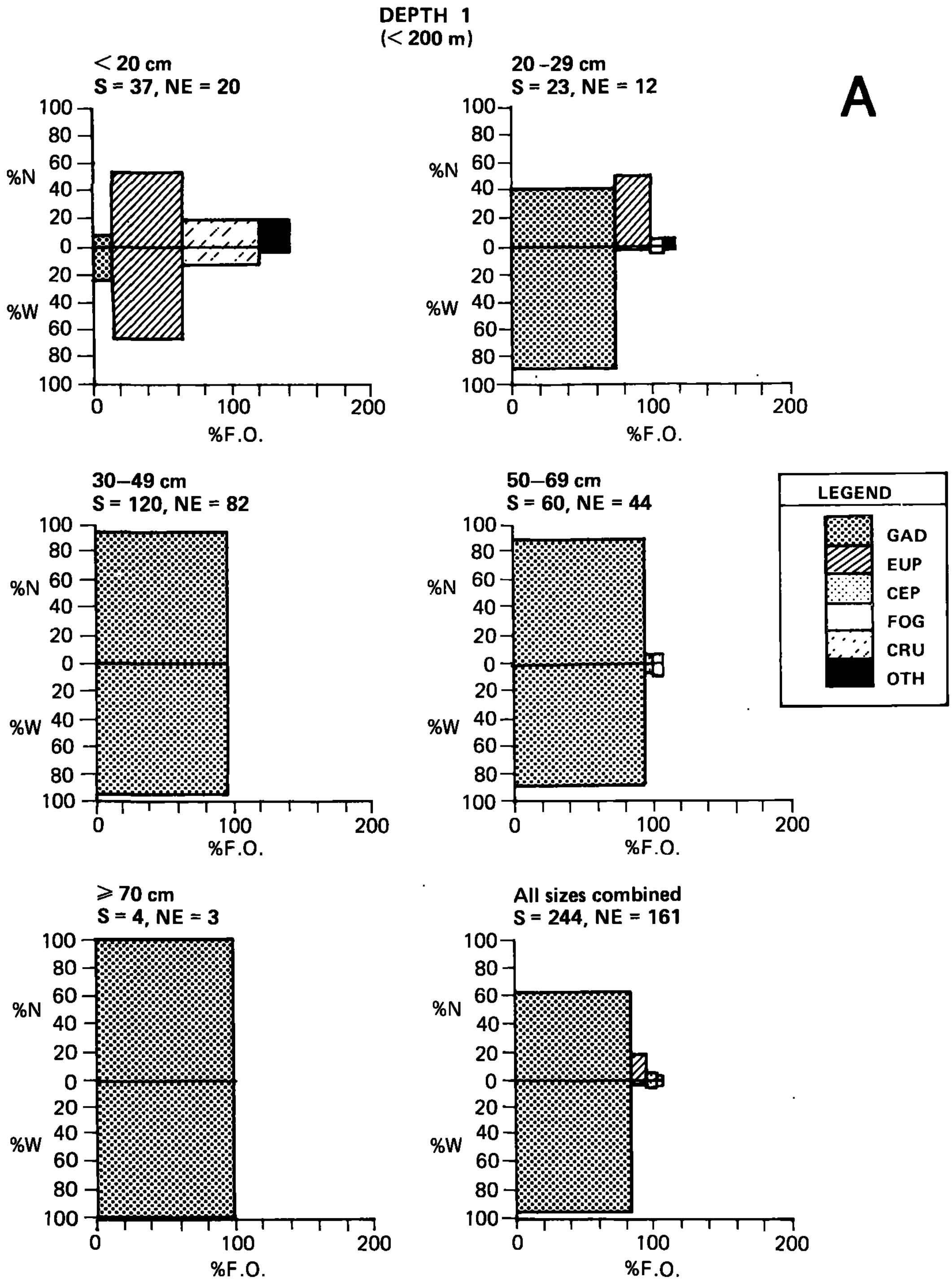

FIGURE 2.—Percent of frequency of occurrence (%FO), percent of prey number (%N), and percent of stomach content weight (%W) of major prey items in the stomach contents of Greenland halibut (by depth and by size). S, total number of stomachs; NE, nonempties; %FO, GAD, Gadids; EUP, Euphausiids; CEP, Cephalopod; FOG, Fish other than gadids; CRU, Crustacean; OTH, Others. A) Depth 1.

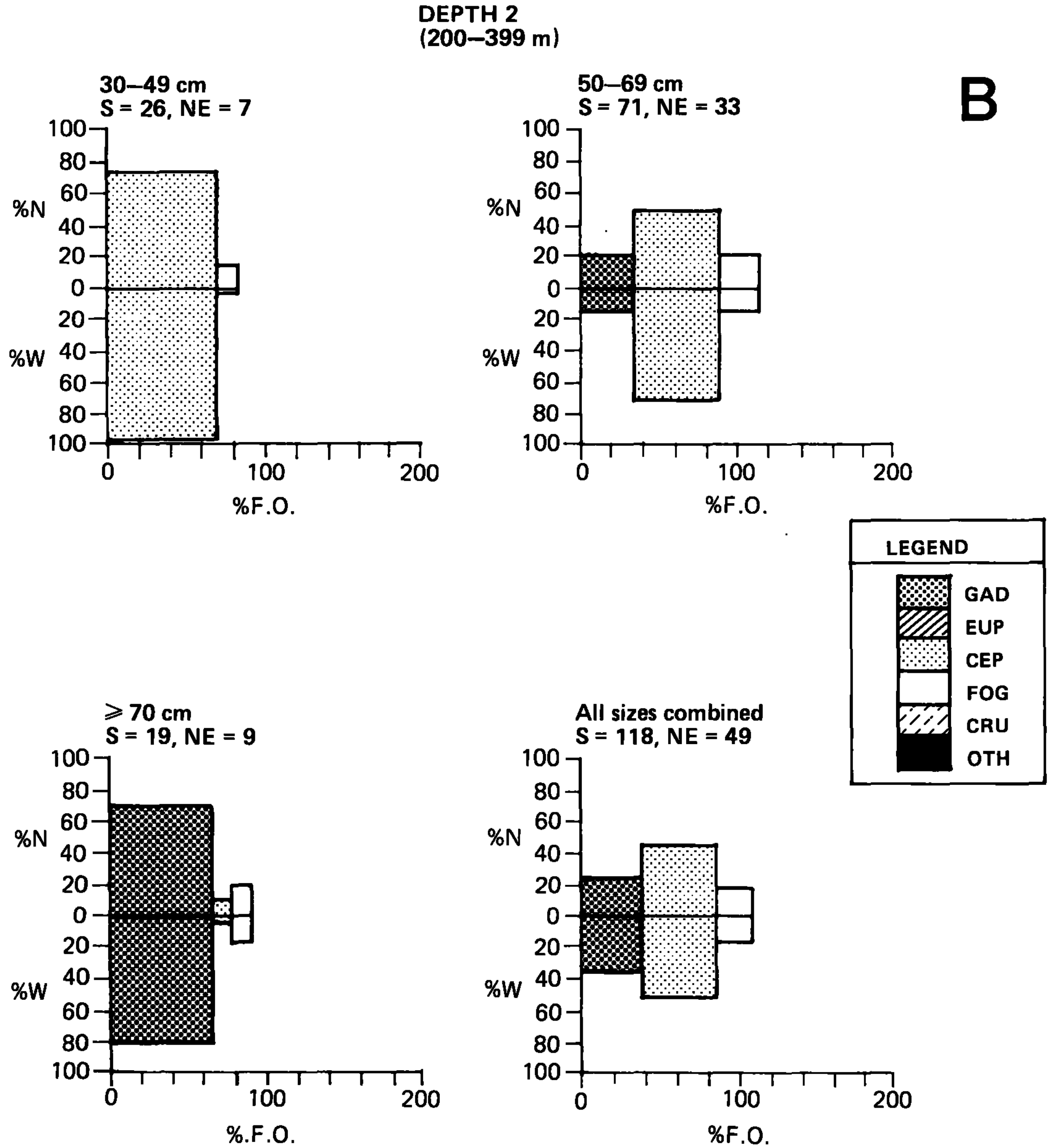

FIGURE 2.—*Continued.*—B) Depth 2.

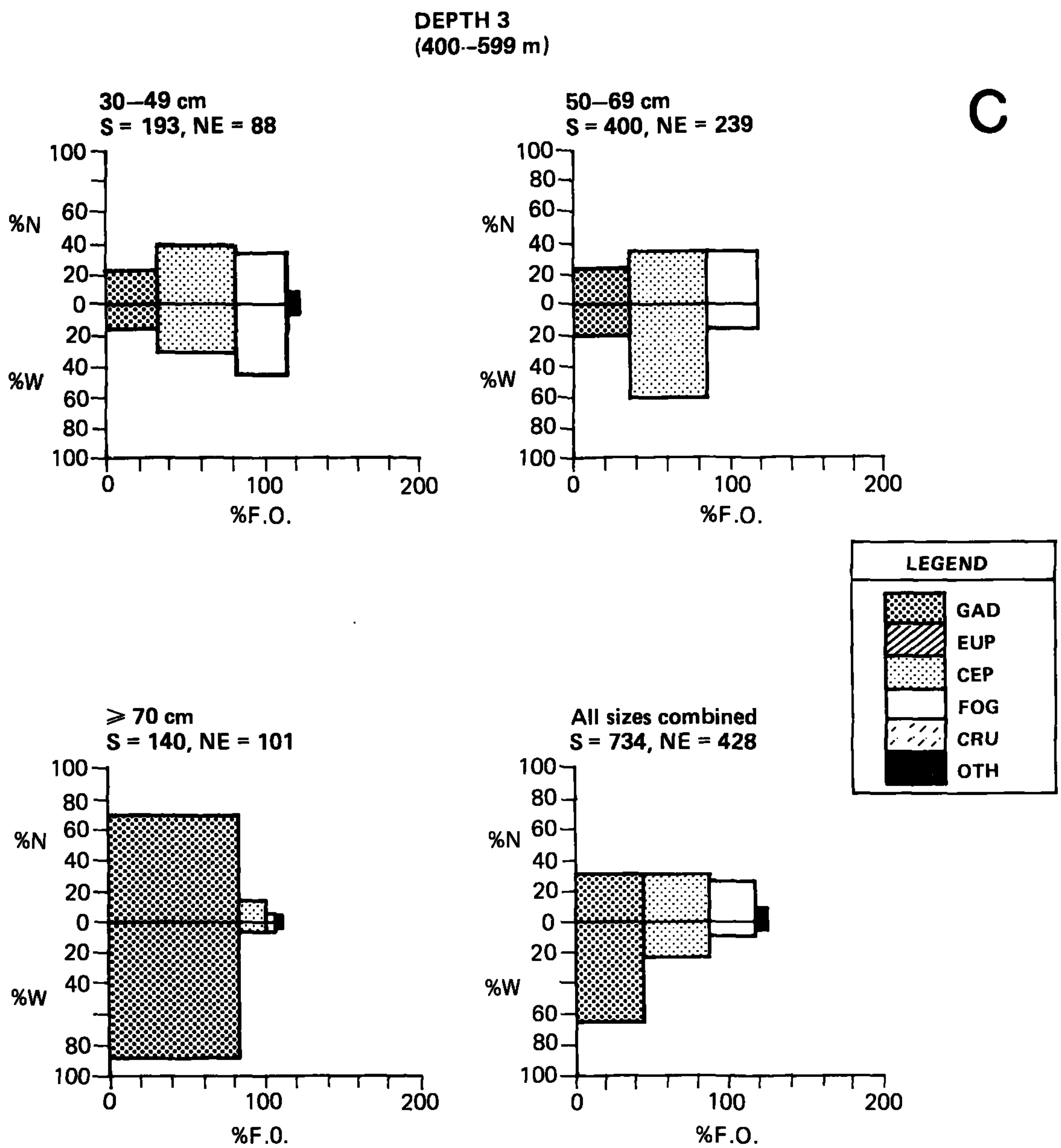

FIGURE 2.—*Continued.*—C) Depth 3.

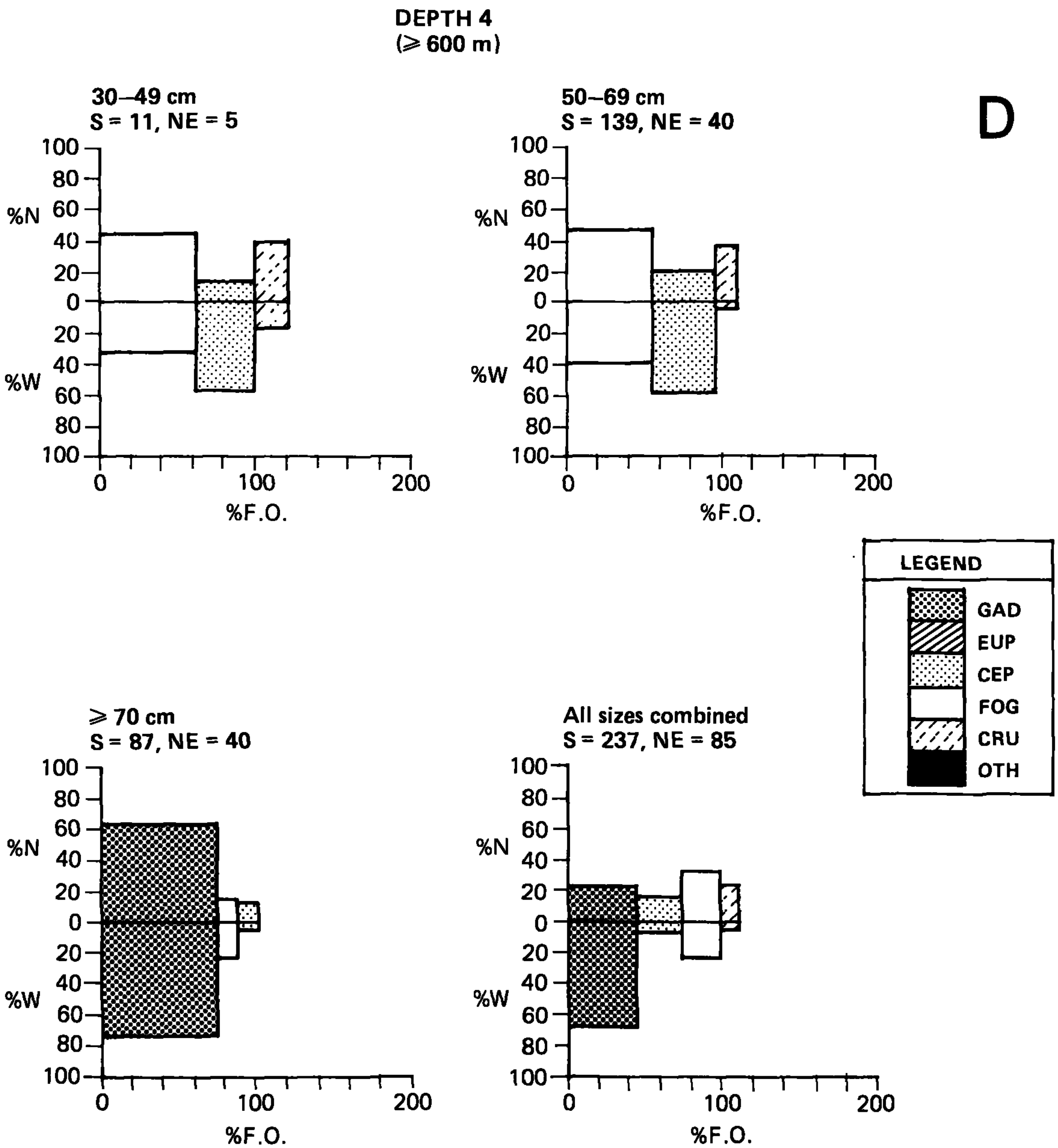

FIGURE 2.—*Continued.*—D) Depth 4.

myctophids, and 0.6% stichaeids. In terms of percent by number and the percent of frequency of occurrence, the fishes other than gadids (FOG in Figure 2D) were more important than the cephalopods. No gadids were found in either the 30–49 cm group or the 50–69 cm group of fishes; however, they were the dominant prey (75% by weight, 64% by number, and 73% by frequency of occurrence) of Greenland halibut ≥70 cm (Fig. 2D, lower left) as in the other three depth groups (Fig. 2A,B,C, lower left). Other food in this size group included macrourids, cyclopterids, and pleuronectids. Even though gadids did not occur in the two smaller size groups, they were important in the Depth 4 group as a whole (Fig. 2D, lower right).

Trends in Fish Consumption

The size of the walleye pollock consumed by Greenland halibut increased dramatically with predator size (Fig. 3). The relationship appears linear with $r^2 = 0.835$. Based on the age-length key for walleye pollock (Halliday and Umeda 1986), the walleye pollock eaten by Greenland halibut were approximately age 0 and age 1 for smaller size fish (<50 cm), age 1 and age 2 for medium size fish (50–69 cm), and age 3 and age 4 for the fish ≥70 cm (Fig. 4).

The importance of prey fishes in the diet of Greenland halibut appears to be depth related (Table 2). Clupeids disappear from the diet in waters ≥200 m deep, while gadids are important in all depths but occur most frquently (85%FO), and comprise most of the diet both in number and weight (65% and 93%, respectively), in the area <200 m deep. Zoarcids appear in stomachs only in the area 200–600 m deep, and bathylagids start appearing at 200–399 m and increase in importance as the water depth increases. Myctophids seem to be more important in the area 400–599 m than in the other depths,

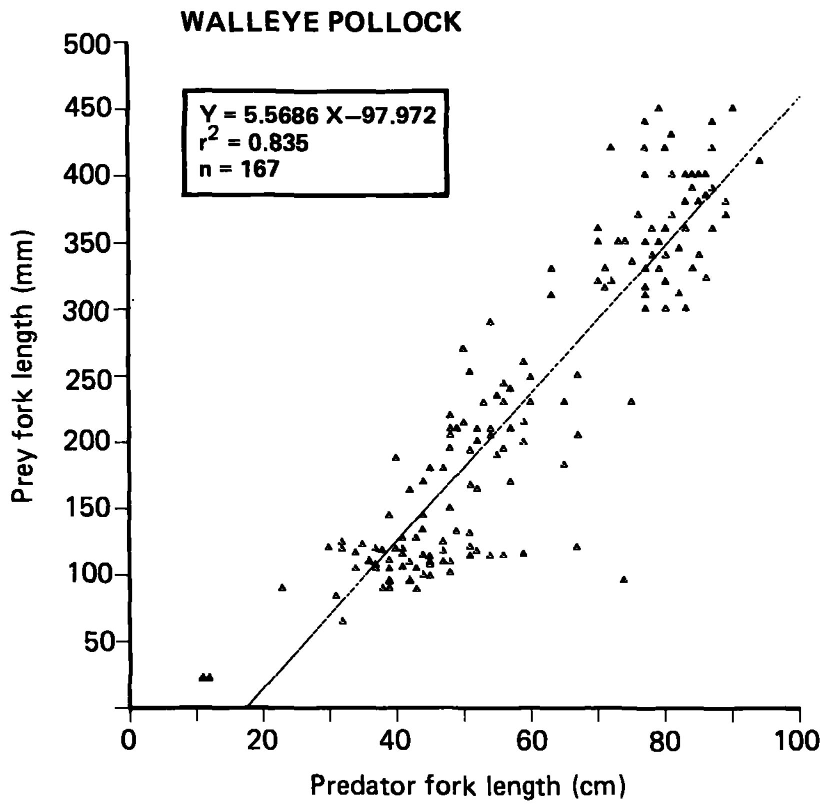

FIGURE 3.—Scatter plot of the fork length of walleye pollock that were consumed by Greenland halibut of different sizes in the eastern Bering Sea.

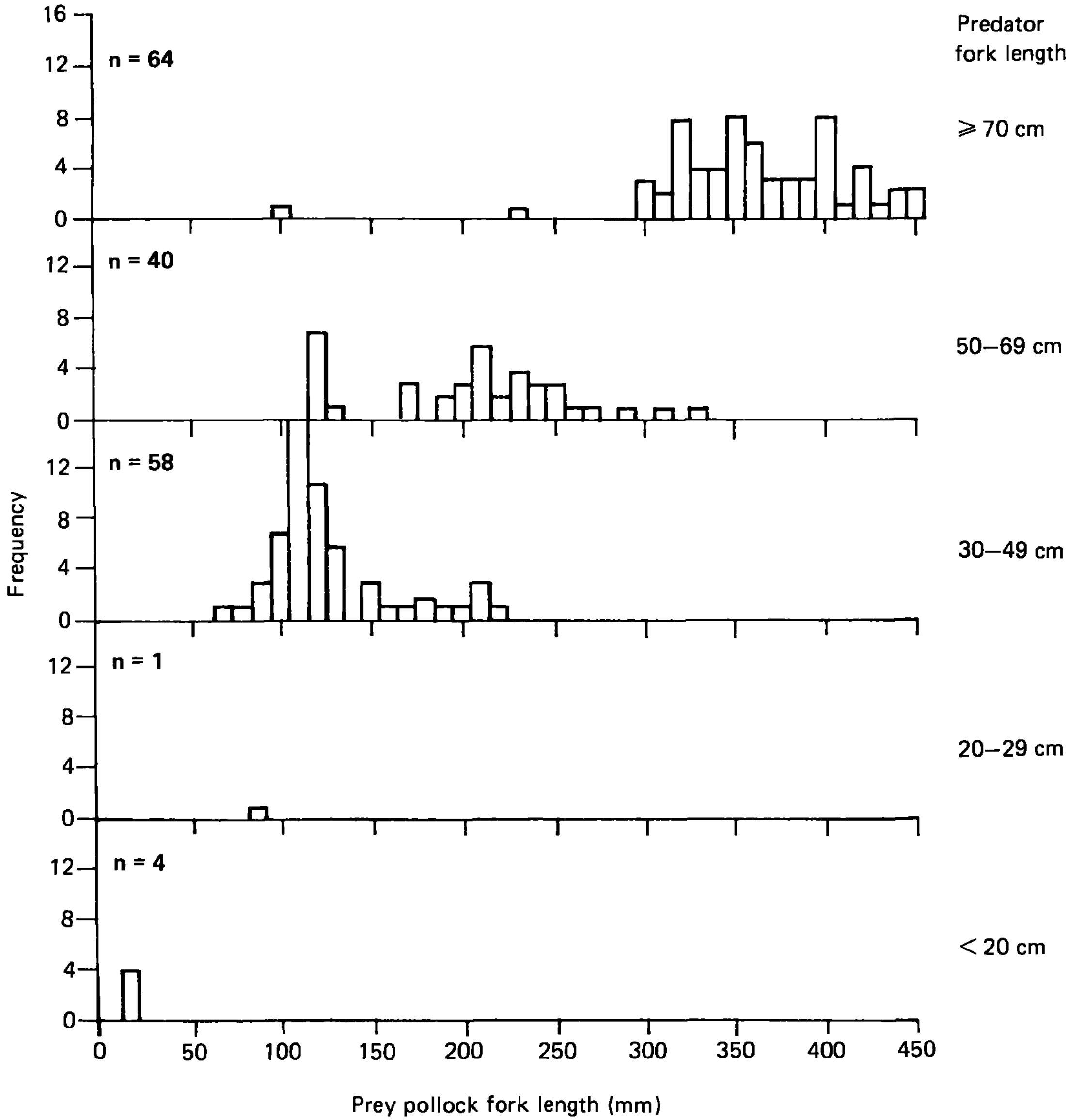

FIGURE 4.—Length-frequency distributions of walleye pollock consumed by Greenland halibut in the eastern Bering Sea.

while macrourids are important prey in even deeper waters (≥600 m).

Trends in Stomach Fullness

Fewer empty stomachs were found in summer than in spring and autumn except in the ≥70 cm size group (Fig. 5). The occurrence of empty stomachs for all size groups was about 35% in summer and 50% in autumn. In spring, samples from the 30-49 cm size group had the greatest percentage of empty stomachs (about 70%), followed by size groups 50-69 cm (about 58%) and ≥70 cm (about 12%).

There were no apparent diel trends in stomach content weight in this study (Fig. 6). The stomach content weight (expressed as percentage of body weight) for large fish (≥70 cm) was fairly constant except for the 0900-1200 h time period. The

TABLE 2.—Importance of the prey fish by depth found in the stomachs of Greenland halibut collected from the eastern Bering Sea. %FO = percent frequency of occurrence, %N = percent by number, %W = percent by weight.

	Depth 1 (<200 m)			Depth 2 (200–399 m)			Depth 3 (400–599 m)			Depth 4 (≥600 m)		
Prey fish	%FO	%N	%W	%FO	%N	%W	%FO	%N	%W	%FO	%N	%W
Clupeidae	0.6	0.3	2.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Osmeridae	0.6	0.3	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Stichaeidae	1.2	0.7	0.4	0.0	0.0	0.0	0.5	0.3	0.1	1.2	0.7	0.1
Gadidae	85.1	64.9	92.7	36.7	26.5	36.2	45.3	31.4	64.4	42.4	25.2	67.9
Zoarcidae	0.0	0.0	0.0	8.2	8.8	7.0	7.4	6.5	4.8	0.0	0.0	0.0
Bathylagidae	0.0	0.0	0.0	6.1	5.9	0.1	9.8	9.4	0.5	11.8	21.7	2.1
Myctophidae	0.6	0.3	0.1	4.1	4.4	0.2	7.2	11.1	1.3	2.4	2.8	0.4
Cottoidei	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.5	0.4	0.0	0.0	0.0
Macrouridae	0.6	0.3	0.5	0.0	0.0	0.0	0.9	0.8	1.1	8.3	4.9	9.4
Cyclopteridae	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.5	1.4	1.2	0.7	6.0
Pleuronectidae	0.0	0.0	0.0	2.0	1.5	6.0	0.2	0.2	0.9	2.4	1.4	4.7

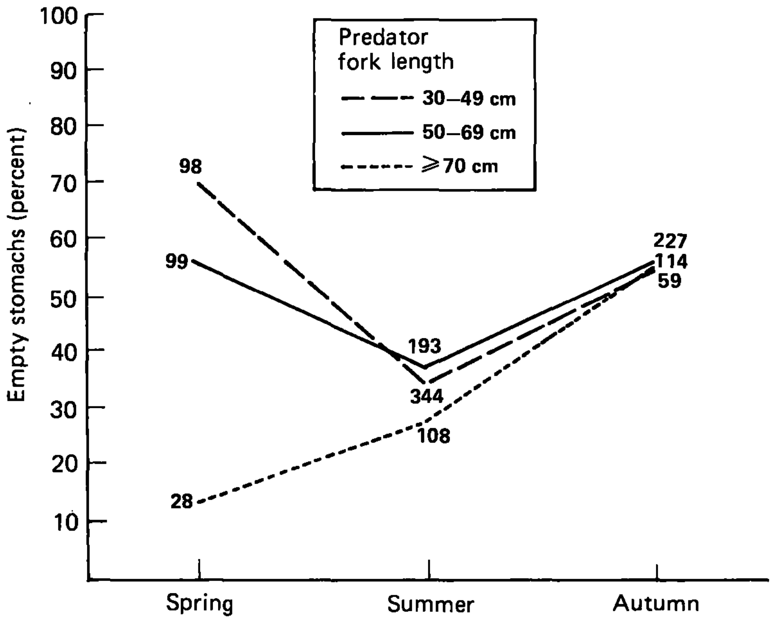

FIGURE 5.—Percent of empty stomachs by season and Greenland halibut size. (Numbers are sample sizes.)

stomach content weight of the fish 50–69 cm was also fairly constant although much less than in the larger fish. Although a midday drop in stomach content weight occurred in the two larger size groups, stomach content weight for the smallest size group appeared to steadily increase from 0100 h to 1200 h. The stomach content weight was highest but most variable in size group 30–49 cm during the 1500-1800 h time period.

Daily Ration

The mean stomach content weight and the daily ration varied among three size groups of Greenland halibut (Table 3). By percent body weight, the mean stomach content weight for 30–49 cm and 50–69 cm size groups were 1.4% and 1.3% respectively. Fish ≥70 cm had the greatest mean stomach content weight (2.4% of body weight). Since gastric evacu-

TABLE 3.—Daily ration (*D.R.*) and mean stomach content weight (%BW ± SE) of Greenland halibut during each 3-h period. BW = body weight; *N* = No. of stomachs (including empty stomachs).

Size class (Temperature)	Time period	*N*	Mean stomach content weight (%BW ± SE)
30–49 cm	2400–0300	64	0.4700 ± 0.1772
(2.64°C)	0300–0600	21	0.9537 ± 0.4470
fish as prey	0600–0900	44	1.1542 ± 0.2926
a = 0.0143	0900–1200	59	1.7173 ± 0.3097
R = 0.0194	1200–1500	27	1.8937 ± 0.5661
D.R. = 0.6644	1500–1800	52	2.5844 ± 1.4731
	1800–2100	49	0.7300 ± 0.2425
squid as prey	2100–2400	34	1.9124 ± 0.3710
a = 0.0079			
R = 0.0107			$\bar{S}$ = 1.4270
D.R. = 0.3665			
50–69 cm	2400–0300	49	0.9141 ± 0.1306
(2.93°C)	0300–0600	78	1.5944 ± 0.3292
fish as prey	0600–0900	108	1.6596 ± 0.3011
a = 0.0143	0900–1200	70	1.0256 ± 0.2566
R = 0.0200	1200–1500	70	1.6406 ± 0.2736
D.R. = 0.6380	1500–1800	87	0.8967 ± 0.2340
	1800–2100	97	1.5372 ± 0.3077
squid as prey	2100–2400	111	1.3652 ± 0.2646
a = 0.0079			
R = 0.0111			$\bar{S}$ = 1.3292
D.R. = 0.3541			
≥70 cm	2400–0300	25	2.8888 ± 0.6365
(2.96°C)	0300–0600	22	2.4635 ± 0.6325
fish as prey	0600–0900	28	3.2101 ± 0.6714
a = 0.0143	0900–1200	21	1.0156 ± 0.3308
R = 0.0201	1200–1500	40	2.8228 ± 0.5439
D.R. = 1.1712	1500–1800	40	1.7294 ± 0.4454
	1800–2100	41	2.5454 ± 0.6559
	2100–2400	33	2.7468 ± 0.4782
			$\bar{S}$ = 2.4272

ation rate (R) is affected by prey type, the constant a, used to calculate R for each size group, was determined by the percentage by weight of the main prey items (fish or squid). In size group 30–49 cm, where fish constituted 72% and squid constituted 25% by weight of the diet, both a = 0.0143 (fish as prey) and a = 0.0079 (squid as prey) were used for calculating R. For size group 50–69 cm, fish constituted 47% of the diet and squid 52%, so gastric evacuation rates were also calculated by using both a = 0.0143 and a = 0.0079. For size group ≥70 cm, prey fish comprised 94% of the diet, and a = 0.0143 was used for calculating the gastric evacuation rate.

Large Greenland halibut (≥70 cm) had the highest daily ration value (1.17%), measured as percentage of body weight per day (BWD), followed by the size group 30–49 cm (0.66% BWD). The 50–59 cm size group had the lowest daily ration value, 0.64% BWD

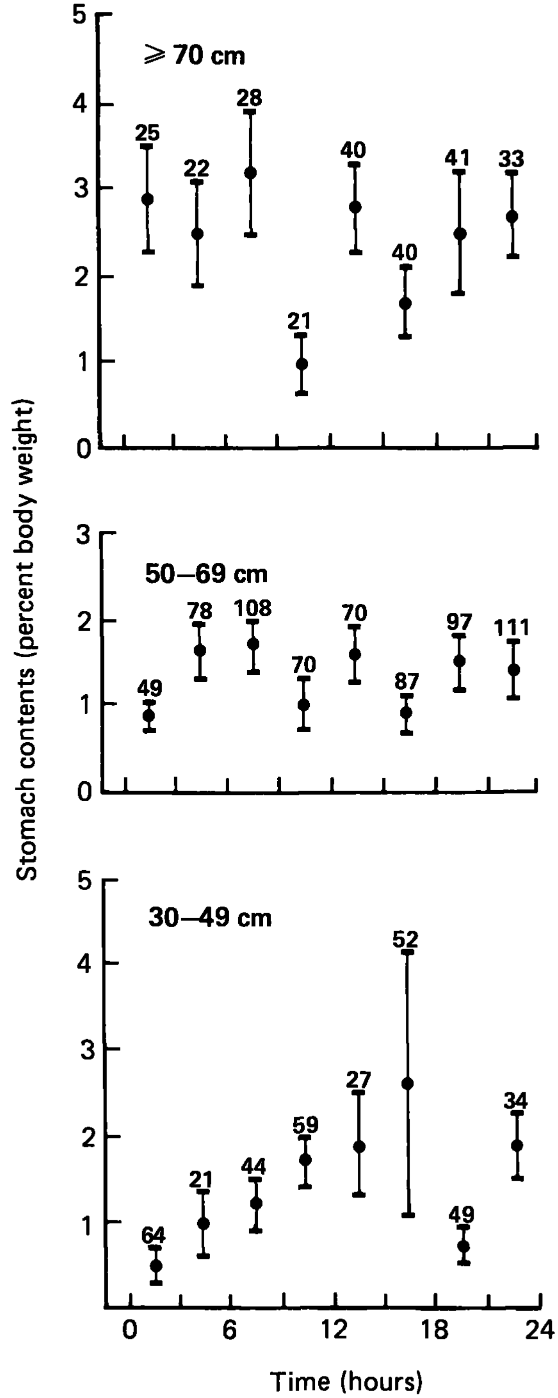

FIGURE 6.—Diel changes in mean stomach content weight (%BW ± SE) in the stomachs of three different size groups of Greenland halibut (the number above each bar was the sample size).

for fish prey and 0.35% BWD for squid prey. Since, fish and squid each constituted about one half of the stomach contents by weight in this size group, the actual daily ration lies within the range of the two values, 0.64% and 0.35%.

DISCUSSION

This study demonstrates size-dependent prey preference by Greenland halibut; halibut <20 cm fed primarily on euphausiids whereas those ≥20 cm were largely fish and squid eaters. It is not surprising to find that walleye pollock was the dominant prey (Table 1) of Greenland halibut because the estimated biomass of walleye pollock in the Bering Sea area is about 10,000,000 metric tons (Bakkala and Wespestad 1983). Livingston et al. (1985[6], 1986) noted that walleye pollock is a major food source not only for marine birds, marine mammals, and man, but also serves as a major food source for dominant components of the eastern Bering Sea groundfish complex. Other studies have also shown the importance of walleye pollock as food of Greenland halibut (Moiseev 1953; Mito 1974; Smith et al. 1978) in the eastern Bering Sea.

In this study, large Greenland halibut (≥70 cm) ate fish almost exclusively. Bowering and Lilly (1985) found that 65–69 cm was the length at which Greenland halibut in the northwestern Atlantic began to switch from smaller pelagic fish (*Mallotus villosus*) to larger groundfish (*Gadus morhua, Sebastes* sp., Anarhichadidae, Pleuronectidae, Zoarcidae) as food. Mikawa (1963) noted increased piscivory with size in Greenland halibut sampled in several areas of the North Pacific. Mito (1974) also showed the same trend; he found that 65–90 cm Greenland halibut ate 20–40 cm long walleye pollock. These observations suggest that large Greenland halibut (≥70 cm) feed on larger sized groundfish which may be lower in the water column whereas the smaller Greenland halibut (<70 cm) feed on smaller sized pelagic fish in the upper water column.

Shuntov (1970) and Mikawa (1963) noted seasonal depth migrations for Greenland halibut and interpreted the summer movement into shallower waters as a feeding migration related to migrations of walleye pollock. Based on the size distribution of walleye pollock in midwater trawl catches near the Pribilof Islands and westward over the Aleutian Basin, Livingston and Dwyer (1986) found that small (age 0) pollock occurred in near-slope and shelf areas, medium (age 1) pollock in shelf areas, while larger (>1 year old) pollock occurred in all areas during summer. Therefore, it can be concluded that in the slope area, where juvenile walleye pollock (age 0 and 1) of the appropriate size for smaller Greenland halibut were not available, the smaller sized (30–69 cm) Greenland halibut ate the available prey, cephalopods and deep-water fishes, while the larger ones (≥70 cm) consumed mostly larger walleye pollock (≥30 cm) and other fish regardless of depth or season.

No clear diel feeding trends were found. The lack of trends may be related to the large variations of the time of sunrise and sunset in different seasons in the Bering Sea. Other studies have varied findings. Mito (1974) reported that Greenland halibut fed primarily from sunset to midnight based on limited sample sizes (six specimens in some time periods). Shuntov (1970) showed that this species fed continuously in the Okhotsk Sea, although feeding was somewhat higher during the night. By comparing day and night catch rates, Chumakov (1969) concluded that Greenland halibut (in the Iceland area) made daily vertical migrations (staying close to the bottom during the day and moving up in the water column at night). However, he did not correlate this behavior with diel feeding. Thus, the literature and this study show no definite diel feeding trend in Greenland halibut.

Daily Ration

Daily ration calculations were based on the evacuation rate of one prey item (pollock or squid) using Elliott and Persson's (1978) model. Other authors (Durbin et al. 1983; Dwyer 1984) have calculated total daily ration by adding up the separate daily rations of the different prey items. Persson (1984) demonstrated that the evacuation of a specific food item can be dependent on the ingestion of other food items. Therefore, it may be erroneous to apply the food consumption model to estimate the consumption of individual prey types separately. Persson (1984) suggested that the only practical solution to calculate the daily rations of different prey items is to calculate the mean weight of each food item remaining in the digestive tract over 24 hours and multiply the fraction it constitutes of the total mean content with the total daily ration. This is necessary

[6]Livingston, P. A., M. S. Yang, and D. Wencker. 1985. The importance of juvenile pollock in the diet of key fish species in the eastern Bering Sea. Unpubl. manuscr., 19 p. Presented as the workshop on comparative biology, assessment, and management of gadoids from the North Pacific and Atlantic Oceans, 24–28 June 1985. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, Seattle, WA 98115.

since the complexity of feeding and evacuation patterns in field populations of fish makes it impossible to estimate the consumption and evacuation of different food items ingested at different times.

Bowering and Lilly (1985) estimated the consumption rate of capelin, *Mallotus villosus*, by Greenland halibut in the northwestern Atlantic, using estimates of gastric evacuation rate for Atlantic cod, *Gadus morhua*, on capelin from Minet and Perodou's (1978) study. Assuming a linear gastric evacuation model, they found the time for Greenland halibut to complete digestion of capelin at 2°–3°C was 3–5 days. By using the gastric evacuation rate calculated from this study, the time needed by large Greenland halibut (≥70 cm) to evacuate 99% of a pollock meal at 3°C was 4.2 days, a value very similar to Bowering and Lilly's (1985) estimate.

Livingston and Dwyer (1986[6]) calculated an average daily ration for arrowtooth flounder of 0.62% of body weight per day. This value is close to the daily ration values calculated from this study. Since Greenland halibut and arrowtooth flounder are ecologically and morphologically similar species, it is not surprising to find their daily ration needs are similar.

Huebner and Langton (1982) performed a gastric evacuation study on winter flounder, *Pseudopleuronectes americanus*. They used squid as food for fish 10–40 cm at 5.5°–7.0°C to get a gastric evacuation rate of 0.079/h and calculated daily ration in the range of 1.8–2.4% BWD. Compared to these values, the daily ration of Greenland halibut calculated in this study is low, possibly due to the lower temperatures in this study.

Greenland halibut ≥70 cm apparently ate a higher daily ration (1.17% of body weight per day) than did those <70 cm (0.66% and 0.64% BWD for size group 30–49 cm and 50–69 cm, respectively). Flowerdew and Grove (1979) studied the effects of body weight and meal size on gastric emptying time in the turbot, *Scophthalmus maximus*. Their results showed that large fish emptied a meal of a given size from the stomach at a faster rate than small fish, and large meals in a given fish were processed at faster rate than small meals. Dwyer (1984) also found a higher daily ration value for larger walleye pollock in the eastern Bering Sea. However, Windell (1978) stated that small fish generally consume proportionately more food per unit weight, and some studies showed this trend; Daan (1973) used a prey size dependent evacuation model and found that ration decreased with increasing fish size for North Sea Atlantic cod. Huebner and Langton (1982) calculated daily ration of winter flounder and found the largest fish (>300 g) had the smallest ration. Other studies (Elliott 1972; Hofer et al. 1982) showed that predator size and meal size have little or no effects on gastric evacuation rate. Durbin and Durbin (1980) concluded from an extensive review of daily ration studies that particle size and meal size relationships on gastric evacuation rates deserve further study. Since the ≥70 cm Greenland halibut in this study, which had the highest daily ration, also consumed much larger walleye pollock than the other predator size groups, a particle size interaction with gastric evacuation rate seems a likely avenue for further research.

[6]Livingston, P. A., and D. A. Dwyer. 1986. Food web interactions of key predatory fish with northern fur seal, *Callorhinus ursinus*, in the eastern Bering Sea during summer 1985. *In* T. R. Loughlin and P. A. Livingston (editors), Summary of joint research on the diets of northern fur seals and fish in the Bering Sea during 1985, p. 57–92. NWAFC 86-19. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115.

ACKNOWLEDGMENTS

We are grateful to Sandra Noel, Karen Conlan, and Wendy Carlson for their excellent work on the figures. Thanks also go to Doug Milward and Geoff Lang for their assistance on the stomach content analyses. We also want to thank the two reviewers for their comments on the earlier manuscript.

LITERATURE CITED

BAKKALA, R. G., AND V. G. WESPESTAD.
1983. Walleye pollock. *In* R. G. Bakkala and L. L. Low (editors), Condition of groundfish resources of the eastern Bering Sea and Aleutian Islands region in 1982, p. 1–27. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-42.

BOWERING, W. R., AND G. R. LILLY.
1985. Diet of Greenland halibut off southern Labrador and northeastern Newfoundland (Div. 2J+3K) in autumn of 1981–82, emphasizing predation on capelin. Northwest Atl. Fish. Org. SCR Doc. 85/109, Ser. No. N1085, 16 p.

CHUMAKOV, A. K.
1969. The Greenland halibut *Reinhardtius hippoglossoides* (Walbaum) in the Iceland area—the halibut fisheries and tagging. J. Ichthyol. 9:909–912. (Engl. Transl. Vopr. Ikhtiol.)

DAAN, N.
1973. A quantitative analysis of the food intake of North Sea cod, *Gadus morhua*. Neth. J. Sea Res. 6:479–517.

DURBIN, E. G., AND A. G. DURBIN.
1980. Some factors affecting gastric evacuation rates in fishes. Int. Counc. Explor. Sea C.M. 1980/L:59.

DURBIN, E. G., A. G. DURBIN, R. W. LANGTON, AND R. E. BOWMAN.
1983. Stomach contents of silver hake, *Merluccius bilinearis*, and Atlantic cod, *Gadus morhua*, and estimation of their daily rations. Fish. Bull., U.S. 81:437–454.

DWYER, D. A.
1984. Feeding habits and daily ration of walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea. M.S. Thesis, Univ. Washington, Seattle, WA, 102 p.

DWYER, D. A., K. M. BAILEY, AND P. A. LIVINGSTON.
1987. Feeding habits and daily ration of walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea, with special reference to cannibalism. Can. J. Fish. Aquat. Sci. 44:1972–1984.

ELLIOTT, J. M.
1972. Rates of gastric evacuation in brown trout, *Salmo trutta* L. Freshwater Biol. 2:1–18.

ELLIOTT, J. M., AND L. PERSSON.
1978. The estimation of daily rates of food consumption for fish. J. Anim. Ecol. 47:977–991.

FLOWERDEW, M. W., AND D. J. GROVE.
1979. Some observations on the effects of body weight, temperature, meal size and quality on gastric emptying time in the turbot, *Scophthalmus maximus* (L.) using radiography. J. Fish Biol. 14:229–238.

HALLIDAY, K., AND Y. UMEDA.
1986. Data Report: 1984 bottom trawl survey of the eastern Bering Sea continental shelf. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-108, 203 p.

HART, J. L.
1973. Pacific fishes of Canada. Bull. Fish. Res. Board Can. 180, 740 p.

HAUG, T., AND B. GULLIKSEN.
1982. Size, age, occurrence, growth, and food of Greenland halibut, *Reinhardtius hippoglossoides* (Walbaum) in coastal waters of western Spitzbergen. Sarsia 68:293–297.

HOFER, R., H. FORSTNER, AND R. RETTENWANDER.
1982. Duration of gut passage and its dependence on temperature in roach, *Rutilus rutilus* L: Laboratory and field experiments. J. Fish Biol. 20:289–299.

HUBBS, C. L., AND N. J. WILIMOVSKY.
1964. Distribution and synonymy in the Pacific Ocean, and variation, of the Greenland halibut, *Reinhardtius hippoglossoides* (Walbaum). J. Fish. Res. Board Can. 21:1129–1154.

HUEBNER, J. D., AND R. W. LANGTON.
1982. Rate of gastric evacuation for winter flounder, *Pseudopleuronectes americanus*. Can. J. Fish. Aquat. Sci. 39:356–360.

LIVINGSTON, P. A., D. A. DWYER, D. L. WENCKER, M. S. YANG, AND G. M. LANG.
1986. Trophic interactions of key fish species in the eastern Bering Sea. Int. North Pac. Fish. Comm. Bull. 47:49–65.

MIKAWA, M.
1963. Ecology of the lesser halibut, *Reinhardtius hippoglossoides* Matsuurae Jordan and Snyder. Bull. Tohoku Reg. Fish. Lab. 29:1–41.

MINET, J. P., AND J. B. PERODOU.
1978. Predation of cod, *Gadus morhua*, on capelin, *Mallotus villosus*, off eastern Newfoundland and in the Gulf of St. Lawrence. Int. Comm. Northwest Atl. Fish. Res. Bull. 13:11–20.

MITO, K.
1974. Food relationships among benthic fish populations in the Bering Sea. M.S. Thesis, Hokkaido Univ., Hokkaido, Jpn.

MOISEEV, P. A.
1953. Treska i Kambaly dalnevestochnykh morei (Cod and flounders of Far-Eastern seas). [In Russ.] Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr. 40:1–287. (Transl. by Transl. Bur. Can. Dep. Secr. State, 576 p., available as Fish. Res. Board Can. Transl. Ser. 119.)

NISKA, E. L., AND A. R. MAGILL.
1967. Occurrence of Greenland halibut and Asiatic flounder off Oregon. Fish. Comm. Oreg., Res. Brief 13:123–124.

PERSSON, L.
1984. Food evacuation and models for multiple meals in fishes. Environ. Biol. Fishes 10:305–309.

SCHMIDT, P. J.
1934. On the zoogeographical distribution of the chief marine food fishes in the western part of the North Pacific. Proc. Pac. Sci. Congr. 5:3795–3799.

SHMIDT, P. Y.
1950. Fishes of the Sea of Okhotsk. Acad. Sci. U.S.S.R. Trans. Pac. Comm., Vol. VI. (Transl. from Russian by Isarael Program for Sci. Transl., Jerusalem, 1965.)

SHUNTOV, V. P.
1970. Sezonnoe respredelenie chernogo i strlozubykh paltusov v Beringovum more (Seasonal distribution of black and arrow-tooth halibuts in the Bering Sea). [In Russ.] Tr. Vses. Nauchno-Issled. Inst. Morsk. Rybn. Khoz. Okeanogr. 70 (Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr. 72):391–401. [Transl. by Isr. Program Sci. Transl., 1972, *In* P. A. Moiseev (editor), Soviet fisheries investigations in the northeastern Pacific, Part 5, p. 397–408. Available Natl. Tech. Inf. Serv., Springfield, VA, as TT 71-501271.]

SMITH, R. L., A. C. PAULSON, AND J. R. ROSE.
1978. Food and feeding relationships in the benthic and demersal fishes of the Gulf of Alaska and Bering Sea. Final Report to NOAA RU284 OCSEAP. Inst. Mar. Sci., Univ. Alaska, p. 33–107. Vol. 1 June 1978.

VODOPOVICH, D. S., AND J. J. HOOVER.
1981. A computer program for integrated feeding ecology analyses. Bull. Mar. Sci. 31:922–925.

WESTRHEIM, S. J., AND F. T. PLETCHER.
1966. First record of the twoline eelpout *Bothrocara brunneum*, Greenland halibut, *Reinhardtius hippoglossoides*, and shortbelly rockfish, *Sebastodes jordani*, in British Columbia waters. J. Fish. Res. Board Can. 23:309–312.

WINDELL, J. T.
1978. Digestion and the daily ration of fishes. *In* S. D. Gerking (editor), Ecology of freshwater fish production, p. 159–183. John Wiley and Sons (Halsted Press), N.Y.