

FOOD HABITS OF YELLOWTAIL FLOUNDER, *LIMANDA FERRUGINEA* (STORER), FROM OFF THE NORTHEASTERN UNITED STATES

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ABSTRACT

Stomachs of 1,021 yellowtail flounder caught in 1973-76 contained primarily polychaetes (43%) and crustaceans (18%) as a percentage weight of total contents. The most important prey were *Spiophanes bombyx* (9.68%) and *Unciola* sp. (13.65%). Predator size had little effect on diet composition whereas geographic distribution did. *Spiophanes bombyx* was three times more important as prey on Georges Bank than in southern New England, and amphipods were more important in southern New England than on Georges Bank. From the middle Atlantic to southern New England to Georges Bank the total weight of stomach contents increased from 0.12% to 0.14% to 0.21% of the fishes' body weight. Year-to-year differences were inconsistent; however, fish stomachs from spring cruises contained more food, 0.20%, than those from autumn cruises, 0.14% body weight. During a composite 24-hour day, peak stomach content weight occurred in the afternoon to early evening. Polychaetes accounted for less of the stomach contents at night while amphipods increased in importance during the night. Sex of the fish had no effect on diet composition although the stomachs of females were fuller than males, 0.15% vs. 0.11% body weight. Neither diet composition nor the percentage of empty stomachs were related to gonadal maturity stages, but stomachs from spawning fish contained the least amount of prey, 0.06%, while resting-stage fish contained the most, 0.24% body weight. Over a 12°C temperature range there was little change in diet composition, but between 3° and 8°C a greater percentage of stomachs contained prey and a larger quantity of prey than between 9° and 15°C. Over a 220 m depth range the stomach content weight increased with depth for smaller fish (<15 cm), while the percentage of empty stomachs increased for larger fish (>21 cm). Diet composition showed the greatest effect of depth with *S. bombyx* dominating the diet in the 74-110 m depth zone (26.6% of the stomach content weight) and *Cragon septemspinosus*, also being dominant in a single depth zone, comprising 39.6% of the diet at 147-183 m.

The yellowtail flounder, *Limanda ferruginea* (Storer), is a right-handed, thin-bodied flounder that occurs along the eastern seaboard of North America from Labrador to Chesapeake Bay (Bigelow and Schroeder 1953; Royce et al. 1959). It has contributed significantly to the total flatfish catch, primarily from southern New England and Georges Bank, since about 1935 (Royce et al. 1959; Sissenwine et al. 1978²). Biological information has been summarized by Bigelow and Schroeder (1953) and updated by Lux and Livingston (in press). These summaries qualitatively describe the diet as consisting of small crustaceans, worms, and molluscs. Quantitative work

on the diet is limited. Inshore yellowtail flounder have been examined by Libey and Cole (1979) off Cape Ann in Massachusetts while Efanov and Vinogradov (1973) surveyed the offshore feeding pattern of yellowtail flounder in southern New England and on Georges Bank. Langton (1979³), Grosslein et al. (1980), and Langton and Bowman (1981) described the diet of fish from the middle Atlantic to western Nova Scotia, and Pitt (1976) conducted a study on the Grand Banks. These papers generally agree that crustaceans, particularly amphipods, and polychaetes are major prey items. However, the absolute quantities of prey in the stomachs differ, being influenced by both biological and abiotic factors. Only one of the studies lists the stomach contents by predator size (Pitt 1976) and none of the studies evaluate comprehensively all factors influencing the diet

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²Sissenwine, M. P., B. E. Brown, and M. M. McBride. 1978. Yellowtail flounder (*Limanda ferruginea*): Status of the stocks, January 1978. Northeast Fisheries Center Woods Hole Laboratory Reference No. 78-02, 27 p.

³Langton, R. W. 1979. Food of yellowtail flounder, *Limanda ferruginea* (Storer). International Council for Exploration of the Sea. C.M. 1979/G:54, 10 p.

of this predator. The purpose of the present paper is to describe the stomach contents of yellowtail flounder and quantitatively evaluate factors influencing the quantity and composition of the animal's stomach contents.

METHODS

Yellowtail flounder stomachs were collected on eight bottom trawl survey cruises conducted from 1973 through 1976. The dates of the cruises are as follows: 16 March-15 May 1973; 26 September-20 November 1973; 12 March-4 May 1974; 20 September-14 November 1974; 4 March-12 May 1975; 15 October-18 November 1975; 4 March-8 May 1976; 20 October-23 November 1976. Fish collections were made from the RV *Albatross IV* or RV *Delaware II*, using a #36 Yankee otter trawl for autumn surveys and a #41 Yankee otter trawl for spring surveys. A scheme of stratified random sampling was carried out in the continental shelf waters between Nova Scotia and Cape Hatteras, N.C. For survey purposes this region has been divided into five geographic areas, which are further subdivided into depth strata as depicted in Clark and Brown (1977) and described by Grosslein (1969⁴).

Yellowtail flounder were selected from the catch in, primarily, two of the five geographic areas, i.e., southern New England and Georges Bank which include the three major fishing grounds and major yellowtail flounder stocks in U.S. waters (Lux 1963). Stomachs were labelled according to vessel, cruise, station, length, sex, and sexual maturity and were preserved individually in a gauze wrapping in 10% Formalin⁵. The sampling strategy was designed to collect fish, more or less at random, from the population without bias towards a specific length, except as described below. We attempted to collect 50 fish per geographic area per cruise for fish both above and below 12 cm TL (total length). Twelve centimeters in length approximates the length of 1- to 2-yr-old fish, and these smaller fish were preserved intact after the body cavity was cut open to insure fixation of the contents.

In the laboratory, individual stomachs were opened, and the contents emptied onto a fine mesh screen and rinsed with seawater. The vari-

ous items were sorted and identified to the lowest possible taxa. Each distinct group was blotted dry and immediately weighed. In the text and tables these weights have been expressed as a percentage of the total weight of stomach contents. In the text these percentages are often given in brackets after the mention of taxa to quantify their relative importance.

Twelve percent of the fish collected fell into the three smallest size classes (Table 1) with a mean length of 7.6 cm. Fish >15 cm TL were equally distributed around the 31-35 cm size class with 70% ($n = 715$) of all fish examined falling between 26 and 40 cm TL. The average length of all fish comprising this peak is 32.8 cm. For some analyses two size-related groupings of fish, representative of this bimodal distribution, have been differentiated while in other cases the data are presented by 5 cm length classes or expressed as a percentage of the fishes' body weight according to the length/weight equation in Wilk et al. (1978). [$W = aL^b$ where $a = 0.4514^{-5}$, $b = 3.1257$, and L is in millimeters.]

RESULTS

Food

Of the 1,021 stomachs examined, 684 contained prey which weighed in total 422 g. The overall mean fish length and standard deviation was 29.4 ± 10.5 cm. The prey were allocated into 148 different categories, which included all taxonomic levels of identification and such miscellaneous categories as sand and unidentifiable animal remains. The most important major taxonomic groupings were polychaetes and crustaceans (Table 1).

Polychaetes accounted for 43% of the stomach contents. The families Spionidae (13.27%), Lumbrinereidae (1.90%), Sabellidae (1.42%), and Nephtyidae (1.19%) were all of some importance. *Spiophanes bombyx* was the major prey, making up 9.68% of the weight of the total stomach contents. Other polychaetes (17.24%) and polychaete tubes (7.94%) accounted for the remainder of the prey in this taxon.

Crustaceans (18.0%) were second in importance, the amphipods (13.65%) being the major prey group. *Unciola* sp. (4.41%), *Leptocheirus pinguis* (2.25%), and *Byblis serrata* (1.72%) were important amphipod prey. Other gammarids (1.92%), ampeliscids (1.56%), and corophiids (0.3%) made up most of the remaining amphipod

⁴Grosslein, M. E. 1969. Groundfish survey methods. Northeast Fisheries Center Woods Hole Laboratory Reference No. 69-2, 34 p.

⁵Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Principal items in stomachs of yellowtail flounder, *Limanda ferruginea*, by 5 cm length classes. Data are expressed as a percentage of the total weight of stomach contents (+ indicates present but <0.01%).

Stomach contents	Fish length intervals in centimeters										
	1-5	6-10	11-15	16-20	21-25	26-30	31-35	36-40	41-45	46-50	51-55
Anthozoa						1.09	0.69	4.24	8.10	3.69	9.71
Other Cnidaria								0.01			
<i>Spiophanes bombyx</i>		11.74			5.82	0.93	10.28	11.97	11.99	11.06	
Spionidae					0.60	1.77	2.71	4.91	9.80		
Sabellidae					2.02	0.97	3.34	0.88	0.16		
Annelida tubes						1.01	4.46	12.12	9.16	14.35	
Lumbrineridae					0.54	3.05	3.49	1.05	0.11	2.22	
Nephtyidae				+	0.54	0.28	2.80	0.92	0.23	0.39	
Other polychaetes		10.82	11.91	13.64	29.19	23.35	21.83	14.51	16.46	12.26	0.33
<i>Byblis serrata</i>		1.73		2.02	0.59	1.24	1.24	2.35	2.50	2.34	0.03
Other Ampeliscidae		14.71	0.79	1.81	0.71	2.45	2.25	1.40	0.54	0.92	
<i>Unciola</i> sp.	+	2.22	3.64	15.28	12.86	12.03	5.36	3.44	0.26	0.60	
Other Corophiidae		4.02	3.31	0.93	0.33	1.34	0.32	0.07		0.01	
Gammaridae	+	3.77	4.96	1.47	1.61	4.21	2.14	1.35	2.79	0.12	
<i>Leptocheirus pinguis</i>	+			8.51	4.77	3.81	1.92	3.11	1.96		
Other Amphipoda		6.24	0.93	1.43	1.27	2.55	1.03	1.53	0.18	3.87	
<i>Crangon septemspinosa</i>	41.38	9.09	11.98		3.25	7.14	2.53	0.71	0.01		
<i>Dichelopandalus leptocerus</i>			31.83			0.64	1.96	0.66	0.09		
Other crustaceans	58.62	19.16	4.37	19.28	6.94	2.32	1.96	0.72	10.65	0.16	
Animal remains	+	15.39	7.28	28.42	24.46	19.30	16.09	15.47		36.79	0.59
Sand		0.93	0.60	1.81	10.19	8.22	10.22	17.34	23.02	10.30	88.45
Other groups	+	0.19	18.40	5.39	0.31	2.28	3.38	1.25	1.99	0.93	0.88
Number examined	39	77	21	23	63	187	337	191	60	18	2
Number empty	22	25	6	9	16	63	108	62	20	4	0
Mean weight per stomach (g)	0.0001	0.021	0.072	0.103	0.230	0.242	0.375	0.563	0.950	2.445	9.652
Mean length (cm)	4.0	8.3	12.0	18.1	23.4	28.3	32.7	37.7	42.3	47.5	51.0

prey. Only two other crustaceans were of significance in the yellowtail flounder's diet, namely, the shrimps *Crangon septemspinosa* (1.89%) and *Dichelopandalus leptocerus* (0.94%).

All other taxonomically distinct groups contributed only 4.96% of the weight of stomach contents. Unidentifiable animal remains (17.18%) and sand (16.92%) accounted for the remainder of the total weight of stomach contents.

Size-Related Feeding Habits

Amphipods were the most important prey for the smaller yellowtail flounder although stomachs from every size class of fish contained amphipods (Table 1). Polychaetes comprise a greater percentage of the stomach contents of the larger fish but, like amphipods, they occur in stomachs from most every size class. The occurrence of anthozoans in the larger size fish (>26 cm) might reflect a tendency for larger yellowtail flounder to be selecting "wormlike" prey.

Geographic Comparison

Composition of the diet of yellowtail flounder in southern New England and on Georges Bank was similar, with polychaetes and amphipods accounting for 50 to 70% of the total weight of stomach contents in both areas (Table 2). Polychaetes were the major prey in both regions with

TABLE 2.—Principal items in stomachs of yellowtail flounder, *Limanda ferruginea*, by geographic area in the northwest Atlantic. Data are presented as a percentage of the total weight of stomach contents (+ indicates present but <0.01%).

Stomach contents	Middle Atlantic	Southern New England	Georges Bank
Anthozoa		1.93	3.52
Other Cnidaria		0.01	
<i>Spiophanes bombyx</i>		4.35	13.18
Spionidae		4.41	3.12
Sabellidae		3.30	0.25
Annelida tubes	5.47	7.53	8.24
Lumbrineridae	+	2.57	1.50
Nephtyidae		2.66	0.28
Other polychaetes	9.80	22.74	13.89
<i>Byblis serrata</i>	8.15	2.18	1.34
Other Ampeliscidae	1.55	2.44	1.01
<i>Unciola</i> sp.	1.50	7.01	2.81
Other Corophiidae	5.36	0.36	0.19
Gammaridae	0.77	2.25	1.72
<i>Leptocheirus pinguis</i>	4.38	3.25	1.58
Other Amphipoda	0.54	1.38	1.58
<i>Crangon septemspinosa</i>		2.16	1.75
<i>Dichelopandalus leptocerus</i>		1.90	0.35
Other crustaceans		1.82	1.34
Animal remains	41.57	15.53	17.85
Sand	20.09	7.75	22.65
Other groups	0.83	2.46	1.86
No. fish examined	16	502	502
No. empty stomachs	4	163	169
Mean weight per stomach ±SD (g)	0.242±0.324	0.323±0.578	0.512±1.452
Mean length ±SD (cm)	28.2±8.2	29.2±9.2	29.7±11.7

Spiophanes bombyx being the most important species identified. On Georges Bank *S. bombyx* was three times more important as prey than in

southern New England. The other major difference between areas was in the quantity of other polychaetes, but a large percentage of this group was unidentified remains (12.93% in southern New England and 11.61% on Georges Bank). The diversity of polychaete prey was very similar in the two areas; 27 families of polychaetes in the stomach contents of fish from southern New England and 24 different families on Georges Bank. Eleven different genera of polychaetes were identified in each area. Six of these were common to both regions, but only *Spiophanes* contributed >1% to the total stomach contents weight.

Amphipods made up almost twice the percentage of the weight of stomach contents in southern New England than on Georges Bank (18.87% vs. 10.23%). The same species were important in both areas (Table 2). There was, however, a slightly greater reliance on *Unciola* sp. and *Leptocheirus pinguis* in southern New England than on Georges Bank. The diversity of amphipod prey was greater on Georges Bank, 16 genera as opposed to 11 genera, although yellowtail flounder from the two areas preyed on 9 of the same genera.

Crustaceans such as *C. septemspinosa* and *D. leptoceurus* played a minor role in the diet of yellowtail flounder as did all other arthropod groups except the amphipods. The only other category of stomach contents that differed substantially between areas was the quantity of sand in the stomachs. This might be related to the heavy predation on *S. bomyx* on Georges Bank, since this polychaete is reported to prefer a fine sand substrate (Light 1978).

The percentage of empty stomachs was virtually the same in southern New England and on Georges Bank, but was less in the Middle Atlantic (Table 2). The mean weight per stomach increased from the Middle Atlantic to Georges Bank and the mean fish length also increased from south to north (Table 2). This size difference did not counterbalance the increase in stomach content weight. The mean weight of stomach contents ranged from 0.12% in the Middle Atlantic to 0.14% in southern New England and 0.21% body weight on Georges Bank.

Yearly, Seasonal, and Diurnal Variation

Data were collected over a 4-yr period in both the spring and autumn and throughout the day-night cycle. It is, therefore, possible to examine the influence of the time of capture on the com-

position of the diet as well as on changes in the absolute quantity of prey in the stomachs.

On a year-to-year basis, polychaete worms were always the most important prey, between 36 and 44% of the diet, followed by amphipod crustaceans, 10 to 33% of the diet. Within these two taxa the actual percentage composition of the various groups fluctuated, but no systematic changes in diet were discernible. Within the Polychaeta, for example, *S. bomyx* made up between 2 and 12% of the diet from 1973 to 1974 and ranged from 9 to 11% between 1975 and 1976, respectively. At the family level, Spionidae, the range increased from 2 to 16% for the first 2 yr and 9 to 18% for the latter 2 yr. When spionids were most important, there was also a very large percentage of sand in the stomachs, 20 and 27% for 1974 and 1976, respectively, which probably relates to predation on these particular polychaetes. Among the amphipods, *Unciola* sp. showed the greatest fluctuation, ranging from 16% of the diet in 1973 to 1% in 1975 but increasing to just under 5% in 1976.

The mean weight of prey showed an increase from 1973 to 1976, but when this was corrected for fish size, there was no pattern evident in these changes. The slightly larger mean fish lengths occurring in 1975 and 1976 counterbalanced the increase in the mean weight of stomach contents. The percentage of empty stomachs also showed no consistent yearly change, fluctuating around the overall mean value of 33%.

Species composition of the diet showed no drastic shift between spring and autumn. Polychaetes were more important in the spring (49%) than in the autumn (35%), and the same was true for amphipods, 19% vs. 13%. Both of the changes may, however, simply reflect the higher percentages of unidentified animal remains and sand in the fish stomachs collected in the autumn.

In all years, except 1976, stomachs collected on spring cruises contained a greater mean weight of prey than stomachs from fish collected in the autumn. Although the mean length of fish in the spring was only slightly larger (30.0 cm vs. 28.8 cm). The 4-yr mean weight of prey in the stomachs was 0.505 g (0.20% body weight) for the spring and 0.298 g (0.14% body weight) in the autumn. The percentage of empty stomachs was also lower in the spring than the autumn; 22.7% of the 574 stomachs examined from spring cruises versus 46.3% of 447 stomachs examined from autumn cruises.

An examination of the data for a composite 24-h day revealed a diurnal feeding pattern.

Although there was a certain degree of hour-to-hour variability, a peak in the weight of stomach contents occurred during the afternoon-early evening period (Fig. 1). In Figure 1 the day has been divided into four periods—dawn (0300-0800 h), day (0900-1400 h), dusk (1500-2000 h), and night (2100-0200 h)—which accounts for seasonally variable day length in the dawn and dusk period. Despite a seasonal change in day length, the composition of the diet also changed over a 24-h period. Polychaetes were less important prey during the night than during any of the other three time periods. They dropped from values ranging from 41-47% to 24% as a percentage of the weight of stomach contents. Conversely, crustaceans, amphipods in particular, were more important at night (values ranging from 15 to 23% vs. 34%). Unidentifiable animal remains also accounted for their smallest percentage of the diet (13.0%) in the dusk period when the fish stomachs were fullest. The greatest percentage of empty yellowtail flounder stomachs was found during the night (46%) and the smallest (19%) during the day with intermediate levels occurring at dawn (34%) and dusk (26%).

To evaluate whether the diurnal feeding pattern shown in Figure 1 is statistically significant, an analysis of variance, including time of day and seasonal factors, was conducted. The results of this analysis are given in Table 3 for transformed data using an inverse hyperbolic sine transformation ($Y' = \sin h^{-1}(\sqrt{Y})$) to account for the extreme skewness of the data (i.e., a large number of empty and almost empty stomachs) (see Bartlett 1947). Both time of day and season are significant factors in determining the weight of stomach contents for yellowtail flounder. This analysis confirms that there are statistically significant differences in stomach content weight over a 24-h period. These results are, however, influenced by the level of interaction between time of day and season, such that it is not clear which of these two factors is the most important

TABLE 3.—Analysis of variance of the weight of stomach contents for yellowtail flounder, expressed as percent body weight, for time of day and season. See text for details.

Source	df	Sum of squares	F
Time of day	3	0.03376	14.59*
Season	1	0.02464	31.93*
Interaction	3	0.00894	3.86*
Error	1,011	0.78005	

*Significant, $P = 0.05$.

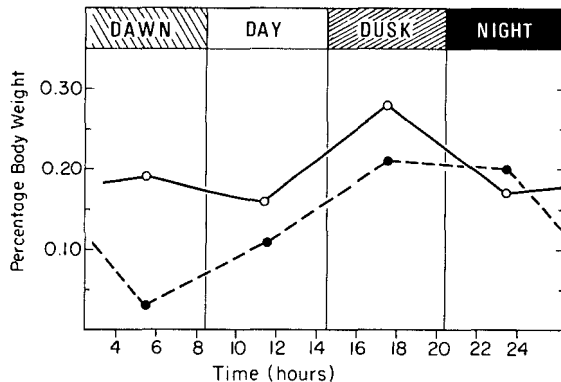


FIGURE 1.—Weight of stomach contents, as a percentage of the body weight, for yellowtail flounder collected during the spring (open circles) and autumn (solid circles) over a composite 24-h day from 1973 through 1976. Data points are 6-h weighted averages for the periods identified in the figure as dawn, day, dusk, and night.

in determining the shape of the curve for the weight of stomach contents over the composite 24-h period. Further study specifically evaluating the effects of time and season on stomach content weight is warranted.

Determining what influence size might have on the feeding periodicity of yellowtail flounder is difficult because of the small number of samples when the data are distributed among both size classes and time. To distinguish between mature and immature fish the data were divided into two size classes, 0-15 cm and 21-49 cm fish, which accounts for the bimodal distribution of fish collected for stomach content analysis (see section on Methods). For the 1-15 cm fish the sample sizes were small and unevenly distributed, and no conclusions can be made as to feeding periodicity. However, 66% of these smaller fish were caught at night and an additional 24% were caught during the dawn period. In contrast, the 21-49 cm fish were taken both day and night in much more equal proportions. Only 30% of the catch was taken at night and 20% was caught during the daytime period. The feeding periodicity of these larger fish is adequately represented by the data in Figure 1. There was a gradual increase in the mean weight of stomach contents from dawn to a peak in the dusk period. The major influence of the smaller, 1-15 cm, fish is that they have relatively more in their stomachs which increases the overall mean in the night period when the numbers of juveniles caught was at a maximum.

Sexual and Maturity Stage Influences

Of 1,021 fish examined for stomach content analysis, 376 were males, 466 females, and 179 were not sexed. Females were slightly larger than males, mean length of 34.4 ± 6.3 vs. 31.8 ± 5.1 cm, respectively, and contained a larger mean quantity of prey in their stomachs, 0.57 ± 1.37 g (0.15% body weight) vs. 0.32 ± 0.76 g (0.11% body weight). Females also had a lower percentage of empty stomachs, 29% vs. 36%, than males. The 179 fish that were not sexed were small and presumably immature with a mean length of 11.7 ± 8.9 cm and mean weight of stomach contents of 0.203 ± 0.83 g.

When the sex of a fish was determined, the maturity stage of the gonads was evaluated subjectively. A percentage of the fish examined were not classified as to their state of sexual maturity and another group, those <15 cm, was routinely classified as immature. The remainder of the fish were classified as either resting, developing, ripe and/or spawning, or spent. Although the average size of individuals in these last four categories was quite similar, there was a substantial difference in the mean weight per stomach. Spawning fish had the least amount of prey in their stomachs, mean = 0.21 g (0.06% body weight), while developing-stage fish contained the most, mean = 0.58 g (0.16% body weight) although on a percentage body-weight basis resting-stage fish contained a larger quantity of prey in their stomachs than developing-stage fish (0.24% vs. 0.16%). The percentage of empty stomachs and the actual composition of the diet showed no pattern to the fluctuation in values which was related to the maturity stage of the gonads.

Physical Factors

Temperature, over the 12°C range in which yellowtail flounders were caught, had no apparent effect on diet composition. In contrast, although the data are variable, the stomach content weights appeared to vary with temperature. The weight was higher at the lower temperatures, with one exception. In the range from 3° to 8°C the stomach content weight ranged from 0.13 to 0.26% body weight. Between 9° and 15°C the range was greater, 0.05 to 0.65%. However, exclusion of the 13°C value of 0.65% reduced the high point of the range to 0.14%. The percentage of empty stomachs was also related to tempera-

ture. Between 3° and 8°C the percentage of empty stomachs averaged 23%, while between 9° and 15°C it averaged 37%. The ranges for these averages were 14-27% and 19-79%, respectively. The value of 79% occurred at the 15°C point, and this may be the result of temperature inhibition of feeding even though 24 fish were collected at this water temperature. Perhaps a more typical range estimate is 19 to 55% with the 55% empty stomachs being recorded at 12°C from a sample size of 118 fish.

To evaluate the relationship between temperature and fish size, the yellowtail flounder data were divided into two size groups, fish between 1 and 15 cm and 21 through 49 cm. For the small size class, fish were collected at temperatures between 4° and 15°C. More fish were collected in the 4° through 7°C temperature range (no samples from 8°C) than the 9° through 15°C range, 80 vs. 51, respectively. Fish from this lower range were also, on the average, larger (9.3 cm vs. 5.3 cm TL) and had a greater quantity of prey in their stomachs, 0.51% vs. 0.35% body weight. Fish in the 21-49 cm size group were also collected in slightly larger numbers, 426 vs. 373, in the lower temperature range. They were slightly larger fish, mean length of 33.6 cm vs. 32.5 cm and the mean weight of stomach contents was greater, 0.15% vs. 0.08% body weight, respectively.

Yellowtail flounder were caught in depths ranging from shallow water to 220 m. To evaluate the influence of depth on the stomach content data the data were divided into 37 m depth intervals. The majority of fish (68%) was taken from waters 38 to 73 m deep with an additional 23% of the fish taken from the next depth category, 74-110 m. The average size of fish and the percentage of empty stomachs fluctuated haphazardly over the depth class groupings. The relation between fish size and depth was further investigated by dividing the data into two size class groupings, 1-15 cm and 21-49 cm. A total of 147 fish fell into the smaller size range and, as with the grouped data, most fish (92%) were caught between 38 and 110 m although the maximum depth from which the smaller fish were taken was only 146 m. There was no obvious relationship between depth and size for these small fish or even for depth and the percentage of empty stomachs. The stomach content weight did, however, increase with depth from 0.28% at 38-73 m, to 1.29% body weight at 111-146 m. For fish in the 21-49 cm group, the major difference from the smaller fish is that the percentage of

empty stomachs showed an increase from 18 to 56% over depth ranges 0-37 m to 111-146 m. At the deepest depth, 147-220 m, the sample sizes were too small (<8 fish) to evaluate this factor. The stomach content weight values were highest at the shallowest depth, 0.28% body weight, but did not systematically decrease with depth.

Certain prey were more prevalent in the stomachs of the yellowtail flounder at different depths. The polychaete *S. bombyx* accounted for 26.6% of the diet of fish in the 74-110 m range and only 9.3 and 2.9% of the stomach content weights for fish in the next lowest and highest depth range, respectively. *Spiophanes* did not occur in stomachs of yellowtail flounder collected outside 38 and 146 m. *Crangon septemspinosa* also predominated in only one depth group, 39.6% of the diet at 147-183 m, although it did occur in stomachs at all depths <147 m. There was no pattern to the occurrence of other prey species in stomachs of yellowtail flounder which could be related to depth.

DISCUSSION

Predator size was of little importance to the diet composition of yellowtail flounder when considering the entire study area. For all sizes of fish, polychaete worms and amphipod crustaceans were the primary prey, although amphipods were somewhat more important for small fish and polychaetes more important for larger fish. Pitt (1976) also observed relatively few changes in diet composition for different-sized yellowtail flounder on the Grand Bank. Size does, however, have an obvious influence on the absolute amount of food in the stomachs with an increase in mean weight of stomach contents increasing with fish size (Table 1).

Predator size also had an observable effect on several other factors which were reflected by differences in the stomach contents. Perhaps the most interesting size (diet?)-related observation is that the majority (66%) of the smaller fish, <15 cm long, were caught at night while the larger fish (21 to 49 cm) were caught both day and night in much more equal proportions. Since the fish were taken at random from the catch, this is likely to be indicative of a behavioral difference between the small and large yellowtail flounder. This same catch pattern has been observed before. Beamish (1966) found a significantly larger catch of small yellowtail flounder (<22.5 cm) at night than during the day, while studying verti-

cal migration by demersal fishes. This difference in catch was not found for the larger fish. Beamish (1966) attributed his results to visual conditions where small yellowtail flounder could escape through the net more easily during the day than at night. Larval yellowtail flounder, however, show strong diel movements and rise towards the surface at night (Smith et al. 1978). It may be that the juvenile yellowtail flounder continue to demonstrate some nocturnal activity, with a resultant increase in vulnerability to the trawl, and this behavior pattern decreases slowly with an increase in fish size. In any event, the larval fish do not appear to be migrating solely for the purpose of feeding (Smith et al. 1978), and the data presented here are inconclusive about any feeding periodicity for these smaller yellowtail flounder. A complete understanding of the factors controlling this size-related difference in catchability, and any relationship that this has to feeding, will have to await further study.

Data on feeding periodicity may be interpreted to suggest that yellowtail flounder are daytime feeders with a peak in food consumption in the afternoon-early evening hours (Fig. 1). However, it is quite likely that the fish are feeding throughout the day, and the stomach contents accumulate at a faster rate than they are digested, resulting in the dusk period stomach content weight maximum followed by the peak in the percentage of empty stomachs at night. In European waters the yellowtail flounder's congener, *Limanda limanda*, has been observed to feed during the day (Arntz 1971). This daytime feeding pattern is consistent throughout the year with the only difference being that there is more food in the stomachs during the spring than in the autumn (compare with Figure 1). Changes in diet composition were also observed which may support the argument that yellowtail flounders are daytime feeders. Polychaetes are less and amphipods more important as prey at night. This shift may simply be the result of a differential digestion rate for these two prey types. The soft-bodied polychaetes would presumably digest more quickly than the crustacean body parts. Studies on digestion and prey selection are needed to understand fully these observed changes in stomach content weight.

Seasonal effects on diet include the difference in the absolute amount of food in stomachs between spring and fall (Fig. 1) and differences related to the reproductive cycle. Yellowtail flounder spawn from March to July with the peak

LITERATURE CITED

usually occurring in mid-May (Lux and Livingston in press). Prior to spawning the gonad goes through various stages of development which were evaluated in relation to the fishes' diet. Spawning fish were found to contain the least amount of prey in the stomachs, which is consistent with Libey and Cole's (1979) observations on feeding intensity related to spawning, and fish with resting-stage and developing gonads contained the greatest quantity of prey. These later two stages were usually observed in late autumn or on spring survey cruises and are reflected in the larger values of the mean weight of stomach contents in the spring. In contrast to the yellowtail flounder's congener, *L. limanda*, there were no seasonal or reproductive stage influences on the actual composition of the diet (Arntz 1971).

The major difference in diet over the geographic range of this study was the change in the mean weight of stomach contents from the Middle Atlantic through southern New England onto Georges Bank. There was, for example, a 75% increase (0.12 to 0.21% body weight) in the relative mean weight of stomach contents from the Middle Atlantic to Georges Bank. This same pattern was observed by Efanov and Vinogradov (1973), who noted that yellowtail flounder feed more intensively on Georges Bank than in southern New England.

In summary, the yellowtail flounder is a benthic predator occurring, for the most part, in depths of 38 to 110 m and at temperatures ranging from 3° to 15°C. All size classes and both sexes of yellowtail flounder prey heavily on polychaetes and amphipods throughout the year and over their entire geographic range. Yellowtail flounder feed more intensively in the spring, prior to spawning, than in the fall. They also feed more intensively on Georges Bank than in other geographic areas and are daytime feeders with a peak in the stomach content weight occurring in the late afternoon to early evening.

ACKNOWLEDGMENTS

Numerous people helped in the collection and stomach content analysis described herein. In particular, I want to thank Edward Brown-Leger, Ray Bowman, Jacqueline Murray, and Barbara North for their assistance and persistence in overcoming the problem in establishing and maintaining an extensive data collection system; Clem Walton for reviewing the paper; and Pat Hoyt for typing the manuscript.

- ARNTZ, W. E.
1971. Die Nahrung der Kliesche (*Limanda limanda* [L.] in der Kieler Bucht. Ber. Dtsch. wiss. Komm. Meeresforsch. Neue Folge 22:129-183.
- BARTLETT, M. S.
1947. The use of transformations. *Biometrics* 3:39-52.
- BEAMISH, F. W. H.
1966. Vertical migration by demersal fish in the Northwest Atlantic. *J. Fish. Res. Board Can.* 23:109-139.
- BIGELOW, H. B., AND W. C. SCHROEDER.
1953. Fishes of the Gulf of Maine. U.S. Fish Wildl. Serv., Fish. Bull. 53, 577 p.
- CLARK, S. H., AND B. E. BROWN.
1977. Changes in biomass of finfishes and squids from the Gulf of Maine to Cape Hatteras, 1963-75, as determined from research vessel survey data. *Fish. Bull.*, U.S. 75:1-21.
- EFANOV, V. N., AND V. I. VINOGRADOV.
1973. Feeding patterns of yellowtail of two New England stocks. *Int. Comm. Northwest Atl. Fish., Redb. Part III*, p. 75-77.
- GROSSLEIN, M. D.
1969. Groundfish survey program at BCF Woods Hole. *Commer. Fish. Rev.* 31(8-9):22-35.
- GROSSLEIN, M. D., R. W. LANGTON, AND M. P. SISSEWINNE.
1980. Recent fluctuations in pelagic fish stocks of the northwest Atlantic, Georges Bank region, in relation to species interactions. *Rapp. P.-V. Réun. Cons. Int. Explor. Mer* 177:374-404.
- LANGTON, R. W., AND R. E. BOWMAN.
1981. Food of eight northwest Atlantic pleuronectiform fishes. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-749, 16 p.
- LIBEY, G. S., AND C. F. COLE.
1979. Food habits of yellowtail flounder, *Limanda ferruginea* (Storer). *J. Fish Biol.* 15:371-374.
- LIGHT, W. J.
1978. Spionidae: *Polychaeta annelida*. Boxwood Press, Pacific Grove, Calif., 211 p.
- LUX, F. E.
1963. Identification of New England yellowtail flounder groups. U.S. Fish. Wildl. Serv., Fish. Bull. 63:1-10.
- LUX, F. E., AND R. LIVINGSTON, JR.
In press. Yellowtail flounder, *Limanda ferruginea*. MESA N.Y. Bight Atlas 15.
- PITT, T. K.
1976. Food of yellowtail flounder on the Grand Bank and a comparison with American plaice. *Int. Comm. Northwest Atl. Fish. Res. Bull.* 12:23-27.
- ROYCE, W. F., R. J. BULLER, AND E. D. PREMETS.
1959. Decline of the yellowtail flounder (*Limanda ferruginea*) off New England. U.S. Fish. Wildl. Serv., Fish. Bull. 59:169-267.
- SMITH, W. G., J. D. SIBUNKA, AND A. WELLS.
1978. Diel movements of larval yellowtail flounder, *Limanda ferruginea*, determined from discrete depth sampling. *Fish. Bull.*, U.S. 76:167-178.
- WILK, S. S., W. W. MORSE, AND D. E. RALPH.
1978. Length-weight relationships of fishes collected in the New York Bight. *Bull. N.J. Acad. Sci.* 28:58-64.