

STOMACH CONTENTS OF SILVER HAKE, *MERLUCCIUS BILINEARIS*, AND ATLANTIC COD, *GADUS MORHUA*, AND ESTIMATION OF THEIR DAILY RATIONS

E. G. DURBIN,¹ A. G. DURBIN,¹ R. W. LANGTON,² AND R. E. BOWMAN³

ABSTRACT

The model of Elliott and Persson was used to estimate the daily ration of silver hake, *Merluccius bilinearis*, and Atlantic cod, *Gadus morhua*, collected in the western North Atlantic between Cape Hatteras and Nova Scotia during the years 1973-76. The model required field measurements of the weight of food in the stomachs during consecutive 3-h periods over 24 h, and laboratory estimates of the exponential gastric evacuation rate. The silver hake and Atlantic cod were each grouped into two size classes for analysis (≤ 20 cm and > 20 cm, and ≤ 30 cm and > 30 cm, respectively). Upper and lower daily ration estimates were 3.2 and 2.9% body weight (BW) per day for hake ≤ 20 cm, 2.2 and 0.8% BW per day for hake > 20 cm, and 1.5 and 0.9% BW per day for cod > 30 cm. There were insufficient small cod to estimate daily ration. These ration estimates are intermediate between two previous estimates for silver hake and Atlantic cod on Georges Bank obtained by different methods.

With the increasing interest in multispecies management and total ecosystem management, it is essential to understand the role of fish predators within the ecosystem. As a part of this, it is necessary to determine the feeding habits and the daily ration of the major species. Here we estimate the daily ration of silver hake, *Merluccius bilinearis*, and Atlantic cod, *Gadus morhua*, in the northwest Atlantic, based on stomach samples collected by the Northeast Fisheries Center, National Marine Fisheries Service. The model of Elliott and Persson (1978) was used to investigate diel feeding periodicity and to estimate the daily ration, based on field measurements of stomach contents, and laboratory estimates of the exponential evacuation rate R .

METHODS

Method of Estimating Daily Food Consumption

Most recent studies have concluded that gastric evacuation is best described by a curvilinear function such as an exponential curve (Tyler 1970; Brett and Higgs 1970; Elliott 1972; Kjørboe 1978; Persson 1979; but see Jobling 1981). In an evaluation of dif-

ferent models to estimate daily ration in fishes, Elliott and Persson (1978) demonstrated that their model, which assumes exponential evacuation, provided accurate estimates of ingestion, whereas models which assumed a constant (linear) gastric evacuation rate (Bajkov 1935 and derivations thereof) significantly underestimated ingestion. Since recent comments support the validity of the exponential model for the field estimation of daily ration on the basis of stomach contents (Cochran 1979; Elliott 1979; Eggers 1979), this approach has been adopted for the present analysis.

In the Elliott and Persson model, the consumption of food (C_t) by a fish over the time interval t_0 to t_i is calculated from the amount of food in the stomach at time t_0 (S_0), the amount in the stomach at time t_i (S_i), and the instantaneous evacuation rate R :

$$C_t = \frac{(S_i - S_0 e^{-Rt}) Rt}{1 - e^{-Rt}} \quad (1)$$

To apply the model, a sample of fish is collected from the field at intervals of t hours for at least 24 h, and the mean stomach content weight is used to estimate S_0 and S_i for each time interval. The estimates of C_t calculated for each time interval t are then summed to give the total daily ration.

The model assumes that the fish feed continuously, at a constant rate, during time interval t . The cumulative amount of food consumed (C_t) therefore increases linearly during time t . However, Elliott and Persson (1978) showed that even if feeding is not

¹Graduate School of Oceanography, University of Rhode Island, Kingston, RI 02881.

²State of Maine, Department of Marine Resources, Marine Resources Laboratory, West Boothbay Harbor, ME 04575.

³Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

continuous, the estimates of C_t will not be seriously biased, provided that stomach samples are collected at intervals of 3 h or less.

The total daily ration can also be calculated in a single step from

$$C_t = 24 R \bar{S} \quad (2)$$

where \bar{S} equals the mean stomach content weight over the 24-h period (Elliott and Persson 1978). However, in order to investigate diel feeding periodicity, it is necessary to calculate ingestion during time intervals <24 h, using Equation (1). For the present analysis the 24-h day was divided into eight consecutive 3-h time periods; data collected within each of these periods were arbitrarily assigned to the midpoint of that time period. Ingestion between that time and the midpoint of the next time interval was then calculated using Equation (1), where $t = 3$ h.

In the Elliott and Persson model, R is assumed to be exponential (i.e., a constant proportion of the stomach content is evacuated per unit time), and unaffected by fish size, food size, meal size, and the frequency of feeding. R is affected by food type, however, and increases with increasing temperature, usually following an exponential or power curve. Gastric evacuation is assumed to begin immediately after the food is ingested, without an appreciable time lag.

The most appropriate values of R to be used in this analysis were determined from a literature review (Appendix 1). The general relationship between R and temperature (t) is that $R = ae^{bt}$ (Elliott 1972), where a and b are constants. The slope (b) of this relationship appears to be fairly constant for different prey types and fish species ($\bar{b} = 0.115$, App. Table 1) but the intercept (a) may change significantly according to the type of food.

For several marine fishes that were fed small prey, the relationship between R and temperature ($^{\circ}\text{C}$) was

$$R = 0.0406 e^{0.111t} \quad (3)$$

(App. Fig. 1). The data indicated that fish prey are digested more slowly than small prey types, however. This effect has not been clearly defined, but the maximum range in R that has been observed within a single fish species was in the Atlantic cod, where the exponential evacuation rate for fish flesh (based on our calculation of data from Bagge 1977) was about 10% of that for a crustacean prey, shrimp tails (Tyler 1970) (App. Fig. 1). A complicating factor is that the food particle sizes in those studies using fish as prey were much larger than in studies using other prey

types, and the effect of large particle size on the evacuation rate is poorly known. Thus we are not presently able to determine whether the reduced evacuation rates observed for fish prey are principally due to the prey type (fish flesh) or to the comparatively large particle sizes used in these studies. A further problem is that we lack information on digestive rates for many important prey species of marine fishes.

Because of these limitations to our knowledge of the rates at which different prey species are evacuated, the stomach contents of the Atlantic cod and silver hake have been grouped into two categories in the present study: "fish prey" and "all other prey." Most of the "other prey" were small organisms, and we used Equation (3) to estimate R for these prey. Because of the uncertainty concerning the value of a for fish prey, we made two estimates of R for this food type: first, where a in Equation (3) = 0.0406, and second where a was 10% of this value, i.e., $a = 0.00406$. These estimates should represent upper and lower limits to the true value of R for fish prey. The temperature for which R was calculated was the mean temperature at which each fish species and size class was collected (see Tables 1, 6, 7).

Description of the Data Set

The survey area from which stomach samples were taken extends from the offshore waters of Cape Hatteras to western Nova Scotia, and is divided into five geographic regions (Fig. 1). Stomach content data gathered during spring and fall cruises (Table 1) during the years 1973-76 were analyzed. Details of the sampling procedure and methods of stomach content analysis are given in Langton et al. (1980). Sampling continued throughout the 24-h day and was designed to provide broad coverage over a wide geographic area rather than intensive surveys within small regions. In order to define the food web, 100 stomachs (50 young-of-the-year and 50 adult fish) were to be collected per geographic region per cruise from each of 17 selected fish species. At each station no more than 10 stomachs per species were to be sampled. The same species was not to be sampled from consecutive stations unless it appeared that, because of low abundance, the desired number of fish could not be collected using the normal sampling scheme. In this case the fish were collected as needed to fill the quota for the geographic area. Young-of-the-year fish were preserved whole in 10% Formalin,⁴ after slitting the gut cavity to ensure quick penetra-

⁴Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

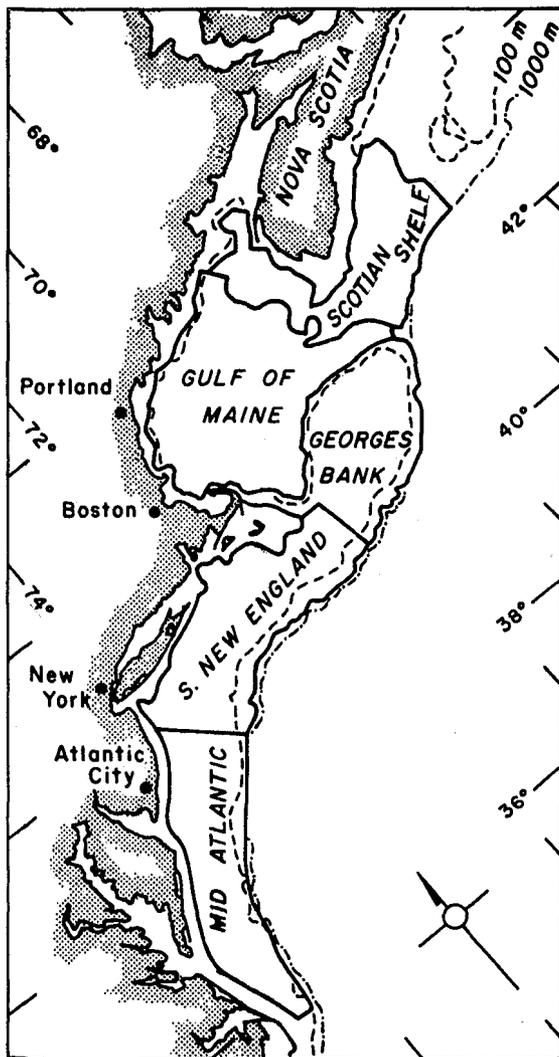


FIGURE 1.—Five geographic areas of the northwest Atlantic composing the sampling area for fish food studies.

tion by the preservative. With the larger fish the length, sex, and maturity were determined at sea, and the stomach was then removed, individually labeled, and preserved in 10% Formalin for later analysis. Fish showing signs of regurgitation (everted stomach, food present in mouth or esophagus) were not included in the samples. In the laboratory the stomach contents were identified to the lowest possible taxon and weighed (wet weight). For the present study, the weight of sand and gravel were subtracted from the total stomach content weight, and stomachs that contained recognizable food in amounts too small to be weighed (<0.01 g) were considered empty.

The weight of each fish was calculated from its total length and length-weight relationships (Wilk et al. 1978) where

$$\text{Wet wt (g)} = 0.3555 \times 10^{-5} \text{ length (mm)}^{3.1109} \\ \text{(silver hake)}$$

$$\text{Wet wt (g)} = 0.6031 \times 10^{-5} \text{ length (mm)}^{3.0979} \\ \text{(Atlantic cod).}$$

Combining all cruises, 1,159 silver hake were collected during the spring, and 1,555 during the fall; the number of fish sampled per tow averaged 8.0 and 8.6, respectively (Table 1). Silver hake were collected almost exclusively in the southern three geographic regions (Middle Atlantic, Southern New England, and Georges Bank), where a total of 2,625 fish were taken in 304 tows. Mean temperatures during spring cruises were several degrees colder than during the fall; however, the mean depth at which the fish were collected was not greatly different during the two seasons (Table 1).

In all cruises combined, 775 Atlantic cod were sampled during spring, and 922 during fall; the average number of fish sampled per tow (5.0 and 4.5, respectively) was lower than for silver hake. Atlantic cod were collected mainly from the northern three geographic regions (Georges Bank, Gulf of Maine, and Western Nova Scotia), where a total of 1,661 fish were sampled from 351 tows. The temperatures at which cod were collected in the spring were colder than those at which they were taken in the fall. Because of the more northerly distribution of the cod, they were taken from colder water temperatures than the silver hake (Table 1). The depths at which hake and cod were taken during the spring were similar (Table 1). However, during fall, the cod were found at somewhat greater depths than hake.

Because of the considerable size range of each species (Fig. 2), and changes in food habits which occurred with increasing size (discussed below), the silver hake and Atlantic cod were divided into two size-classes for further analysis: ≤ 20 cm (small) and > 20 cm (large) for hake, and ≤ 30 cm (small) and > 30 cm (large) for cod. Mean lengths and weights of each size class during spring and fall are presented in Table 2.

For the present study, the data from the four spring cruises were combined to provide a composite picture of diel changes in stomach contents of each species over the entire study area. Data from the four fall cruises were similarly combined. Possible differences in diel feeding patterns or feeding rate that may have existed in different regions or years are not

TABLE 1.—Total number of tows from which silver hake and Atlantic cod were sampled, total number of fish sampled, mean number of fish sampled per tow, and mean temperature and depth of capture. Cruise dates were: (Spring) 3/3 to 15/5 1973; 12/3 to 4/5 1974; 4/3 to 12/5 1975; 4/3 to 8/5 1976; (Fall) 26/9 to 20/11 1973; 20/9 to 14/11 1974; 15/10 to 18/11 1975; 20/10 to 23/11 1976.

	Total no. of tows	Total no. of fish sampled	No. of fish per tow \bar{x}	Temperature of capture (°C) $\bar{x} \pm 95\%$ C.L.	Depth of capture (m) $\bar{x} \pm 95\%$ C.L.
Silver hake					
Spring					
All fish	144	1,159	8.0	8.08 \pm 0.17	88.4 \pm 3.8
≤20 cm				7.63 \pm 0.23	64.1 \pm 3.7
>20 cm				8.45 \pm 0.23	108.6 \pm 5.7
Fall					
All fish	180	1,555	8.6	11.86 \pm 0.10	82.6 \pm 2.3
≤20 cm				11.94 \pm 0.15	75.5 \pm 3.2
>20 cm				11.76 \pm 0.13	90.1 \pm 3.3
Atlantic cod					
Spring					
All fish	155	775	5.0	5.76 \pm 0.16	90.3 \pm 2.9
≤30 cm				5.72 \pm 0.48	89.6 \pm 5.9
>30 cm				5.77 \pm 0.17	90.4 \pm 3.2
Fall					
All fish	204	922	4.5	9.15 \pm 0.15	104.8 \pm 3.1
≤30 cm				8.46 \pm 0.30	87.1 \pm 4.6
>30 cm				9.30 \pm 0.17	108.6 \pm 3.5

TABLE 2.—Mean length and estimated wet weight of silver hake and Atlantic cod.

	n	Total length (cm)			Wet weight (g)		
		$\bar{x} \pm 95\%$ C.L.	Minimum	Maximum	$\bar{x} \pm 95\%$ C.L.	Minimum	Maximum
Silver hake							
Overall	2,714	20.3 \pm 0.5	3	64	125.8 \pm 6.6	0.1	1,908
Spring							
Overall	1,159	23.0 \pm 0.7	3	64	156.0 \pm 11.4	0.1	1,908
≤20 cm	496	10.2 \pm 0.4	3	20	9.9 \pm 1.0	0.1	51.2
>20 cm	663	32.6 \pm 0.5	21	64	265.3 \pm 15.4	59.6	1,908
Fall							
Overall	1,555	18.3 \pm 0.6	3	55	103.3 \pm 7.5	0.1	1,191
≤20 cm	797	7.2 \pm 0.2	3	20	4.1 \pm 0.6	0.1	51.2
>20 cm	758	30.1 \pm 0.4	21	55	207.7 \pm 11.3	59.6	1,191
Atlantic cod							
Overall	1,697	53.2 \pm 1.2	4	150	2,861 \pm 170	0.6	41,649
Spring							
Overall	775	54.5 \pm 1.8	4	133	3,062 \pm 259	0.6	28,693
≤30 cm	143	18.8 \pm 1.3	4	30	104.5 \pm 16.5	0.6	285
>30 cm	632	62.6 \pm 1.5	31	133	3,732 \pm 293	315	28,693
Fall							
Overall	922	52.2 \pm 1.5	5	150	2,692 \pm 225	1.1	41,649
≤30 cm	161	17.9 \pm 1.2	5	30	90.5 \pm 13.6	1.1	285
>30 cm	761	59.5 \pm 1.4	31	150	3,243 \pm 256	315	41,649

considered; evaluation of such differences would require a separate study, with additional, more intensive field surveys designed to investigate these problems (see Pennington et al. (in press) for a discussion of the required sampling design).

As stated above, for the analysis of diel changes in stomach contents and the calculation of daily ration, data from tows within each successive 3-h period of the day were grouped together and arbitrarily assigned to the midpoint of the time period. The number of tows taken during each period is shown for each species by season and size class in Tables 6 and 7. Large silver hake and large Atlantic cod were fairly evenly sampled throughout the day. Small hake were caught in larger numbers by night, however. Small cod were few, and generally the sample sizes for each time period were very small (<10 individuals).

In order to compare mean values from different sub-

sets of the data, an F -test for the equality of variances was first performed. If the variances were not significantly different ($P < 0.05$), a Student's t -test was applied to test for the significance of the difference in the mean values of the two subsets. If the variances were unequal, Satterthwaite's approximation (Steel and Torrie 1960) was used to compute the degrees of freedom associated with the approximate t value, using a computer program which is available in the Statistical Analysis System (SAS 79) statistical package (SAS Institute, Inc.).

RESULTS

Stomach Contents

In both Atlantic cod and silver hake, the food habits and the mean amount of food in the stomachs changed with increasing fish length (Tables 3, 4). The

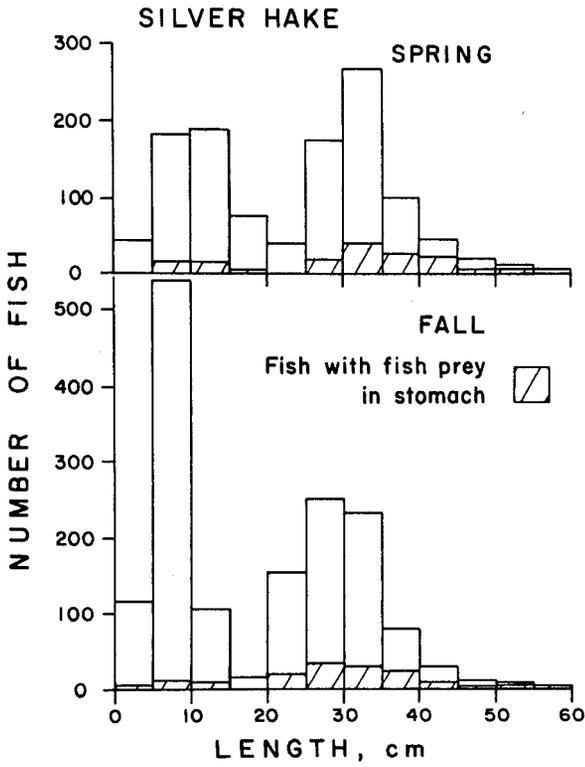
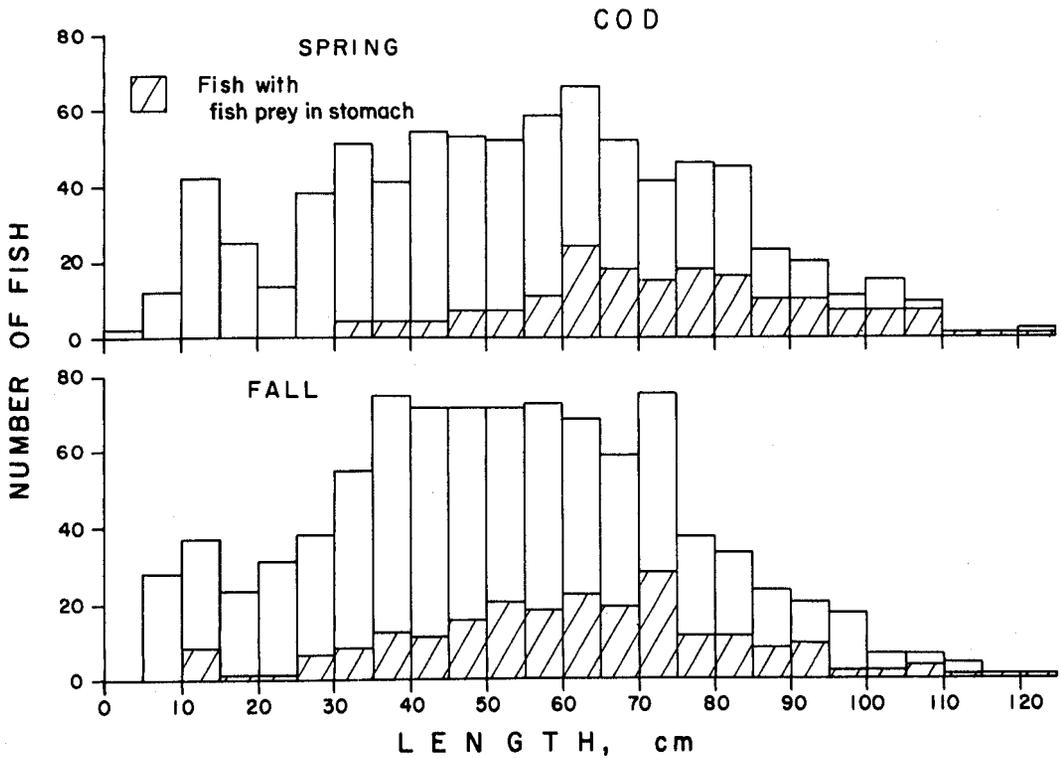


FIGURE 2.—Size-frequency distribution of silver hake and Atlantic cod collected during the spring and fall in the study area. The number of fish in each size class containing fish prey in their stomachs is also shown.



proportion of fish prey in the diet increased as the fish grew larger. This change in food habits was accompanied by an increase in the mean weight of stomach contents as a percent of body weight (Tables 3, 4). Thus, on the average, the stomachs of

large fish contained more food, as a percent of body weight, than the stomachs of small fish (see especially the mean values for fish with nonempty stomachs, last three columns in Tables 3 and 4).

In silver hake, the "other prey" category was im-

TABLE 3.—Mean weight of stomach contents of silver hake, in 10 cm length classes, during spring and fall. BW = body weight.

Size class (cm)	Total no. of fish examined (No. of empty stomachs)	Mean stomach contents of all fish, including those with empty stomachs						Stomach contents, excluding fish with empty stomachs		
		Total wet wt per fish (g)	Fish prey wt per fish (g)	Other prey wt per fish (g)	Total % BW per fish	Fish prey % BW per fish	Other prey % BW per fish	Total % BW per fish	Fish prey % BW per fish	Other prey % BW per fish
Spring										
1-10	283(79)	0.022	0.005	0.017	0.73	0.15	0.58	1.01	0.21	0.80
11-20	213(42)	0.19	0.024	0.16	0.86	0.14	0.72	1.08	0.18	0.90
21-30	264(95)	0.84	0.30	0.54	0.63	0.22	0.41	0.98	0.35	0.64
31-40	332(147)	3.15	2.19	0.95	1.00	0.67	0.33	1.79	1.20	0.59
41-50	53(18)	21.99	19.82	2.17	3.10	2.80	0.30	4.70	4.24	0.46
51-60	13(6)	24.54	24.51	0.027	2.29	2.29	0	4.26	4.25	0.00
61-70	1(1)	0	0	0	0	0	0	0	0	0
All Fish	1,159(388)	2.41	1.88 (78.0%)	0.53 (22.0%)	0.93	0.46 (49.2%)	0.47 (50.8%)	1.40	0.69 (49.3%)	0.71 (50.7%)
Fall										
1-10	697(144)	0.016	0.001	0.015	1.08	0.08	1.00	1.36	0.10	1.26
11-20	100(28)	0.17	0.046	0.12	0.92	0.19	0.73	1.28	0.27	1.01
21-30	448(218)	0.32	0.18	0.14	0.29	0.17	0.13	0.57	0.33	0.24
31-40	264(113)	2.66	2.25	0.41	0.83	0.68	0.15	1.45	1.19	0.27
41-50	38(22)	10.07	10.04	0.032	1.71	1.70	0.01	4.06	4.04	0.01
51-60	8(3)	15.84	15.80	0.047	1.59	1.58	0	2.54	2.53	0.01
61-70	0	0	0	0	0	0	0	0	0	0
All fish	1,555(528)	0.89	0.76 (85.4%)	0.13 (14.6%)	0.82	0.26 (31.4%)	0.56 (68.6%)	1.24	0.39 (31.5%)	0.84 (67.7%)

TABLE 4.—Mean weight of stomach contents of Atlantic cod, in 10 cm length classes, during spring and fall. BW = body weight.

Size class (cm)	Total no. of fish examined (No. of empty stomachs)	Mean stomach contents of all fish, including those with empty stomachs						Stomach contents, excluding fish with empty stomachs		
		Total wet wt per fish (g)	Fish prey wt per fish (g)	Other prey wt per fish (g)	Total % BW per fish	Fish prey % BW per fish	Other prey % BW per fish	Total % BW per fish	Fish prey % BW per fish	Other prey % BW per fish
Spring										
1-10	13(1)	0.0064	0	0.0064	0.59	0	0.59	0.64	0.00	0.64
11-20	71(11)	0.11	0	0.11	0.39	0	0.39	0.46	0.00	0.46
21-30	59(5)	1.15	0.0017	1.15	0.52	0	0.52	0.57	0.00	0.57
31-40	92(7)	2.63	0.28	2.35	0.57	0.07	0.50	0.61	0.07	0.54
41-50	107(6)	5.31	0.43	4.87	0.49	0.04	0.45	0.52	0.04	0.48
51-60	114(11)	13.12	0.87	12.25	0.66	0.04	0.62	0.73	0.05	0.69
61-70	110(5)	34.42	13.42	21.00	1.09	0.42	0.68	1.15	0.44	0.71
71-80	86(5)	45.52	25.38	20.14	0.90	0.50	0.40	0.96	0.53	0.43
81-90	66(1)	38.53	25.85	12.68	0.55	0.36	0.19	0.55	0.37	0.19
91-100	28(2)	99.02	58.21	40.82	0.99	0.59	0.40	1.06	0.63	0.43
101-110	23(3)	190.02	160.80	29.22	1.39	1.18	0.21	1.59	1.36	0.24
111-120	2(0)	27.30	12.70	14.60	0.13	0.06	0.07	0.13	0.06	0.07
121-130	3(0)	627.96	575.92	52.04	2.50	2.28	0.22	2.50	2.28	0.22
131-140	1(0)	658.00	658.00	0	2.29	2.29	0	2.29	2.29	0.00
All fish	775(57)	28.86	17.13 (59.4%)	11.73 (40.6%)	0.71	0.23 (32.6%)	0.48 (67.4%)	0.77	0.25 (32.5%)	0.51 (66.2%)
Fall										
1-10	35(10)	0.034	0.002	0.032	0.75	0.02	0.73	1.05	0.03	1.02
11-20	63(14)	0.095	0.008	0.087	0.28	0.04	0.24	0.36	0.05	0.31
21-30	63(9)	1.14	0.53	0.61	0.72	0.40	0.31	0.84	0.47	0.37
31-40	144(12)	2.15	0.44	1.72	0.42	0.08	0.34	0.46	0.09	0.37
41-50	149(8)	6.82	2.98	3.84	0.62	0.27	0.34	0.65	0.29	0.36
51-60	128(16)	11.96	6.75	5.22	0.64	0.37	0.27	0.73	0.42	0.31
61-70	129(14)	17.92	11.39	6.53	0.56	0.35	0.20	0.62	0.39	0.23
71-80	109(13)	23.39	16.79	6.60	0.48	0.34	0.14	0.55	0.39	0.16
81-90	49(7)	62.39	54.23	8.16	0.83	0.72	0.11	0.97	0.84	0.13
91-100	34(4)	113.95	63.65	50.30	1.08	0.61	0.46	1.22	0.69	0.53
101-110	11(3)	48.12	39.21	8.91	0.36	0.30	0.06	0.50	0.42	0.08
111-120	4(0)	399.86	96.17	303.70	2.36	0.56	1.80	2.36	0.56	1.80
121-130	3(0)	709.41	709.41	0	2.82	2.82	0	2.81	2.81	0.00
131-140	0	0	0	0	0	0	0	0	0	0
141-150	1(0)	98.02	0	98.02	0.24	0	0.24	0.24	0.00	0.24
All fish	922(110)	20.70	13.52 (65.3%)	7.17 (34.6%)	0.59	0.30 (51.4%)	0.29 (48.6%)	0.67	0.35 (52.2%)	0.33 (49.3%)

portant in the diet up to a size of about 40 cm; hake >40 cm fed almost exclusively on fish. The mean weight of "fish prey" exceeded that of "other prey" in all silver hake size classes >30 cm during spring, and >20 cm during fall (Table 3).

In contrast to silver hake, Atlantic cod in all size classes fed on "other prey" to a significant degree. Fish prey was absent from the diet of cod ≤30 cm during the spring, but was observed in all size classes in the fall (Table 4). Fish prey constituted a significant portion of the diet in cod >60 cm during spring, and >30 cm during fall, but the mean weight of fish prey did not exceed that of other prey except in cod >70 cm (spring) or >50 cm (fall).

The total weight of food as a percentage of body weight was significantly greater ($P < 0.05$) in the hake than in the cod during both the spring and the fall (Table 5). During spring, hake contained significantly more fish prey (% BW) than cod, but the amount of "other" prey was not significantly different ($P < 0.05$) (Table 5). During the fall, the amount of fish prey was not significantly different, but hake contained significantly more "other" prey than cod.

The mean stomach content weight as a percentage of body weight of the large silver hake was significantly greater ($P < 0.05$) than the small silver hake during spring, while during the fall the stomach content

weight of the small hake was greater. During both seasons, large hake contained significantly ($P < 0.05$) more fish prey than the small hake (Table 5); the large hake contained 66.2 and 77.3% fish prey as a percentage of body weight during spring and fall, respectively, and the small hake 18.7 and 8.5%, respectively.

Fish prey constituted 0 and 32.1% of the stomach contents of small Atlantic cod, and 37.4 and 55.1% of the stomach contents of large Atlantic cod during spring and fall, respectively. During spring, small cod contained a lower mean stomach content, as a percentage of body weight, than large cod (Table 5). This was due to the lack of fish prey in the diet of small cod, since the amount of food in the "other" category did not differ significantly between the two size classes. During fall, the mean stomach contents (total, fish and "other" prey) as a percentage of body weight did not differ ($P < 0.05$) between the two size classes of cod.

The mean weight of food in the stomachs of each group of fish did not exceed 1.0% BW (body weight), but the range of values observed in individual fish extended from 0 to 23.7% (Table 5). In general, the maximum observed values for the fish prey category were larger than those for the other prey category (especially in Atlantic cod). Among silver hake, the maximum values for large fish were greater than for small

TABLE 5.—Overall mean and 95% confidence limits, minimum and maximum values, and median stomach contents of the different categories of silver hake and Atlantic cod. BW = body weight.

		Stomach contents, all fish including those with empty stomachs					Stomach contents, excluding fish with empty stomachs				
		No. of fish	Mean ± 95% C.L. (% BW)	Min (% BW)	Max (% BW)	Median (% BW)	No. of fish	Mean ± 95% C.L. (% BW)	Median (% BW)		
Silver hake	≤20 cm	Spring	Total food	496	0.785 ± 0.104	0	12.86	0.439	375	1.039 ± 0.127	0.741
			Fish prey	496	0.147 ± 0.083	0	12.86	0	375	0.195 ± 0.110	0
			Other prey	496	0.638 ± 0.071	0	4.55	0.374	375	0.844 ± 0.083	0.586
	Fall	Total food	797	1.056 ± 0.094	0	10.37	0.583	625	1.348 ± 0.110	0.891	
		Fish prey	797	0.090 ± 0.046	0	10.37	0	625	0.115 ± 0.058	0	
		Other prey	797	0.966 ± 0.084	0	9.63	0.498	625	1.232 ± 0.098	0.866	
	>20 cm	Spring	Total food	663	1.044 ± 0.216	0	22.05	0.035	396	1.747 ± 0.345	0.309
			Fish prey	663	0.691 ± 0.194	0	20.07	0	396	1.157 ± 0.318	0
			Other prey	663	0.353 ± 0.106	0	22.05	0	396	0.590 ± 0.174	0.107
Fall		Total food	758	0.565 ± 0.152	0	20.08	0.005	402	1.066 ± 0.276	0.116	
		Fish prey	758	0.437 ± 0.138	0	20.08	0	402	0.825 ± 0.255	0	
		Other prey	758	0.128 ± 0.065	0	17.13	0	402	0.241 ± 0.121	0.039	
Atlantic cod	≤30 cm	Spring	Total food	143	0.462 ± 0.087	0	3.66	0.340	126	0.525 ± 0.094	0.397
			Fish prey	143	0.000 ± 0.000	0	0.00	0	126	0.000 ± 0.000	0
			Other prey	143	0.462 ± 0.087	0	3.66	0.340	126	0.525 ± 0.094	0.397
	Fall	Total food	161	0.554 ± 0.313	0	23.65	0.178	128	0.697 ± 0.390	0.270	
		Fish prey	161	0.178 ± 0.288	0	23.65	0	128	0.224 ± 0.363	0	
		Other prey	161	0.376 ± 0.133	0	9.57	0.112	128	0.473 ± 0.164	0.214	
	>30 cm	Spring	Total food	632	0.765 ± 0.097	0	9.66	0.342	592	0.817 ± 0.102	0.385
			Fish prey	632	0.266 ± 0.083	0	9.66	0	592	0.305 ± 0.088	0
			Other prey	632	0.479 ± 0.058	0	7.77	0.185	592	0.511 ± 0.081	0.209
Fall		Total food	761	0.601 ± 0.102	0	14.12	0.149	684	0.869 ± 0.113	0.201	
		Fish prey	761	0.331 ± 0.094	0	12.45	0	684	0.369 ± 0.104	0	
		Other prey	761	0.270 ± 0.042	0	7.21	0.073	684	0.300 ± 0.046	0.105	

fish, whereas no consistent pattern emerged between large and small Atlantic cod.

A significant proportion of the stomachs in the samples was empty, especially among silver hake (Tables 3, 4). Moreover, among those fish containing measurable amounts of food in their stomachs, the distribution of stomach content weight was strongly skewed towards small values. For these two reasons, the median stomach content weight was always considerably less than the mean weight (Table 5).

The mean and median stomach content weights within the entire population, which includes fish that had empty stomachs, were less than the corresponding values when only those fish containing measurable quantities of food were considered (last three columns of Tables 3 and 4; last two columns of Table 5). The differences were greater for silver hake than Atlantic cod, because of the large percentage of hake with empty stomachs. These data show that, even when the analysis is restricted to the fish that have recently fed (i.e., the fish with nonempty stomachs), the amount of food in the stomachs is, on the average, very much less than the maximum amount that the fish are physically capable of ingesting (as indicated by the maximum observed values, Table 5).

The mean stomach contents by season for each species, all sizes combined, are presented in grams and as a percentage of body weight in Tables 3 and 4. When the stomach contents are expressed in terms of weight (grams), the apparent importance of fish prey in the diet is greater than when the stomach contents are expressed as a percentage of body weight. This disparity occurs because the large, more piscivorous, fish contain a much greater weight of food in their stomachs, and have a disproportionate effect compared with the more numerous, but less piscivorous, small fish. This bias is eliminated if the stomach content weight is normalized to the weight of the fish (percent body weight) for the calculation of mean stomach contents. This also allows intercomparison of samples with different size-distributions of fish. We have, therefore, expressed the stomach content data as percent body weight for the analysis of diel changes in stomach fullness and daily ration.

Diel Changes in Stomach Contents

The diel feeding patterns of large and small silver hake appeared to differ. The weight of the stomach contents of small hake fluctuated over the 24-h day, but did not show any trends indicative of diel periodicity in feeding intensity during either spring or fall (Fig. 3). However, large hake exhibited a strong

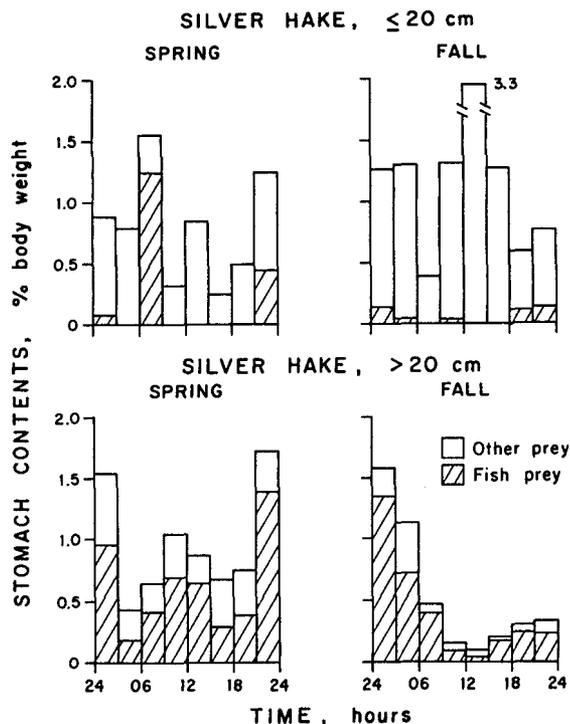


FIGURE 3.—Diel changes in "total stomach content weight," "fish prey," and "other prey" in the stomachs of small and large silver hake during spring and fall.

pattern of nocturnal feeding during the fall (Fig. 3). This pattern was less clear during spring, when comparatively large amounts of food were observed in the stomachs during the daytime. However, maximum amounts of food occurred at night, between 2100 and 0300.

Among small silver hake, the number of empty stomachs averaged 23.4% during spring over the 24-h day, with highest values observed between 1500 and 2400 (see Fig. 5). During the fall, the mean number of empty stomachs was 21.9%, with no apparent diel pattern. Among large hake, the number of empty stomachs averaged 40.4% during spring and 47.8% during fall. The percentage remained fairly constant throughout the day except for peaks between 1500 and 2100 during spring and 0900 and 1500 during fall. These peaks corresponded to the periods when the minimum mean weight of stomach content was observed (Fig. 3).

In contrast to silver hake, there were no apparent diel trends in the stomach contents of Atlantic cod (Fig. 4). The percentage of empty stomachs was lower in cod than in hake, and there was no diel pattern (Fig. 5). Among large cod, the percentage of empty stomachs over the day averaged 6.4% during spring

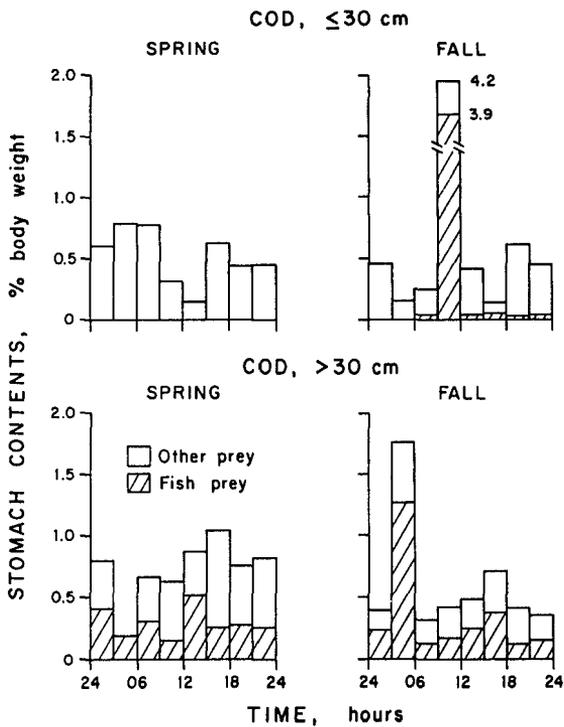


FIGURE 4.—Diel changes in “total stomach content weight,” “fish prey,” and “other prey” in the stomachs of small and large Atlantic cod during spring and fall.

and 10.2% during fall. Among small cod, the respective percentages were 10.6 and 14.7%.

Daily Ration

In order to describe the average feeding behavior of all fish in the samples, the mean stomach content weights, which included fish with empty stomachs, were used to estimate the mean feeding rate for each 3-h period during the day (Tables 6, 7). Ingestion estimates fluctuated considerably, and negative as well as positive values occurred. The negative ingestion estimates resulted when the decline in amount of food in the stomach from one period to the next was greater than predicted from the evacuation rate used in the calculation. Daily rations were obtained by summing the amount of food ingested during each 3-h period.

With the exception of small silver hake in the fall, the daily ration estimates for the two species were not greatly different: small hake, 1.82 and 4.65% BW during spring and fall, respectively; large hake, 2.40 and 1.92%; and large Atlantic cod 1.42 and 1.66% BW (Tables 6, 7). Overall, hake consumed more than large cod; the daily ration of small cod was not estimated because of the small sample size. The daily ration of small hake and large cod was higher, and of large hake was lower, during the fall than during

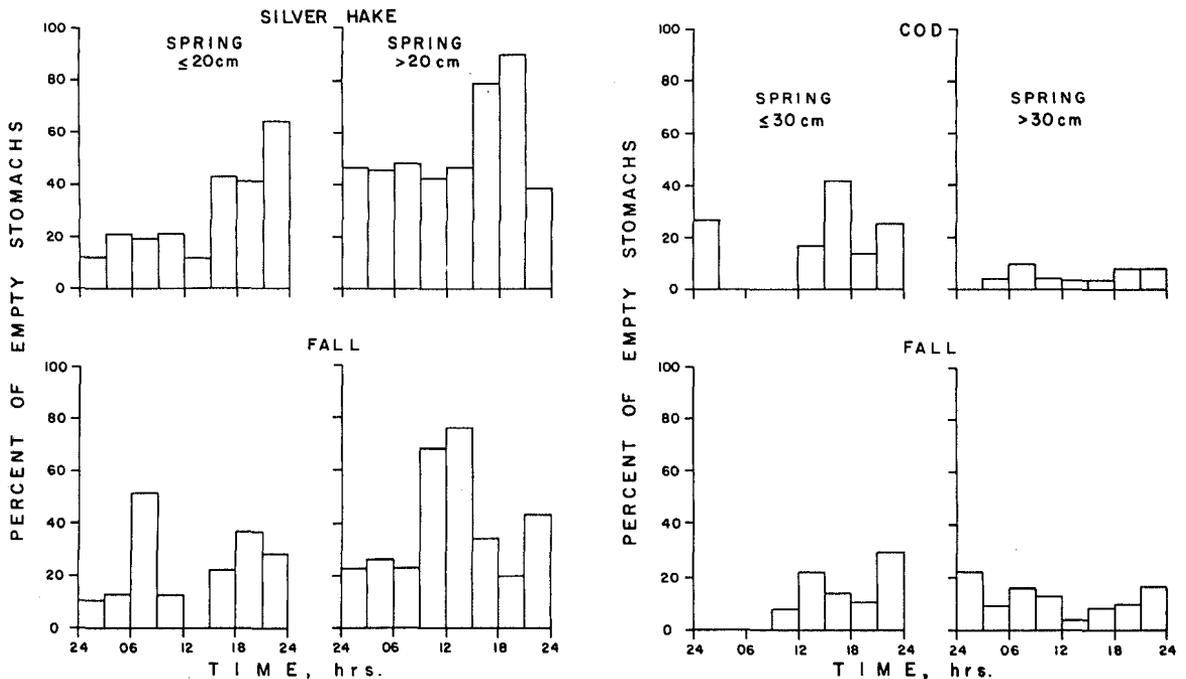


FIGURE 5.—Diel changes in the percentage of empty stomachs of silver hake and Atlantic cod collected during each 3 h time period.

TABLE 6.—Number of fish caught, amount (% BW) of food in the silver hake stomachs ($\bar{x} \pm$ standard error of mean), and estimated mean amount of food ingested during each 3-h period. BW = body weight.

Time	Total no. of fish (No. of tows)	Total food		Fish prey		Other prey		
		Stomach contents (% BW)	Ingestion (% BW)	Stomach contents (% BW)	Ingestion (% BW)	Stomach contents (% BW)	Ingestion (% BW)	
Silver hake ≤ 20 cm								
Spring								
Temp = 7.63°C R = 0.0947	24-3	136 (13)	0.888 \pm 0.079		0.083 \pm 0.024		0.805 \pm 0.078	
	3-6	101 (7)	0.795 \pm 0.093	0.145	0.009 \pm 0.007	-0.061	0.786 \pm 0.092	0.207
	6-9	36 (4)	1.557 \pm 0.400	1.101	1.252 \pm 0.412	1.430	0.305 \pm 0.078	-0.329
	9-12	14 (4)	0.325 \pm 0.135	-0.973	0 \pm 0.0	-1.083	0.325 \pm 0.135	0.110
	12-15	17 (2)	0.848 \pm 0.124	0.693	0 \pm 0.0	0	0.848 \pm 0.124	0.693
	15-18	30 (5)	0.244 \pm 0.089	-0.453	0.007 \pm 0.005	0.008	0.237 \pm 0.089	-0.481
	18-21	128 (7)	0.497 \pm 0.057	0.360	0.004 \pm 0.004	-0.001	0.493 \pm 0.056	0.361
	21-24	34 (7)	1.249 \pm 0.390	1.005	0.443 \pm 0.382	0.505	0.806 \pm 0.156	0.500
				-0.060		-0.288		0.228
			$\bar{x} = 0.800$	$\Sigma = 1.818$	$\bar{x} = 0.225$	$\Sigma = 0.510$	$\bar{x} = 0.576$	$\Sigma = 1.309$
Fall								
Temp = 11.94°C R = 0.153	24-3	145 (15)	1.262 \pm 0.116		0.143 \pm 0.062		1.118 \pm 0.095	
	3-6	204 (16)	1.299 \pm 0.106	0.625	0.046 \pm 0.033	-0.055	1.253 \pm 0.102	0.682
	6-9	35 (4)	0.385 \pm 0.105	-0.544	0 \pm 0.0	-0.036	0.385 \pm 0.105	-0.507
	9-12	31 (6)	1.309 \pm 0.183	1.329	0.030 \pm 0.030	0.037	1.278 \pm 0.187	1.290
	12-15	6 (3)	3.226 \pm 0.692	2.991	0 \pm 0.0	-0.024	3.226 \pm 0.692	3.016
	15-18	86 (8)	1.275 \pm 0.168	-0.952	0.010 \pm 0.007	0.012	1.266 \pm 0.169	-0.963
	18-21	76 (11)	0.601 \pm 0.102	-0.255	0.117 \pm 0.063	0.138	0.484 \pm 0.086	-0.394
	21-24	214 (17)	0.770 \pm 0.079	0.487	0.144 \pm 0.065	0.087	0.626 \pm 0.053	0.399
				0.967		0.065		0.901
			$\bar{x} = 1.266$	$\Sigma = 4.648$	$\bar{x} = 0.061$	$\Sigma = 0.224$	$\bar{x} = 1.205$	$\Sigma = 4.424$
Silver hake > 20 cm								
Spring								
Temp = 8.45°C R = 0.104	24-3	99 (16)	1.542 \pm 0.408		0.963 \pm 0.319		0.579 \pm 0.274	
	3-6	46 (7)	0.430 \pm 0.170	-0.813	0.179 \pm 0.153	-0.612	0.251 \pm 0.084	-0.201
	6-9	60 (11)	0.639 \pm 0.254	0.377	0.407 \pm 0.246	0.321	0.232 \pm 0.082	0.056
	9-12	92 (17)	1.043 \pm 0.300	0.670	0.693 \pm 0.275	0.460	0.350 \pm 0.141	0.210
	12-15	102 (15)	0.875 \pm 0.227	0.130	0.639 \pm 0.225	0.153	0.236 \pm 0.065	-0.024
	15-18	79 (18)	0.673 \pm 0.163	0.038	0.287 \pm 0.128	-0.210	0.366 \pm 0.113	0.248
	18-21	78 (12)	0.747 \pm 0.228	0.296	0.383 \pm 0.171	0.201	0.364 \pm 0.158	0.095
	21-24	107 (14)	1.726 \pm 0.389	1.373	1.390 \pm 0.369	1.292	0.336 \pm 0.083	0.081
				0.324		-0.083		0.388
			$\bar{x} = 0.959$	$\Sigma = 2.395$	$\bar{x} = 0.618$	$\Sigma = 1.542$	$\bar{x} = 0.342$	$\Sigma = 0.853$
Fall								
Temp = 11.76°C R = 0.150	24-3	115 (19)	1.575 \pm 0.359		1.340 \pm 0.335		0.235 \pm 0.149	
	3-6	85 (14)	1.134 \pm 0.310	0.161	0.724 \pm 0.240	-0.162	0.411 \pm 0.205	0.324
	6-9	84 (13)	0.468 \pm 0.234	-0.317	0.392 \pm 0.235	-0.086	0.076 \pm 0.023	-0.231
	9-12	71 (9)	0.144 \pm 0.070	-0.192	0.096 \pm 0.069	-0.191	0.048 \pm 0.015	-0.0006
	12-15	70 (13)	0.099 \pm 0.031	0.009	0.043 \pm 0.025	-0.023	0.055 \pm 0.020	0.030
	15-18	94 (18)	0.201 \pm 0.122	0.171	0.171 \pm 0.121	0.178	0.029 \pm 0.014	-0.007
	18-21	155 (23)	0.304 \pm 0.090	0.218	0.245 \pm 0.090	0.169	0.080 \pm 0.013	0.052
	21-24	84 (18)	0.337 \pm 0.132	0.178	0.227 \pm 0.127	0.088	0.110 \pm 0.031	0.089
				1.689		1.484		0.205
			$\bar{x} = 0.533$	$\Sigma = 1.917$	$\bar{x} = 0.405$	$\Sigma = 1.457$	$\bar{x} = 0.128$	$\Sigma = 0.461$

spring.

When the daily ration was estimated using an R value for fish prey derived from Equation (3) (Tables 6-8), then fish prey constituted 28.1 and 4.8% of the daily ration of small hake during spring and fall, respectively. In large cod, fish prey constituted 38.2 and 55.1% of the daily ration, whereas in large silver hake, fish prey constituted 64.4 and 76.0% (Tables 6-8). However, if the lower estimate of the evacuation rate for fish prey items is used in the calculation, the importance of fish prey in the diet of all groups was sharply reduced (Table 8). The effect on the total estimated daily ration was small for hake ≤ 20 cm, because this size class did not feed heavily upon fish prey. However, since large hake and large cod feed extensively upon fish prey, a change in the R value for this prey type significantly affected the total estimated daily ration (Table 8).

DISCUSSION

Application of the Elliott and Persson Model

The Elliott and Persson model was originally described for field samples collected in a restricted area from the same population over time. Present data were obtained from extensive surveys over large areas rather than intensive surveys of single populations. As applied here, the model provides a broad overview of ingestion by fish located over a very large geographic area. Resolution of this composite picture to include possible differences in fish behavior in different years or areas would have required additional intensive field surveys and was beyond the scope of the present study.

Daily ration estimates, which are based on field

TABLE 7.—Number of fish caught, amount (% BW) of food in the Atlantic cod stomachs ($\bar{x} \pm$ standard error of mean), and estimated mean amount of food ingested during each 3-h period. BW = body weight.

Time	Total no. of fish (No. of tows)	Total food		Fish prey		Other prey	
		Stomach contents (% BW)	Ingestion (% BW)	Stomach contents (% BW)	Ingestion (% BW)	Stomach contents (% BW)	Ingestion (% BW)
Atlantic cod ≤ 30 cm							
Spring							
Temp = 5.72°C	24-3	5 (2)	0.603 \pm 0.241		0 \pm 0.0		0.603 \pm 0.241
	3-6	14 (4)	0.790 \pm 0.262		0 \pm 0.0		0.790 \pm 0.262
	6-9	4 (1)	0.785 \pm 0.235		0 \pm 0.0		0.785 \pm 0.235
	9-12	24 (6)	0.316 \pm 0.042		0.001 \pm 0.001		0.314 \pm 0.041
	12-15	9 (3)	0.154 \pm 0.103		0 \pm 0.0		0.154 \pm 0.103
	15-18	7 (2)	0.635 \pm 0.282		0 \pm 0.0		0.635 \pm 0.282
	18-21	63 (10)	0.442 \pm 0.053		0 \pm 0.0		0.442 \pm 0.053
	21-24	17 (9)	0.451 \pm 0.152		0 \pm 0.0		0.451 \pm 0.152
			$\bar{x} = 0.522$		$\bar{x} = 0$		$\bar{x} = 0.522$
Fall							
Temp = 8.46°C	24-3	30 (11)	0.461 \pm 0.113		0 \pm 0.0		0.461 \pm 0.113
	3-6	6 (5)	0.151 \pm 0.076		0.006 \pm 0.006		0.145 \pm 0.076
	6-9	7 (5)	0.252 \pm 0.083		0.040 \pm 0.040		0.212 \pm 0.090
	9-12	6 (6)	4.213 \pm 3.889		3.942 \pm 3.942		0.271 \pm 0.124
	12-15	12 (7)	0.418 \pm 0.150		0.039 \pm 0.030		0.379 \pm 0.126
	15-18	24 (5)	0.140 \pm 0.044		0.053 \pm 0.026		0.087 \pm 0.038
	18-21	30 (7)	0.615 \pm 0.111		0.028 \pm 0.028		0.587 \pm 0.108
	21-24	46 (6)	0.448 \pm 0.208		0.045 \pm 0.021		0.403 \pm 0.208
			$\bar{x} = 0.837$		$\bar{x} = 0.519$		$\bar{x} = 0.318$
Atlantic cod > 30 cm							
Spring							
Temp = 5.77°C	24-3	58 (16)	0.795 \pm 0.125		0.406 \pm 0.126		0.389 \pm 0.061
R = 0.0769	3-6	64 (17)	0.575 \pm 0.089	-0.063	0.191 \pm 0.075	-0.147	0.384 \pm 0.054
	6-9	81 (18)	0.660 \pm 0.146	0.228	0.300 \pm 0.122	0.166	0.360 \pm 0.066
	9-12	116 (20)	0.628 \pm 0.086	0.116	0.147 \pm 0.066	-0.102	0.481 \pm 0.059
	12-15	88 (17)	0.865 \pm 0.168	0.410	0.509 \pm 0.170	0.439	0.356 \pm 0.052
	15-18	80 (16)	1.039 \pm 0.183	0.394	0.255 \pm 0.135	-0.167	0.784 \pm 0.134
	18-21	60 (20)	0.757 \pm 0.121	-0.076	0.270 \pm 0.087	0.076	0.487 \pm 0.100
	21-24	85 (22)	0.820 \pm 0.151	0.245	0.261 \pm 0.126	0.052	0.558 \pm 0.096
			$\bar{x} = 0.787$	$\Sigma = 1.415$	$\bar{x} = 0.292$	$\Sigma = 0.540$	$\bar{x} = 0.475$
							$\Sigma = 0.876$
Fall							
Temp = 9.30°C	24-3	91 (28)	0.398 \pm 0.087		0.234 \pm 0.084		0.164 \pm 0.032
R = 0.114	3-6	94 (24)	1.783 \pm 0.323	1.748	1.271 \pm 0.298	1.304	0.492 \pm 0.128
	6-9	103 (25)	0.314 \pm 0.060	-1.108	0.119 \pm 0.055	-0.926	0.195 \pm 0.029
	9-12	95 (24)	0.418 \pm 0.092	0.230	0.168 \pm 0.083	0.099	0.249 \pm 0.047
	12-15	111 (31)	0.483 \pm 0.085	0.220	0.245 \pm 0.070	0.148	0.238 \pm 0.050
	15-18	84 (22)	0.714 \pm 0.158	0.438	0.373 \pm 0.158	0.235	0.341 \pm 0.048
	18-21	87 (20)	0.415 \pm 0.061	-0.109	0.119 \pm 0.058	-0.172	0.296 \pm 0.034
	21-24	96 (21)	0.355 \pm 0.076	0.071	0.149 \pm 0.066	0.076	0.206 \pm 0.046
			$\bar{x} = 0.608$	$\Sigma = 1.662$	$\bar{x} = 0.335$	$\Sigma = 0.915$	$\bar{x} = 0.273$
							$\Sigma = 0.745$

TABLE 8.—Upper and lower estimates of R for fish prey, and the effect upon the estimated daily ration, where: $R_{fish, max} = 0.0406 e^{0.111t}$; $R_{fish, min} = 0.00406 e^{0.111t}$, and $R_{other} = 0.0406 e^{0.111t}$. Basic data from Tables 6 and 7. BW = body weight.

	Fish prey (% BW)	Other prey (% BW)	Total (% BW)	Fish prey % of total
Silver hake ≤ 20 cm				
Spring				
$R_{fish, max}$	0.510	1.309	1.818	28.1
$R_{fish, min}$	0.051	1.309	1.360	3.8
Fall				
$R_{fish, max}$	0.224	4.424	4.648	4.8
$R_{fish, min}$	0.022	4.424	4.446	0.5
Silver hake > 20 cm				
Spring				
$R_{fish, max}$	1.542	0.853	2.395	64.4
$R_{fish, min}$	0.154	0.853	1.007	15.3
Fall				
$R_{fish, max}$	1.457	0.461	1.917	76.0
$R_{fish, min}$	0.146	0.461	0.607	24.1
Atlantic cod > 30 cm				
Spring				
$R_{fish, max}$	0.540	0.876	1.415	38.2
$R_{fish, min}$	0.054	0.876	0.930	5.8
Fall				
$R_{fish, max}$	0.915	0.745	1.662	55.1
$R_{fish, min}$	0.092	0.745	0.837	11.0

stomach content data, require information on digestion rate of the various prey types. Equation (3) is based on maximum evacuation rates observed in the laboratory for small, easily digested food items. Evacuation rates determined from this equation should provide an upper limit to estimates of ingestion rates (Table 8). Since there are indications that fish prey may be digested more slowly, the daily ration was also estimated using the lowest observed values of evacuation rate for fish prey (Table 8). This reduced the estimate of ingestion of fish prey by a factor of 10, and provided a lower limit for the probable ingestion rates. The potential significance of this 10-fold range in the R value is well illustrated by the case of silver hake > 20 cm, where during the spring, for example, fish prey constituted 66.2% of the stomach contents by weight, yet the calculated ingestion of fish ranged from as much as 64% to as little as 15% of the diet, depending on the R value used.

This illustrates the need for additional information on the digestion rates of a variety of different prey items, particularly fish prey. If different prey types are digested at different rates, then the static picture of the food web as provided by stomach content analysis may not truly indicate the relative rates of flow of the different elements through the food web.

Food Habits and Stomach Content Weight

The food habits and stomach content weight of silver hake and Atlantic cod in the present study are in general agreement with the results of other studies (Rae 1967, 1968 a, b; Tyler 1971; Vinogradov 1972; Daan 1973; Langton and Bowman 1980).

Rae (1967, 1968a, b) provided a detailed description of the food habits of Atlantic cod in the North Sea, the Faroes, and Iceland, and Vinogradov (1972) described the food habits of silver hake in the North Atlantic. These studies are not directly comparable with the present study because they presented the diet by the frequency of occurrence of prey, not by weight. However, Rae reported that in general, fish prey were seldom eaten by cod <21 cm, but became increasingly important in the diet as the cod grew larger. Cod >50 cm fed mostly on fish. Vinogradov also found that hake became increasingly piscivorous with increasing size, and that hake >40 cm fed almost entirely on fish. These results are consistent with the present study.

Langton and Bowman (1980) have described the food habits of silver hake and Atlantic cod (>20 cm in length) that were caught during 1969-72 in the same area as the present study. Silver hake averaged 27.5 cm in length, their mean stomach content weight was 2.5 g, and the proportion of fish in the diet was 70.9% by weight. Atlantic cod averaged 54.7 cm in length, their mean stomach content weight was 27.9 g, and fish prey constituted 64.0% of the diet by weight. These are very close to our present results with hake >20 cm [mean length = 31.2 cm, mean weight of stomach contents = 2.9 g (0.79% BW), proportion of fish in the diet = 81.7% by weight], and cod >30 cm [mean length = 60.9 cm, mean weight of stomach contents = 29.6 g (0.68% BW), and mean proportion of fish in the diet = 62.3% by weight]. These results imply that no large-scale changes in the mean weight of stomach contents in the two species occurred in the study area between 1969 and 1976. Possible changes in factors such as prey species or prey size, however, are not evaluated in this report.

The weight of the stomach contents of 15-40 cm

Atlantic cod from Passamaquoddy Bay, New Brunswick, was reported by Tyler (1970: figure 7). During spring, the stomach content weights were very similar to those of 15-40 cm cod reported here. However, during late summer-fall, cod in Tyler's study generally had more food in their stomachs (usually >1% BW; range 0.4-2.7% BW) than fish in this study.

Daan (1973) investigated the food habits of Atlantic cod from the northern and southern portions of the North Sea. In general, the weights of the stomach contents of cod (divided into 10 cm size classes) in his study were considerably higher than in the present study (compare Daan's table XI with our Table 4). Daan's samples were collected principally during the daytime, but he considered that diel feeding periodicity was not significant in his study area. In addition, Daan's cod were more piscivorous than the cod collected during the present study (compare his figure 2 with our Table 4). He found that fish prey became increasingly important in the diet with increasing size of cod. These results are in agreement with the present study.

The percentage of empty stomachs observed during our study is in agreement with those reported by Tyler (1971), Daan (1973), and Langton and Bowman (1980).

Diel Changes in Stomach Contents

Edwards and Bowman (1979) and Bowman and Bowman (1980) concluded that silver hake >20 cm were principally nocturnal feeders. Results of the present study also indicate that hake >20 cm feed more intensively at night. However, the lack of significant diel changes in the stomach content weight of hake ≤20 cm indicates that these small fish may feed continuously throughout the day.

The lack of evident feeding periodicity in Atlantic cod was consistent with an extensive study by Rae (1967) and with observations by Daan (1973). Sattersdal (1967) reviewed several studies on feeding periodicity in gadoids, and also concluded that with cod, feeding may take place at any time during the night or day.

Daily Ration

Daan (1973) estimated the daily ration of Atlantic cod from the North Sea, where the mean temperature (5°-9°C) was similar to that experienced by Atlantic cod in the present study. Although these fish, on the average, contained more food in their stomachs, the estimates of the daily food intake were relatively

lower than in the present study, declining from 1.3% BW/d in a 40 cm cod to 0.8% BW/d in a 60 cm fish, to 0.5% BW/d in a 100 cm fish.

Grosslein et al. (1980) used energy budget calculations to estimate the daily ration of six major fishes (Atlantic cod, silver hake, yellowtail flounder, haddock, herring, and mackerel) in the northwest Atlantic during 1963-72. The mean daily ration of silver hake was calculated to be 1.3% BW/d; the daily ration of Atlantic cod was 0.9% BW/d. During 1963-72, the daily food consumption by hake averaged 24.2% of the total consumption by the six species; the daily ration of the cod was 3.7% of the total.

A study by Edwards and Bowman (1979) estimated the daily ration of silver hake to be 3.1% BW/d, and Atlantic cod to be 2.3% BW/d. These authors also concluded that the hake is a major consumer in the food web of the northwest Atlantic.

These daily ration estimates compare with mean upper and lower estimates of 3.2 and 2.9% BW/d for silver hake ≤ 20 cm, 2.2 and 0.8% BW/d for hake > 20 cm, and 1.5 and 0.9% BW/d for Atlantic cod > 30 cm in the present study (Table 8, assigning spring and fall estimates equal weight for the determination of mean ingestion).

Differences in the estimates of daily ration in the above studies reflect differences in the mean stomach content weight of the fish, as well as differences in the methods used to estimate daily ration. However, estimates of daily ration in silver hake were consistently found to be greater than in the Atlantic cod.

The high proportion of empty stomachs among silver hake, and the fact that the average amount of food in the stomachs of both silver hake and Atlantic cod were small, is intriguing from an ecological viewpoint. For example, the results may simply reflect the innate feeding behavior of these two predators, i.e., they feed at a modest rate even when food is plentiful and easily obtained. On the other hand, the results could mean that food is either scarce, or if abundant, difficult for the fish to locate or capture. It would be of interest, in future work, to explore the question of whether the major fish predators in the northwestern Atlantic are food limited, since this will greatly affect the importance of different predator-prey links in the food web and the intensity of competition among different fishes for food.

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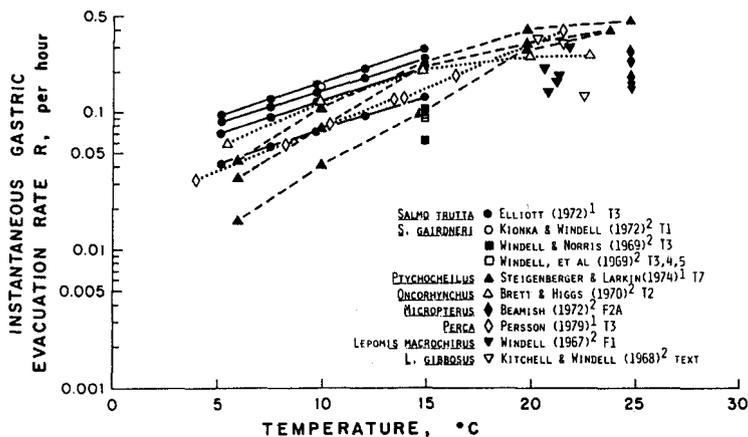
APPENDIX 1

Estimation of the Instantaneous Gastric Evacuation Rate, *R*

A number of factors may affect the instantaneous rate of gastric evacuation, *R*. These include temperature, food type, food particle size, meal size, fish size, autolysis of food in the stomach, swimming activity, prestarvation, experimental stress, experimental

error, and time lags between ingestion and the beginning of gastric evacuation.

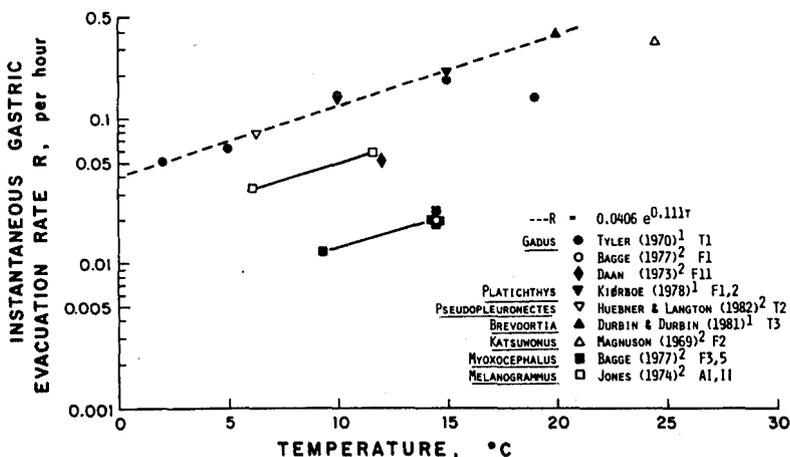
R values from the more complete studies of marine and freshwater fishes are presented as a function of temperature in Appendix Figures 1 and 2.



¹ Author's calculation of *R*.

² Our calculation of *R*, from data presented in the study and assuming evacuation is an exponential process.

APPENDIX FIGURE 1.—The relationship between the instantaneous gastric evacuation rate (*R*, per hour) and temperature in several marine fishes. Note that the body temperature of *Katsuwonus* was probably greater than that of the water temperature shown here. Dashed line and equation based on data from Tyler (1970, 2°-15°C), Kjørboe (1978), Durbin and Durbin (1981), and Huebner and Langton (1982). Source of data, where T = Table, F = Figure, and A = Appendix is shown.



¹ Author's calculation of *R*.

² Our calculation of *R*, from data presented in the study and assuming exponential evacuation.

APPENDIX FIGURE 2.—The relationship between the instantaneous gastric evacuation rate (*R*, per hour) and temperature in several freshwater fishes. Sources of data as in Appendix Figure 1.

TEMPERATURE

The gastric evacuation rate R appears to follow an exponential or power curve relationship with temperature t (Elliott 1972):

$$R = ae^{bt}. \quad (1)$$

Evacuation rates of brown trout that were fed small, rapidly digested prey (*Gammarus*, *Baetis*, Oligochaetes, chironomids), were described by the relationship

$$R = 0.053 e^{0.112t}. \quad (2)$$

In further experiments with other foods (*Protonemura*, *Hydropsyche*, *Tenebrio*) Elliott (1972) found that the intercept (a) in Equation (2) was dependent on prey type, but that the slope (b) was constant and independent of prey type. Data from other freshwater and marine fishes (within their preferred temperature range) indicate that the value of b is fairly close to that found by Elliott for the brown trout (Appendix Table 1; $\bar{b} = 0.115$). At temperatures outside the preferred range, evacuation rates were depressed (i.e., Atlantic cod at 19°C, Tyler 1970). The value of a varies widely in different studies, apparently because of the different prey types used.

The fastest evacuation rates have been reported for a variety of small food organisms. These rates, when adjusted for differences in experimental temperature, were fairly similar among several marine and freshwater fishes: Atlantic cod, fed 0.5 g chunks of shrimp (*Pandalus*) tails (Tyler 1970); the flounder *Platichthys*, fed 0.1 g polychaetes (Kjørboe 1978); winter flounder *Pseudopleuronectes*, fed 0.5-1.0 cm pieces of squid (Huebner and Langton 1982); Atlantic menhaden, fed 80 μ m diatoms (Durbin and Durbin 1981)¹; brown trout, fed 1 and 15.7 mg *Gammarus*, 0.9 and 7.8 mg *Baetis*, 0.33 and 3.3 mg chironomids, and 29 mg oligochaetes (Elliott 1972); sockeye salmon, fed small commercial pellets (Brett and Higgs 1970); pumpkinseed sunfish fed damselfly larvae (Kitchell and Windell 1968); and bluegill sunfish fed 180 mg crayfish (Windell 1967) (App. Figs. 1, 2).

The marine species ingesting these readily digested foods followed a common R -temperature relationship (App. Fig. 1):

$$R = 0.0406 e^{0.112t}. \quad (3)$$

The a and b values are similar to those observed by Elliott (1972) for the brown trout feeding on easily digested foods (0.053 and 0.112, respectively); b is also similar to the overall mean value in Appendix Table 1.

APPENDIX TABLE 1.—Slope (b) of the relationship between the instantaneous evacuation rate (R , per hour) and temperature (°C) for several freshwater and marine fishes, where: $R = ae^{bt}$. The intercept (a) varies with food type.

Species	Slope (b)	Experimental temp. range (°C)	Author
Brown trout, <i>Salmo trutta</i>	0.112	5.2-15.0	Elliott (1972) ¹
Northern squawfish, <i>Ptychocheilus oregonensis</i>	0.131	6.0-24.0	Steigenberger and Larkin (1974) ¹
Perch, <i>Perca fluviatilis</i>	0.140	4.0-21.7	Persson (1979) ¹
Cod, <i>Gadus morhua</i>	0.108	2.0-15.0	Tyler (1970) ¹
<i>Ophiocephalus punctatus</i>	0.137	2.0-28.0	Gerald (1973) ²
Haddock, <i>Melanogrammus aeglefinus</i>	0.095	6.1-11.6	Jones (1974) ²
Flounder, <i>Platichthys flesus</i>	0.081	10.0-15.0	Kjørboe (1978) ¹
$\bar{b} \pm \sigma = 0.115 \pm 0.022$			

¹Based on author's calculations of R .

²Based on our calculation of R from data in study, and assuming that evacuation is an exponential process.

FOOD TYPE

Studies have shown that there are differences in evacuation rates with different food types. While these results may reflect inherent differences in the digestibility of the food, they may also indicate an interaction between food type, particle size, and meal size. In practice, these factors may be difficult to resolve, particularly when the results of different studies are being compared.

However, certain small prey organisms were digested significantly more slowly than those cited above. This may reflect the chemical composition of the prey. For example, slower digestion of *Tenebrio* and *Hydropsyche* by bluegill and brown trout was attributed to the high fat content of these organisms (Kitchell and Windell 1968; Elliott 1972). Pure fat retards

¹Gastric evacuation rate R in menhaden was estimated from the feces elimination rate R' .

evacuation in rainbow trout (Windell et al. 1969) as well as in vertebrates other than fishes (Quigley and Meschan 1941). Artificial pelleted food, which is high in organic content, is also digested more slowly than natural food (Windell and Norris 1969; Windell et al. 1969). The degree of external protection of the prey can also affect the digestion rate. For example, rainbow trout digested the caddisfly *Arctopsyche*, and the cottid *Enophrys* digested *Calliphora* larvae, more slowly than other prey types, evidently because the integument of the prey was resistant to the penetration of the gastric juices (Reimers 1957; Western 1971). MacDonald et al. (1982) also reported that the shell in *Yoldia* retarded the evacuation rate in several marine fishes.

The lowest evacuation rates which have been observed were from fish feeding on fish flesh, usually in fairly large particle and meal sizes [Atlantic cod, fed whole 14 g sprats, meal sizes about 3.7% BW (Daan 1973), Atlantic cod, fed to satiation on 2-3 g pieces of greater weever (Bagge 1977); haddock *Melanogrammus aeglefinus*, fed saithe, 1-7% BW (Jones 1974); skipjack tuna, fed 10.2 g osmerids, 8.6% BW (Magnuson 1969); *Ophiocephalus*, fed small fish 7.9% BW (Gerald 1973); sea scorpion fed to satiation on 5 g pieces of greater weever (Bagge 1977); northern squawfish, fed small *Salmo* (Steigenberger and Larkin 1974); largemouth bass, fed 1.22 g emerald shiners, 2-8% BW (Beamish 1972) (App. Figs. 1, 2)]. These reductions in R may be significant: for example, with Atlantic cod and sea scorpion, the instantaneous evacuation rates for fish flesh were only about one-tenth those predicted by Equation (3) for easily digested foods.

Whether these reduced evacuation rates were due primarily to the food type (fish), or to the large particle sizes, compared with those of the small prey which were digested more rapidly, cannot be determined from the data.

Additionally, in a few studies, after several food types were tested individually and found to have similar evacuation rates, meals composed of mixtures of these food types were given (Windell 1967; Elliott 1972). The evacuation rate of the mixed meal was not significantly different from that of the individual food types. However, evacuation rate of mixed meals containing food types which have individually different R values does not appear to have been investigated.

FOOD PARTICLE SIZE

The exponential model predicts that the evacuation rate, R , depends only on the weight of food in the

stomach, i.e., $dW/dt = -RW$. Thus R should be independent of food particle size. A meal of a given weight, composed of a number of small particles, should be evacuated at the same rate as a meal of equal weight, but composed of a single large particle. However, if digestion occurs at the surface of particles, then the surface area as well as the weight or volume of the food may influence digestion. A surface-area dependent model predicts that small particles should be digested more rapidly than large particles because of their greater surface area per unit volume, i.e., $dW/dt = -RW^{2/3}$.

Few studies have considered the effect of particle size on R .

Elliott (1972) found no effect of food particle size on the gastric evacuation rates of brown trout fed small invertebrates. However, the particle sizes tested were quite small and may have been below some critical size which has a measurable effect on R .

The evacuation rates of Atlantic cod that were fed whole fish or large pieces of fish flesh (Daan 1973; Bagge 1977) were lower than those of Atlantic cod fed small pieces of shrimp (Tyler 1970). However, it is not clear whether this difference is an effect of food particle size or food type.

Swenson and Smith (1973) examined gastric evacuation of walleye and sauger fed 0.8, 1.1-1.9, and 3.1-5.0 g minnows. The two smallest size classes were evacuated at a significantly faster rate than the 3.1-5.0 g fish. However, the difference between the evacuation rates was small, and the different food particle sizes therefore did not have a major effect on the evacuation rate.

MEAL SIZE

Experimental data on the effect of meal size on the gastric evacuation rate is conflicting.

The exponential model predicts that gastric evacuation is not affected by meal size. Studies using small prey as the food have confirmed this prediction: Brown trout, fed 0.06-0.5% BW meals of *Gammarus* and 0.35-1.4% BW of *Tenebrio* (Elliott 1972); pumpkinseed sunfish, fed 1.2 and 2.7% BW of damselfly naiads (Kitchell and Windell 1968); Atlantic cod fed 0.25-0.78% BW on shrimp tails (Tyler 1970); flounder, fed variable meal sizes of polychaetes (Kjørboe 1978); and Atlantic menhaden, fed 0.7-7.0% BW on the diatom *Ditylum* (Durbin and Durbin 1981). Some studies using fish flesh as the food also indicated that meal size did not affect R : Sea scorpion, fed 5.5-11.1% BW on greater weever (Bagge 1977); skipjack tuna, fed various meal sizes averaging 8.6% BW on fish (Magnuson 1969).

However, some authors have suggested that in their studies (where fish flesh was the food), evacuation was slower for large meals than for small (Steigenberger and Larkin 1974; Jones 1974). These authors found that significant time lags, on the order of hours, elapsed between ingestion and the onset of gastric evacuation. Similar lags have been reported by other investigators who used fish as the prey type (Daan 1973; Gerald 1973). Some question therefore remains as to whether meal size had a direct effect on R in these studies, or whether the primary effect of increasing meal size was to cause a progressive increase in the time lag before the onset of gastric evacuation.

EFFECT OF MULTIPLE MEALS

Most digestion rate studies have examined stomach evacuation rates following a single meal. However, in nature most fish do not normally feed in this manner, but rather feed on a more or less continuous, or a periodic, basis. In this situation the time for food to pass through the stomach and the relation between the amount of food in the stomach and evacuation rates will be more complex.

Elliott (1972) fed brown trout three meals, 6 h apart. He then determined the stomach contents 4 h after the last meal. This amount was in good agreement with that calculated from the exponential model, and Elliott concluded that multiple meals, and the presence of food already in the stomach, did not affect R or the exponential model of gastric evacuation.

Tyler (1970) fed Atlantic cod three meals, 24 h

apart at 5°C. He too used an exponential model to predict the amount of food remaining in the stomach after the third meal. The actual amount was slightly, but significantly, lower (by about 7%) than the predicted. He concluded that, overall, the fit was adequate.

In the studies of Kiørboe (1978) and Huebner and Langton (1982), individual fish were fed a number of meals in sequence. Although the data showed a significant degree of variability, reflecting differences in the voluntary food intake of the fish, the mean values followed a common exponential relationship, which implies that multiple meals did not affect R .

CONCLUSIONS

In summarizing this brief discussion, several conclusions can be drawn:

- 1) The exponential model of gastric evacuation provides a good fit to most experimental data, and also provides good estimates of ingestion rate when used in the Elliott and Persson (1978) model.
- 2) The two factors which are known to most strongly influence the instantaneous gastric evacuation rate R are temperature and food type. Multiple meals do not affect the value of R . The available evidence indicates that particle size and meal size probably do not affect R (at least with small prey items), but these questions need further investigation.
- 3) The slopes (b) of the R -temperature relationships among several marine and freshwater fishes were similar, although the intercepts (a) varied according to the type of food.