ASSIMILATION EFFICIENCY AND NITROGEN EXCRETION OF A FILTER-FEEDING PLANKTIVORE, THE ATLANTIC MENHADEN, *BREVOORTIA TYRANNUS* (PISCES: CLUPEIDAE)

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ABSTRACT

Experiments were carried out at 20° C with adult Atlantic menhaden, *Brevoortia tyrannus*, to follow the time course of changes in feces elimination rate, assimilation efficiency, nitrogen excretion rate, and oxygen:nitrogen ratios during and after a 7-hour period of feeding on the diatom *Ditylum brightwelli*. Assimilation efficiency for wild zooplankton dominated by *Acartia tonsa* is also reported.

The elimination of a meal was exponential (mean = 0.366/hour) and thus meals of different size reached the same stage of digestion at the same time. Changes in stomach contents and evacuation rates with time were calculated using the model of Elliott and Persson. These corresponded closely with observed changes in feces elimination rates following a meal. Assimilation, as indicated by the patterns of nitrogen excretion, and the elimination of a meal were rapid: 50% of the exogenous nitrogen excretion occurred within 1 or 2 hours after 50% of the meal was ingested; 50% of the feces were eliminated within a mean of 5.7 hours after the midpoint of feeding.

Mean carbon, nitrogen, and caloric assimilation efficiencies for *D. brightwelli* were 86.4, 92.4, and 89.5%; for zooplankton these were 86.7, 91.3, and 87.7%, respectively. Assimilation efficiencies decreased when fecal elimination rates declined below 0.3 mg dry weight/g dry weight per hour. This resulted in lower assimilation at the beginning and end of each experiment, and a slight decrease in the overall assimilation efficiency in low ration experiments, where the fecal elimination rates were also low.

Nitrogen excretion consisted of 69.6% ammonia and 30.4% dissolved organic nitrogen. The mean excretion rate of fish unfed for 36 hours (10.72 μg nitrogen/g dry weight per hour) increased as much as 17-fold when the fish were digesting and assimilating the food. Exogenous nitrogen excretion was a constant proportion of the ingested and the assimilated rations (61.6 and 65.5%, respectively).

Oxygen:nitrogen ratios indicated that Atlantic menhaden use protein as a metabolic fuel at all times. The mean oxygen:nitrogen (28.2) of fish unfed for 36 hours decreased to values as low as 5.0 during feeding.

In the development of an energy budget for fish it is necessary to determine the proportion of the ingested ration which is lost in the feces and the excretory products. The remainder represents physiologically useful energy available for growth and metabolism.

Here we examine digestion rates, assimilation efficiency, nitrogen excretion rates, and oxygen:nitrogen (O:N) ratios of adult Atlantic menhaden, *Brevoortia tyrannus*, a filter-feeding planktivore. Since Atlantic menhaden normally feed for a prolonged period each day, the experiments were designed to permit observations on the fish before, during, and after a 7-h feeding period during which food was made available at a constant rate. This study is part of a larger effort to determine the energy budget of Atlantic menhaden in Narragansett Bay, R.I.

METHODS

All experiments were carried out on a school of 12 Atlantic menhaden, with a mean wet weight of 302 g, dry weight of 101 g, and fork length of 26 cm. Experiments were carried out during 26 July-9 September 1977 at a temperature of 20.0 ± 1.0° C and a salinity of 31‰. Details of the procedures used for maintenance of the fish and for carrying out the experiments are given in Durbin et al. (1981).

Before an experiment the tank was thoroughly cleaned and the inflowing water was filtered through a GAF[2] polypropylene bag filter of nominal 5 μm pore size. The fish were deprived of food for 36 h to eliminate the remains of the previous meal. The experiment began with a measurement of the excretion rate of the unfed fish between 0600

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and 0800 h. Plankton was then siphoned into the tank at a constant rate over a 7-h period from about 0800 to 1500 h. At intervals prior to, during, and for about 20 h after the feeding period, respiration rates and voluntary swimming speeds were measured (Durbin et al. 1981), and samples of the tank water were collected for determination of ammonia and dissolved organic nitrogen (DON) excretion rates. Feces were periodically siphoned from the tank during the feeding period and for 41 h thereafter for the determination of assimilation efficiency. The tank was briefly flushed with filtered seawater at the end of the feeding period to reduce the ammonia concentration. Control measurements on the tank and tank water with and without plankton, demonstrated that these did not measurably effect ammonia or dissolved oxygen concentrations during the experiments.

Seven experiments were carried out using cultures of the solitary diatom *Ditylum brightwelli*, and three using Narragansett Bay zooplankton consisting mainly of adult *Acartia tonsa* and a small number of unidentified crab zoeas. Details of the culturing and processing of the *D. brightwelli* during experiments are given in Durbin et al. (1981). Narragansett Bay zooplankton were collected with 0.5 m diameter, 300 μm mesh nets on the day before an experiment and maintained alive in 1.2 m diameter tanks overnight.

During each experiment the plankton was concentrated into seven equal batches of about 18 l. Each batch was then siphoned into the tank over a 1-h period, providing an approximately constant input of food over the 7-h period without greatly changing the volume of the tank (1,400 l). Each batch of phytoplankton was subsampled for determination of C and N (Durbin et al. 1981). Each hourly batch of zooplankton was concentrated onto a 100 μm mesh and weighed just before use. A subsample of this was removed for determination of the dry weight:wet weight ratio, C and N content (Hewlett-Packard Model 185B CHN Analyzer), ash (combustion at 475° C for 4 h), caloric (Parr adiabatic bomb calorimeter), and chitin (Windell 1966) content. The remaining sample was dispersed in about 18 l of water and siphoned into the tank. By changing the concentration of plankton in the batches, we obtained different concentrations of food in the tank and different ration sizes. Turbulence produced by the swimming of the fish kept the water and plankton in the tank well mixed at all times.

Feces settled to the bottom of the tank, and were collected at 1-6 h intervals depending on the rate at which they were eliminated. Feces were gently siphoned into a plastic bucket and allowed to settle; the water was then aspirated off, and the feces were briefly rinsed with a little distilled water and transferred to preweighed aluminum dishes. Fecal pellets formed cohesive, cylindrical rods; the loss of material during collection and concentration was nominal. These dishes were then freeze-dried and reweighed to determine the dry weight of the feces. Each sample of feces was subsequently analyzed for carbon and nitrogen (3 replicates), ash (4-8 replicates), and calories (4 replicates). Each sample of feces from the phytoplankton experiments was also analyzed in triplicate for particulate silicon (Durbin 1977).

Samples for dissolved nitrogen analysis were siphoned from the tank into a clean, acid washed container, and then filtered through prerinsed glass fiber filters. The sampling interval was 1-4 h, depending on the excretion rate. All determinations were carried out in triplicate.

Ammonia determinations were carried out immediately with a modification of the method of Solorzano (1969), using 10 ml samples which were incubated in the dark for 4 h for color development. The range of values for 3 replicates was <0.1 μM of ammonia.

Total dissolved nitrogen was determined using the alkaline persulphate method of D'Elia et al. (1977). Nitrate formed during digestion of the samples was determined using a Technicon AutoAnalyzer II. At the same time, nitrate, nitrite, and ammonia concentrations were also determined on noncombusted subsamples using the AutoAnalyzer. These concentrations were subtracted from the total dissolved nitrogen determined from the persulphate digestion to give a measure of DON. Ammonia concentrations of the samples which had been frozen were always very similar to the concentrations determined from fresh samples immediately after collection. The range of values for three replicates of each measurement of total dissolved N was ≤ 0.5 μM N.

Excretion rates of the nonfeeding fish were low, and thus changes in total dissolved nitrogen concentration in the tank water were small. Although the ammonia excretion rate could always be satisfactorily determined, the greater errors inherent in the DON determination made it impossible to accurately measure DON excretion except during and soon after feeding, when the N excretion rates were high. During feeding the increase in NH_3

and DON concentrations in the tank was approximately linear, and linear regressions were calculated to estimate the excretion rates. The ratio of the DON:NH_3 regression slopes was similar in all experiments (overall means $\Delta DON/\Delta NH_3$ = 0.437, σ = 0.088). We assumed that this average value would provide the best estimate of DON excretion in both feeding and nonfeeding fish, and therefore multiplied the observed NH_3-N excretion rates by 0.437 to calculate DON-N excretion.

The Atlantic menhaden did not excrete any measurable quantities of nitrate, nitrite, or dissolved silicon. The latter was measured because of the large amounts of particulate silicon in the phytoplankton used as food. Nitrate, nitrite, and silicate were determined in triplicate on selected samples using methods described in Strickland and Parsons (1972).

Assimilation efficiency was calculated in two ways: by calculating the overall assimilation efficiency of C, N, and calories, and by following the time course of changes in the assimilation efficiency during each experiment. Both methods were based on the assumption that all of the feces were quantitatively collected.

The overall assimilation of C, N, or calories was determined by subtracting the total amount of each of these constituents that remained in the feces, from the amount in the food for each experiment. The C assimilation efficiency (percent), for example, was calculated:

$$\text{C assimilation} = \frac{C_{food} - C_{feces}}{C_{food}}(100). \quad (1)$$

In the second method, assimilation was calculated separately for each sample of feces. Since silicon (Si) was not absorbed by the fish, the Si content of each sample of feces was used to calculate the quantity of food (C, N, calories) which corresponded to each fecal sample. This was done by using the C:Si, N:Si, and calories:Si ratios of the food for each experiment, which were calculated from the measurements of the C, N, and calories in the food, and the total Si content of the feces. The assimilation efficiency was then determined in a manner analagous to Equation (1), using the back-calculated amount of C, N, and calories in the food which corresponded to each fecal sample, and the actual amount of C, N, and calories remaining in the sample.

The assumptions that all of the feces were collected quantitatively, and that Si was not absorbed by the fish, were verified in a phytoplankton experiment in which Si was used as a tracer. Subsamples of the phytoplankton were centrifuged and the Si content of the freeze-dried pellets then determined. This gave an estimate of 1.87 g for the total Si in the ration, which was very similar to that actually collected in the feces, 1.98 g.

A small but unknown amount of seawater remained interstitially within the pellets of both the phytoplankton and the feces, the salt content of which may have contributed to the estimates of ash content (Table 1). Because of this it was not possible to use ash content as a tracer to calculate assimilation efficiency. However, it should be noted that since the calculations of assimilation were based on direct measurements of C, N, and Si in the food and feces, they were not affected by the presence of trace amounts of seawater in the samples.

Nitrogen excretion and feces elimination by Atlantic menhaden are reported per gram dry weight, as micrograms N per gram dry weight per hour and milligrams per gram dry weight hour, respectively. It should be noted that measurements of oxygen consumption by the Atlantic menhaden during these experiments were reported in Durbin et al. (1981) as milligrams O_2 per gram wet weight per hour, to conform to the usual manner of reporting respiration rates in the literature.

RESULTS

The chemical composition of Atlantic menhaden, zooplankton, and *D. brightwelli* differed considerably (Table 1). Atlantic menhaden contained more C and calories, and less ash, per gram dry weight than the plankton, and were intermediate in N content between *D. brightwelli* and zooplankton. The composition of the fecal pellets was considerably altered from that of the food (Table 1). Atlantic menhaden assimilated N more efficiently than C, causing the C:N ratios of the fecal pellets to be higher than in the food.

The total dry weight of plankton fed to the 12 fish in each experiment ranged from 7.20 to 17.67 g of zooplankton, and 9.60 to 94.79 g of phytoplankton (Table 2). However, since the chemical composition of Atlantic menhaden differs from that of the plankton, the food rations are equivalent to different percentages of Atlantic menhaden dry weight, C, N, and calories. For example, the phytoplankton rations represented from 0.79% to

TABLE 1.—Chemical composition (mean ± σ) of *Brevoortia tyrannus*, plankton food organisms, and *B. tyrannus* fecal pellets.

Item	Dry wt as % of wet wt	Percent of dry weight					C:N	kcal/g dry wt	kcal/g ash-free dry wt
		Carbon	Nitrogen	Chitin	Silicon	Ash[1]			
B. tyrannus[2]	33.4±1.80	56.61±3.18	8.03±0.78	—	—	10.94±1.40	7.05	6.238±0.481	7.002±0.450
Zooplankton[3] mostly *Acartia tonsa*	10.86±0.20	40.05±2.34	10.91± .86	5.42±0.69	—	19.96±3.81	3.67	4.278± .161	5.348± .059
Chitin	—	39.37± .89	5.88± .17	—	—	—	6.70	—	—
Phytoplankton[4]: *Ditylum brightwelli*	—	18.52± .19	3.04± .05	—	9.28±0.16	55.24± .37	6.09	1.872± .072	4.179± .160
Fecal pellets[5]:									
Zooplankton	—	10.34±1.20	1.85± .34	—	—	72.3±2.14	5.59	1.013± .037	3.666± .297
Phytoplankton	—	9.29±1.34	.80± .11	—	25.7±7.35	74.6±1.20	11.61	.715± .042	2.818± .111

[1]May be an overestimate for plankton and fecal pellets; see text.
[2]Dry weight was determined on experimental fish; other constituents estimated from measurements on Atlantic menhaden collected from Narragansett Bay, R.I. (Durbin et al. unpubl. manuscr.).
[3]Mean ± σ of Experiments 1-3.
[4]*D. brightwelli* from Experiment 7; mean ± σ of four replicate determinations.
[5]Mean ± σ from Experiments 1-3 (zooplankton) and 4-10 (phytoplankton).

TABLE 2.—Food rations fed to 12 Atlantic menhaden.

Food type	Experiment no.	Duration of feeding (h)	Feeding rate[1] (mg food/g dry wt fish per h)	Food rations[2]				
				Dry weight[1]		Carbon (% of fish)	Nitrogen (% of fish)	kcal (% of fish)
				g	% of fish			
Zooplankton mostly *Acartia tonsa*	1	5.6	2.61	17.67	1.46	0.97	1.81	0.96
	2	8.1	1.19	11.58	.96	.71	1.39	.68
	3	3.8	1.55	7.20	.59	.42	.82	.41
Phytoplankton *Ditylum brightwelli*	6	7.1	10.99	94.79	7.80	2.56	3.01	2.35
	4	7.3	9.79	86.93	7.15	2.35	2.60	2.15
	5	7.0	7.93	67.46	5.55	1.82	2.13	1.67
	9	6.7	3.39	27.64	2.27	.75	.75	.68
	7	6.8	2.51	20.76	1.71	.56	.61	.51
	8	6.9	1.84	15.43	1.27	.42	.42	.38
	10	6.9	1.14	9.60	.79	.26	.29	.24

[1]Dry weight of zooplankton was measured in each experiment. Phytoplankton dry weight was estimated from C measurements in each experiment, and the conversion factor milligram C = 0.1852 (mg dry wt) (Table 1).
[2]Based on 12 fish = 1,212 g dry weight, 686.1 g C, 97.3 g N, and 7,560 kcal.

7.8% of the Atlantic menhaden dry weight, but only 0.26% to 2.56% of the estimated carbon content of the fish.

Each of the 12 fish was assumed to have obtained the same proportion (1/12) of the plankton added to the tank. This appeared reasonable since they were of similar size and swam at the same average speed during feeding (Durbin et al. 1981), and thus filtered similar volumes of water.

In the zooplankton experiments the duration of the feeding period was variable because of a problem caused by crab zoeas present in low numbers in the plankton. It was apparent that the sharp, 5 mm spines of these zoeas irritated the gill rakers of the Atlantic menhaden, because in three of four experiments attempted, the fish fed normally at first, then stopped feeding and began shaking their heads and repeatedly flaring their gill rakers. They stopped this unusual behavior as soon as the zoeas were washed out of the tank with filtered seawater. The fish were not satiated, since trial experiments demonstrated that once the zoeas were removed, the fish would feed readily on salmon food. The number of zoeas was least in Experiment 2, and in this instance the fish fed in their normal manner for as long as zooplankton was made available, 8.1 h. Because of these problems, only total assimilation efficiency will be reported from the zooplankton experiments.

Feces Elimination

In the phytoplankton experiments, feces began to appear about 2.4 h after the beginning of feeding (Table 3, column 2). The rate of elimination continually increased during the feeding period. The peak rates increased with increasing meal size, and occurred during the first 1 or 2 h following feeding (Figures 1, 2, 3). The elimination of feces began an approximately exponential decline 2 or 3 h after the end of feeding (Figure 1). With the exception of Experiment 6, these rates were all similar (overall $\overline{X}$ = 36.6%/h, or 38.1%/h if Experiment 6 is excluded) (Table 3, column 8). The exponential period lasted until about 14 h after the end of feeding, after which elimination continued at a low, nearly constant rate for the next 27 h (Figures 2, 3).

One consequence of the exponential elimination of the feces was that different sized rations

TABLE 3.—Feces elimination and nitrogen excretion of a school of 12 Atlantic menhaden, in relation to a 7-h period of feeding on the diatom *Ditylum brightwelli*, where time t_0 = the beginning, $t_{0.5}$ = the midpoint, and t_1 the end of the feeding period. At $t_{0.5}$, 50% of the ration has been ingested. Column numbers, in parentheses, are for text reference.

	Elapsed time (h)						
	After t_0	After $t_{0.5}$		After t_1			
Experiment no. (1)	Elimination begins (2)	50% Si eliminated (3)	50% N excreted (4)	90% Si eliminated (5)	90% N excreted (6)	Elimination rate ≥0.3 mg/g per h (7)	Exponential decline in elimination rate (per h) after t_1 (8)
6	2.0	5.5	2.3	10.0	2.9	13	−0.275
4	2.0	5.8	1.9	6.6	1.3	10	− .363
5	1.4	5.7	1.3	7.5	2.8	10	− .344
9	3.9	5.8	1.1	8.9	3.3	6	− .372
7	2.5	5.3	1.0	6.6	5.3	6	− .406
8	2.2	6.1	1.0	7.7	.7	7	− .392
10	2.6	6.0	1.5	7.0	.8	5	− .409
Mean ± σ	2.4 ± 0.8	5.7 ± 0.3	1.4 ± 0.5	7.8 ± 1.3	2.4 ± 1.6		−.366 ± .046

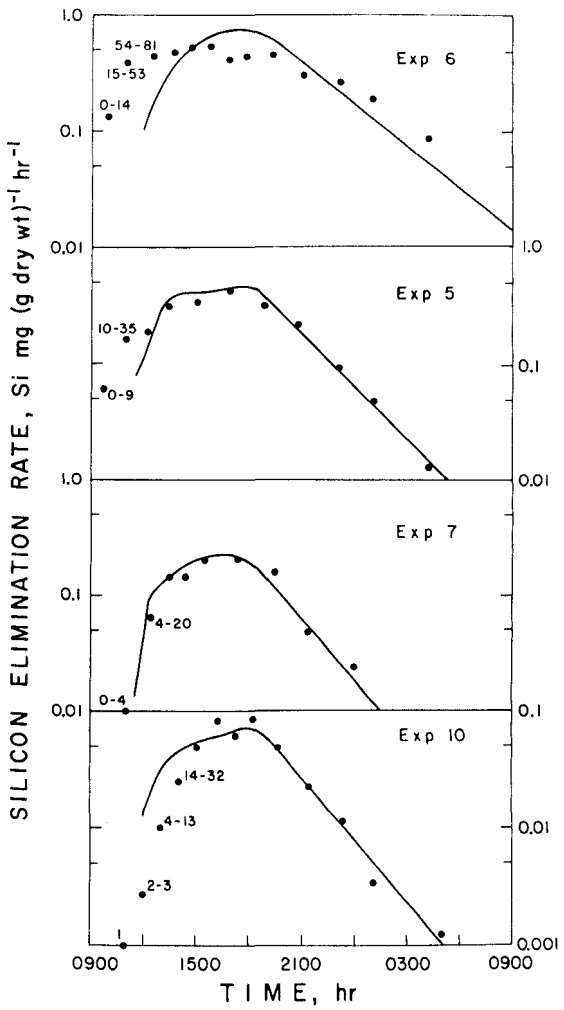

FIGURE 1.—Silicon elimination rate (circles) of a school of 12 *Brevoortia tyrannus*, during and after a 7-h (0800-1500 h) period of feeding on the diatom *Ditylum brightwelli*. Curve representing the calculated stomach evacuation rate is fitted to the feces elimination data; further explanation in text. Numbers refer to the elapsed time (minutes) in the feeding period when food corresponding to the fecal sample was ingested.

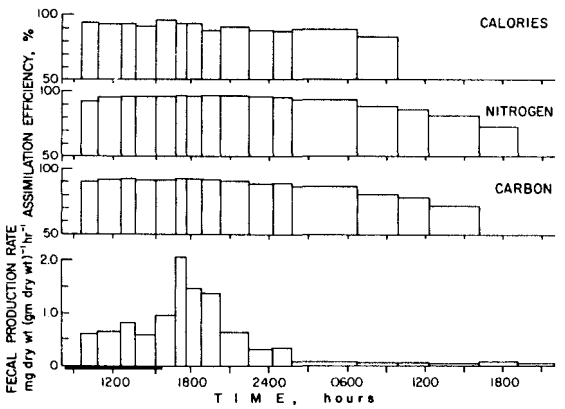

FIGURE 2.—Experiment 4 (high ration, Table 4). Changes in the fecal elimination rate of 12 *Brevoortia tyrannus*, and carbon, nitrogen, and caloric assimilation efficiency during and after a 7-h period of feeding (dark line on the x-axis) on *Ditylum brightwelli*.

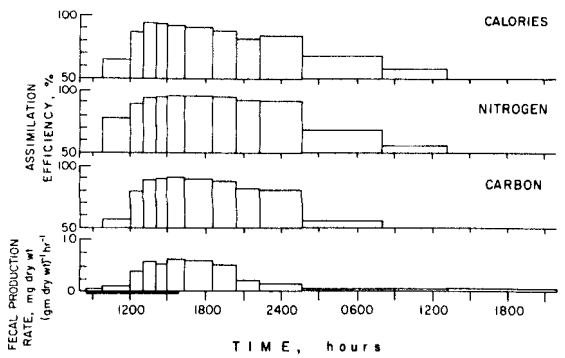

FIGURE 3.—Experiment 7 (low ration, Table 4). Symbols are as in Figure 2.

reached the same stage of elimination (i.e., 50%, 90%) at about the same time (Table 3, columns 3, 5).

Particulate Si in the feces was used to trace the passage of phytoplankton through the gut, since Si was not digested by the fish. Elimination of the experimental meal was rapid; 50% of the Si from the food was recovered in the fecal pellets within an average of 5.7 h after the midpoint of the feeding period (the time at which 50% of the food had been ingested) (Figure 4; Table 3, column 3). Because of the exponential decline in feces production following feeding, Si from the second half of the ration was egested more slowly, particularly the final 10%. Ninety percent of the Si in the food was recovered within a mean of 7.8 h after the end of feeding (Figure 4; Table 3, column 5) and a mean of 94.3% was recovered by 10 h after the end of feeding. Much of the fecal material eliminated during the next 31 h appeared to have sloughed from the gut since the C:Si ratios were higher in these samples. The amount of Si released during the interval between 14 and 41 h after the end of feeding was small, corresponding on the average to the food ingested during the final 10 min of the 7-h feeding period.

Assimilation Efficiency

The assimilation efficiency was high and similar for both phytoplankton and zooplankton (Table 4, columns 3, 4, 7). In the phytoplankton experiments, there was a slight positive trend between assimilation and increasing meal size, except in the largest ration experiment. In this experiment, assimilation appeared to be reduced.

It is not known whether Atlantic menhaden are able to digest chitin. The chitin content of the

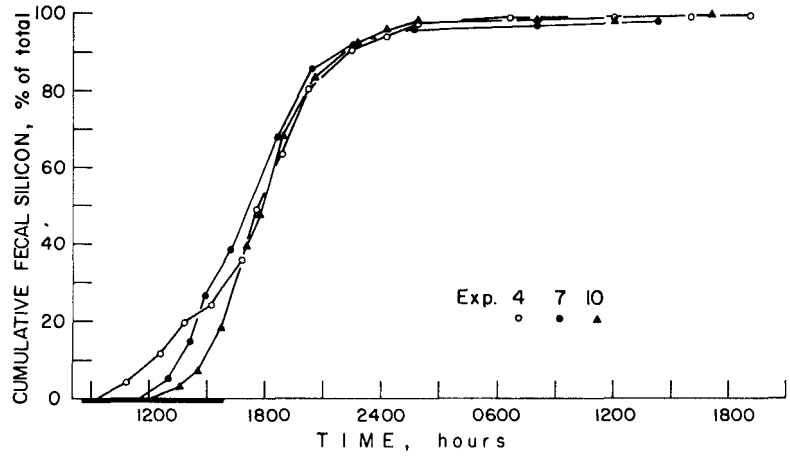

FIGURE 4.—Cumulative fecal silicon eliminated by 12 *Brevoortia tyrannus* in Experiments 4, 7, and 10 during and after the 7-h feeding period.

TABLE 4.—Assimilation efficiency of *Brevoortia tyrannus*, and the percentage of the total feces which were eliminated at a rate ≤0.3 mg/g dry weight per h. A) Overall assimilation efficiency. B) Assimilation during the period when fecal production was ≥0.3 mg/g dry weight per h. C) Calculated assimilation after subtraction of the chitin C and N from the total. Column numbers, in parentheses, are for text reference.

			Assimilation efficiency (%)						
			Carbon			Nitrogen			
Food type (1)	Experiment no. (2)	kcal A (3)	A (4)	B (5)	C (6)	A (7)	B (8)	C (9)	% of total elimination ≤0.3 mg/g per h (10)
Zooplankton	1	89.01	86.55	—	91.79	90.23	—	93.25	—
mostly	2	88.19	87.09	—	91.10	91.78	—	94.01	—
Acartia	3	85.80	86.39	—	91.39	91.88	—	94.72	—
tonsa	Mean ± σ	87.67 ± 1.67	86.68 ± 0.37		91.43 ± 0.35	91.30 ± 0.93		93.99 ± 0.74	
Phytoplankton	6	89.76	86.86	87.23	—	92.48	92.57	—	10.81
Ditylum	4	92.20	91.08	91.49	—	95.28	95.53	—	7.50
brightwelli	5	—	89.39	89.91	—	94.47	94.81	—	9.02
	9	—	86.99	89.15	—	92.66	94.15	—	43.04
	7	86.67	83.90	87.84	—	91.64	93.37	—	28.11
	8	—	84.43	87.55	—	90.22	92.49	—	35.08
	10	—	81.84	86.43	—	90.08	92.38	—	66.06
	Mean ± σ	89.54 ± 2.77	86.36 ± 3.22	88.51 ± 1.76		92.40 ± 1.97	93.61 ± 1.25		

zooplankton food (Table 1) was measured gravimetrically, but it was not possible to obtain an accurate measurement of chitin in the feces because of their very high ash content. However, if it is assumed that chitin (39.37% C and 5.88% N by weight) was not assimilated by Atlantic menhaden, and the chitin C and N are then subtracted from the total C and N in the food and the feces, the calculated assimilation efficiency for zooplankton would be increased slightly, to 91.43% (C) and 93.99% (N) (Table 4, columns 6, 9).

Changes in assimilation efficiency within experiments followed the general trend of the elimination of feces (Figures 2, 3). During feeding, assimilation efficiency increased from initial low values to a peak, which was sustained for several hours after the end of feeding and thereafter declined. The peak assimilation was reached sooner, and remained elevated for longer, in the high ration experiments (Figures 2, 3). With the two smallest rations, assimilation was still ascending when the feeding period was terminated.

Assimilation remained high as long as the fecal elimination rate exceeded about 0.3 mg/g dry weight per h (Figure 5). At lower elimination rates, assimilation declined precipitously. The reduced assimilation efficiencies at the beginning and near the end of feces production were associated with the presence of a mucuslike material which the fish released with the feces when the elimination rate was low. This material resulted in high C:Si and N:Si ratios in these feces. Any such input of C and N to the feces other than from the food would reduce the calculated assimilation efficiency. With the smaller meal sizes a greater proportion of the feces were eliminated at a low rate (Table 4, column 10), and the materials produced by the digestive tract of the fish constituted a significant fraction of the total fecal material. This reduced the apparent overall assimilation efficiency (Table 4, columns 3, 4, 7). If the feces produced at low rates (<0.3 mg/g dry weight per h) are excluded from the calculation, the dependence of assimilation efficiency on ration size is reduced (Table 4, columns 5, 8).

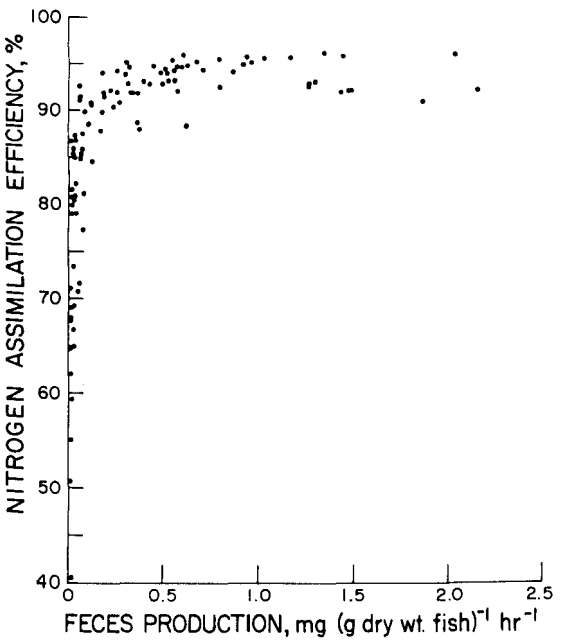

FIGURE 5.—Relationship between fecal elimination rate of *Brevoortia tyrannus* and the assimilation efficiency for nitrogen.

Nitrogen Excretion

When the fish were not feeding, their excretion rates were low and changes in the concentration of ammonia and DON in the tank were small. However, during feeding the excretion of the fish increased rapidly, and produced a rapid and nearly linear increase in the ammonia and DON concentrations (Figure 6). Excretion declined soon after the fish stopped feeding (Figure 7).

The mean ratio between DON and NH_3 excreted during the feeding period in all experiments was:

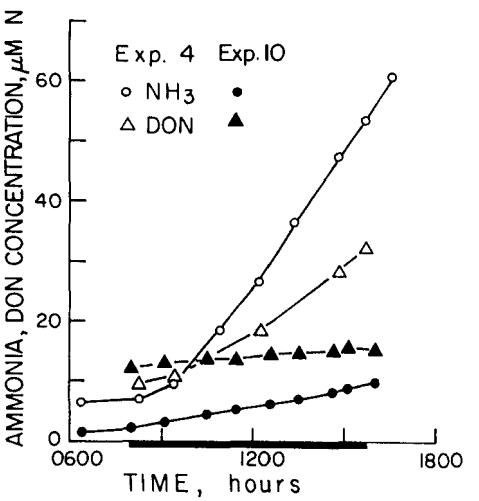

FIGURE 6.—Changes in ammonia and dissolved organic nitrogen concentration in the tank water due to excretion by 12 *Brevoortia tyrannus* during and after feeding. A high ration (Exp. 4) and a low ration (Exp. 10) experiment are illustrated.

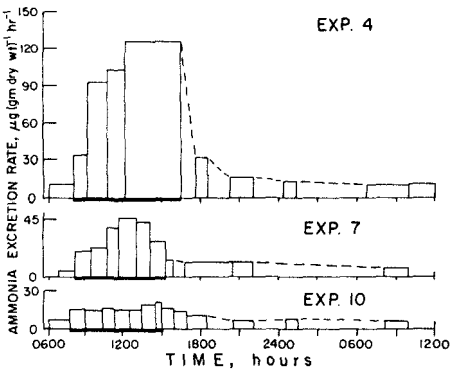

FIGURE 7.—Ammonia excretion rates of *Brevoortia tyrannus* before, during, and after a 7-h period of feeding on three ration sizes of *Ditylum brightwelli*.

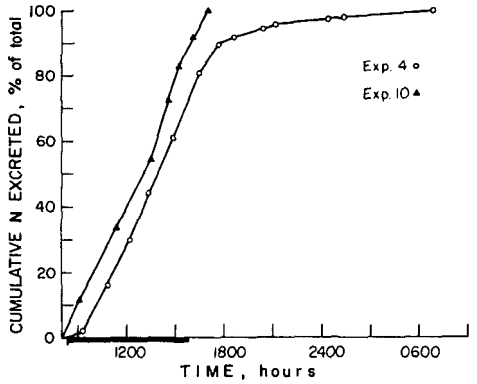

FIGURE 8.—Cumulative total exogenous nitrogen excreted by 12 *Brevoortia tyrannus* during and after feeding on *Ditylum brightwelli*. A high ration (Exp. 4) and a low ration (Exp. 10) experiment are illustrated.

$$\bar{X}\,\frac{\text{DON}-\text{N}}{\text{NH}_3-\text{N}} = 0.437, \quad \sigma = 0.088. \qquad (2)$$

Thus 30.4% of the total N excretion was in the form of DON, and 69.6% was in the form of ammonia.

The mean ±95% confidence limits of the ammonia excretion rate of fish unfed for 36 h (corresponding to measurement no. 1 in Durbin et al. 1981) was 7.46±2.54 µg NH_3-N/g dry weight per h. Using Equation (2), the total excretion was calculated to be 10.72±3.65 µg total N/g dry weight per h.

The amount of exogenous N excretion (that derived from the food) was calculated by subtracting the basal N excretion (10.72 µg N/g dry weight per h) from the total during the period of elevated excretion. Excretion rates were considered to have returned to basal when they reached the upper 95% confidence limit on the mean prefeeding rate, 14.4 µg N/g dry weight per h. Assimilation and N excretion did not lag far behind ingestion of the food. The time required for 50% of the exogenous N excretion to occur was only 1 or 2 h after 50% of the food was ingested ($\bar{X}$ = 1.4 h, Figure 8; Table 3, column 4). This indicates that all of the N ingested during the first 5.6 h of feeding (80% of the total) was assimilated during the feeding period.

The immediate decline in excretion rate after the fish stopped feeding was in accord with the decline in the elimination rate. In spite of this decline, 90% of the total exogenous excretion was completed within a mean of 2.4 h after the end of feeding (Figure 8; Table 3, column 6). The digestion and assimilation of *D. brightwelli* is therefore much more rapid than its complete elimination from the gut (i.e., compare Table 3, columns 4, 6 with columns 3, 5).

The total exogenous N excreted (E_N, milligrams/gram dry weight) increased linearly with both the total N ingested in the ration (R_N, milligrams) (Figure 9) and the N assimilated from the ration (pR_N, milligrams). The least squares linear regressions were:

$$E_N = 0.616R_N - 0.020 \qquad (3)$$
$$r = 0.99$$

$$E_N = 0.655pR_N - 0.016 \qquad (4)$$
$$r = 0.99$$

where p is the assimilation efficiency for N. These regressions indicate that approximately 61.6% of

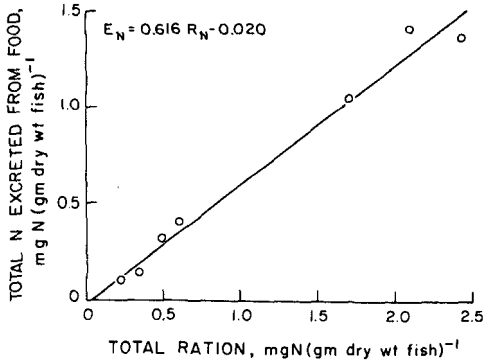

FIGURE 9.—Total exogenous nitrogen excreted by *Brevoortia tyrannus*, as a function of the amount of nitrogen ingested from *Ditylum brightwelli*. The least squares linear regression is shown.

the N in the ingested ration, and 65.5% of the N in the assimilated ration, were excreted.

If the total basal N excreted per day (0.257 mg N/g dry weight per d) is incorporated into Equations (3) and (4), the relationship between the total N excreted per day and the ingested N ration becomes:

$$E_N = 0.616R_N + 0.237 \text{ mg N/g dry weight per d} \quad (5)$$
$$r = 0.99$$

and the relationship between total daily N excretion and the assimilated N ration becomes (Figure 10):

$$E_N = 0.655pR_N + 0.241 \text{ mg N/g dry weight per d} \quad (6)$$
$$r = 0.99.$$

Equation (6) can be used to calculate, on a daily basis, the efficiency with which Atlantic menhaden retain N for growth as a function of N in the ration. This is analagous to calculating the net growth efficiency K_2:

$$K_2 = \frac{G}{pR} \quad (7)$$

where G = growth, grams/day
p = assimilation efficiency
R = ration, grams/day.

In the present case, growth in N (G_N, milligrams N/gram dry weight per day) will be equal to the N in the assimilated ration (pR_N) minus the total amount of N excreted per day (E_N total):

$$G_N = pR_N - E_N \quad (8)$$

$$= pR_N - (0.655\,pR_N + 0.241) \text{ mg N/g dry weight per d} \quad (9)$$

$$= 0.345\,pR_N - 0.241 \text{ mg N/g dry weight per d} \quad (10)$$

and

$$K_2 = \frac{0.345\,pR_N - 0.241}{pR_N} \quad (11)$$

K_2 calculated from Equation (11) for different assimilated ration sizes is shown in Figure 11. At an assimilated ration of 0.70 mg N/g dry weight per d there would be no net gain or loss of N. If Atlantic menhaden are composed of 8.03% N by weight (Table 1), this maintenance ration would correspond to 0.87% of their body N per day. The amount of N provided in the four lowest ration experiments was less than this daily maintenance requirement. The asymptotic value of K_2 at high ration levels was 0.345 (Figure 11). For K_2 = 0.20 and 0.30, the Atlantic menhaden would have to assimilate 1.66 and 5.36 mg N (2.1 and 6.7% of their body N, respectively) per day, with resultant growth rates of 0.42 and 2.01% of body N per day.

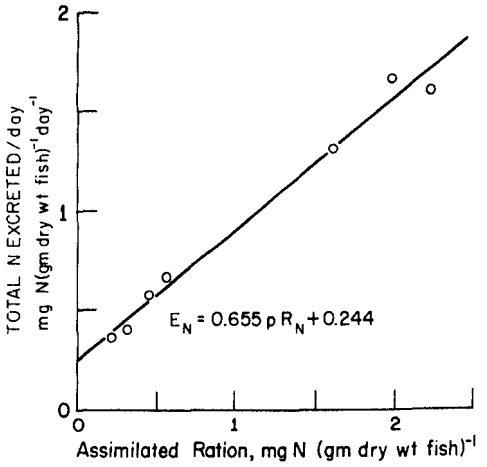

FIGURE 10.—Relationship between the amount of nitrogen assimilated from the daily ration, and the total daily nitrogen excretion by *Brevoortia tyrannus*.

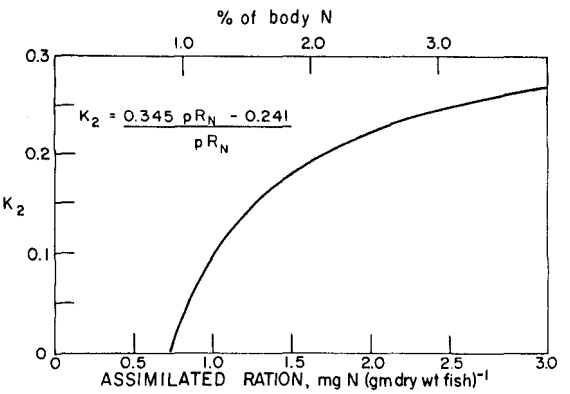

FIGURE 11.—Calculated efficiency of the utilization of nitrogen for growth by *Brevoortia tyrannus*, as a function of the nitrogen content of the assimilated ration.

Oxygen:Nitrogen Ratios

The ratio of O_2 consumed to N excreted (by atoms) has been used to give an indication of the type of food the fish are metabolizing. The O:N ratio during the combustion of protein is about 7.4 (Kutty 1972), while the ratio for carbohydrate is infinity, and for fat is about 415 (Ikeda 1977).

The change in the O:N ratio with time is shown for four phytoplankton experiments (Figure 12). The mean O:N for all initial prefeeding measurements in the phytoplankton experiments was 28.2, σ = 9.8. There was a slight increase of the O:N immediately after the beginning of feeding in most of the experiments. This was because the increase in the voluntary swimming speed of the fish during feeding produced an immediate increase in O_2 consumption, whereas N excretion increased more gradually. Swimming speeds and respiration rates during feeding in the three high ration experiments (nos. 4, 5, 6) averaged about 41.3 cm/s and 0.48 mg O_2/g wet weight per h, respectively. In these experiments, the O:N ratios declined to very low levels (between 5 and 10) soon after the initiation of feeding and remained at these low levels for the rest of the feeding period (Figure 12). In the four smaller ration experiments, the swimming speed during feeding ranged between 29.3 and 36.5 cm/s and O_2 consumption between 0.221 and 0.354 mg O_2/g wet weight per h.

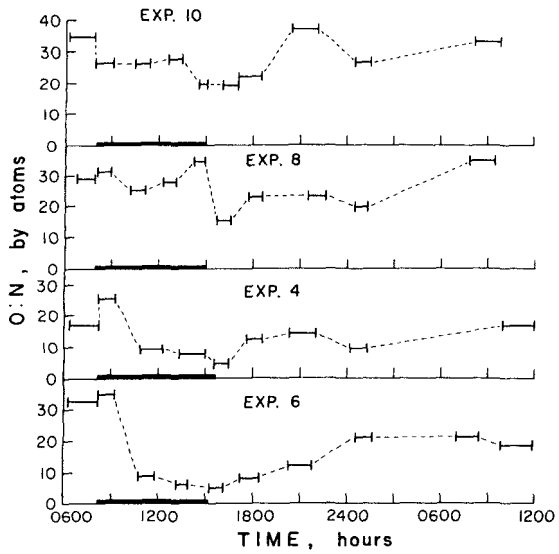

FIGURE 12.—O:N ratios of *Brevoortia tyrannus* before, during, and after feeding on *Ditylum brightwelli*. Oxygen data are from Durbin et al. (1981).

The decline in the O:N ratios during feeding was much less than in the high ration experiments. Swimming speeds and O_2 consumption rates of nonfeeding fish averaged about 12.2 cm/s and 0.10 mg O_2/g wet weight per h, respectively.

In all of the experiments, the lowest O:N ratio occurred immediately following feeding. This was because after the plankton was gone the fish immediately reduced their voluntary swimming speed and O_2 consumption, whereas their ammonia excretion remained high. Following this the O:N ratio gradually increased to the high prefeeding values.

DISCUSSION

Elimination of Food From the Gut

There has been some controversy concerning whether digestion rates and elimination rates are linear or exponential (Fänge and Grove 1979). In the linear model, a constant amount (g) is evacuated per unit time and therefore the instantaneous evacuation rate continually changes. In the exponential model, a constant proportion of the food present in the stomach is evacuated per unit time; thus, while the exponential rate remains constant, the actual amount of food (g) evacuated per unit time continually decreases.

In some studies the linear model has been explicitly used, by fitting a linear regression through the data points representing the food remaining in the stomach vs. time (e.g., Swenson and Smith 1973; Bagge 1977). In other studies the time to 100% evacuation of the stomach has been determined (e.g., Hunt 1960; Molnar and Tölg 1962; Edwards 1971; Jobling et al. 1977). Here there is usually an implicit assumption that evacuation is a linear process. Several recent careful studies, however, have found that gastric evacuation was clearly a curvilinear process which was closely approximated by an exponential curve (Brett and Higgs 1970; Tyler 1970; Elliott 1972; Elliott and Persson 1978). Beamish (1972) also concluded that evacuation is exponential over a major part of the digestion period, but that it may deviate at the beginning and near the end of digestion. In the initial stages this may occur if there is a lag between the ingestion of a meal, and the beginning of gastric evacuation. The final stages of evacuation are obviously not exponential, since completely empty stomachs are frequently seen in fishes.

With the Atlantic menhaden the exponential model seems appropriate since fecal elimination rates showed an exponential decline after the fish stopped feeding. This exponential fecal elimination rate (R'), determined from the decrease in fecal silicon elimination rate with time, is different from the exponential rate of gastric (stomach) evacuation (R), which is the factor measured in most studies. However, if the time required for food to travel the length of the intestine is constant, then the estimate of R' based on measurements of fecal elimination will be the same as R determined directly from measurements of the decline in stomach contents with time. In order to more fully investigate this, and to understand the patterns of change in feces elimination by Atlantic menhaden, especially during feeding, we have fit the data to a modified version of a model proposed by Elliott and Persson (1978). This theoretical model was then compared with our observed elimination rate data. A good agreement between the two would indicate that stomach evacuation is exponential, that R' is a good estimator of R, and that stomach evacuation is the principal factor governing the fecal elimination rate. Such an analysis may also serve to indicate whether systematic deviations between predicted and observed data occur as ration size changes.

The model of Elliott and Persson (1978) assumes that the fish feed at a constant rate, and that the gastric evacuation rate R is exponential. Thus the rate of change in stomach content (S) is given by:

$$(dS/dt) = F - RS. \tag{12}$$

The actual amount of food (S_t, milligrams/gram dry weight) present in the stomach after t hours is given by:

$$S_t = S_0 e^{-Rt} + \frac{F}{R}(1 - e^{-Rt}) \tag{13}$$

where S_0 is the initial amount of food in the stomach and F is the amount of food consumed per hour. As $F \to 0$, $S_t \to S_0 e^{-Rt}$. The amount of food (SE_t, milligrams/gram dry weight) which has been evacuated from the stomach by time t is simply:

$$SE_t = C_t - S_t \tag{14}$$

where C_t is the total amount of food (milligrams/gram dry weight) consumed in t hours. Thus SE_t and C_t are cumulative quantities measured since the onset of feeding, whereas S_t is the instantaneous amount present in the stomach at time t. For the present analysis we assumed that $R' = R$, and substituted R' into Equation (13). From values of R', F, and C_t for each experiment we then calculated S_t and SE_t for hourly intervals during and after feeding. All calculations were in terms of silicon, since this was not digested by the fish.

Curves illustrating C_t, S_t, and SE_t for the 12 fish are shown in Figure 13 for Experiment 7. The value of R' was 0.406/h and F was 0.241 mg Si/g dry weight per h. Since the ingestion rate was constant, C_t increased linearly with time. The amount of Si present in the stomach (S_t) increased curvilinearly during the feeding period, then declined exponentially after feeding stopped. The cumulative Si evacuated (SE_t) increased sigmoidally, with the inflection point at the time the fish stopped feeding. While most of the Si had been evacuated from the stomach within 5 h after the end of feeding, small amounts continued to be evacuated for many hours as the evacuation rates declined exponentially to very low levels.

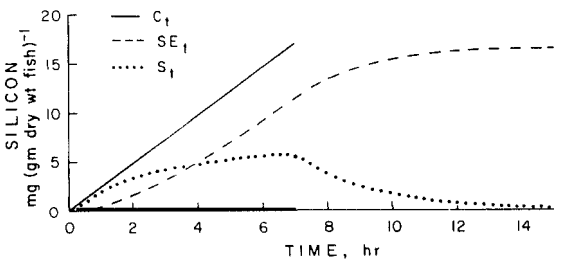

FIGURE 13.—Experiment 7. Cumulative ingestion of silicon (C_t), and model calculations of the instantaneous amounts of silicon present in the stomach (S_t) and the cumulative amounts of silicon which have been evacuated from the stomach (SE_t) during and after a 7-h feeding period.

The time lag between the ingestion of a particle and its elimination in the feces is the digestive tract residence time for that particle. Similarly the stomach residence time is the time lag between the ingestion and the gastric evacuation of a particle. The total digestive tract residence time was determined by subtracting the time required for the fish to ingest a given amount of Si, from the observed time when that same amount of Si was eliminated in the feces. The gastric residence time was similarly calculated from the observed feeding rate and the predicted values of SE_t. In each experiment the calculated gastric residence time followed a pattern similar to the digestive tract residence time (Figure 14). The two curves were

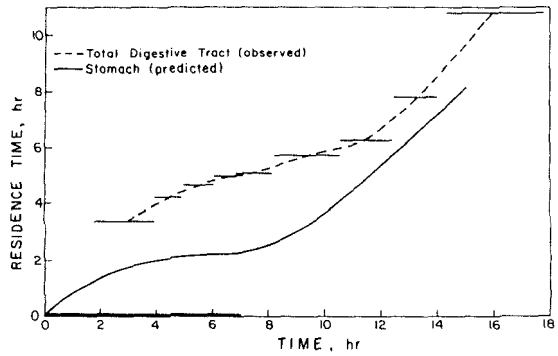

FIGURE 14.—Experiment 7. Changes in the digestive tract residence time of silicon (measured) and the stomach residence time of silicon (calculated) during and following a 7-h feeding period.

offset by the time required for Si to travel the length of the intestine; in the example shown, about 2 h.

Figure 14 demonstrates that particles eaten at the beginning of a feeding period have the shortest residence times. Residence time increases asymptotically during feeding, and then exponentially once the fish have stopped feeding. At the end of feeding the observed digestive tract residence time ranged between 5 and 6 h in all but the largest ration experiment, in which the residence time was only 4.5 h.

This model provides a quantitative explanation of the earlier observations by Noble (1973) and D. J. W. Moriarty and C. M. Moriarty (1973) that during continuous feeding, small food particles ingested early in the feeding period travel through the stomach more quickly than particles eaten later. In addition, observations that food particles eaten during continuous feeding will pass through the stomach more rapidly than when they are eaten as a single meal (i.e., Laurence 1971; Noble 1973) are also consistent with this model, since residence time remains short as long as feeding continues, but increases rapidly after the fish stop feeding.

Finally, the observed fecal elimination rates by the Atlantic menhaden (milligrams Si/gram dry weight per hour) were compared with the predicted gastric evacuation rates (milligrams Si/gram dry weight per hour) calculated from the model. Since the two curves were offset in time by the travel time of particles in the intestine, a comparison of the two is facilitated by lagging the stomach evacuation curve by the amount of the intestinal travel time. This time lag was graphically determined for each experiment by overlaying the curve of stomach evacuation on the curve of feces elimination rate such that the periods of exponential decline coincided. These lag times were quite similar for all experiments (overall mean $\pm\sigma$ = 2.17 $\pm$ 0.18 h). These values agree well with the average time for the first appearance of feces after the onset of feeding (2.4 h).

These plots of the observed fecal elimination rates and the predicted gastric evacuation rates (Figure 1) showed that in general there was good agreement between the two. There were, however, some systematic deviations with change in ration size. At high food rations, the observed elimination rates of the first fecal samples were higher than predicted by the model, indicating that these passed through the digestive tract more rapidly than predicted. In contrast, at the lowest rations the initial elimination rates were lower than predicted. Since the presence of food directly stimulates gastric motility and the secretion of digestive enzymes (Fänge and Grove 1979), it may be that the larger rations have a greater stimulatory effect on the digestive tract than small rations. It should be noted, however, that these deviations observed in the first two or three fecal samples represent food ingested quite early during the feeding period (Figure 1). Subsequent samples more closely followed the model.

The largest ration experiment (no. 6) also deviated from the model during the postfeeding period. The model predicts that if the exponential evacuation rate is <1 (i.e., in the present case = 0.366), food will continuously accumulate in the stomach during feeding (Figure 13). The largest amount of material in grams is therefore evacuated at the end of the feeding period (Figure 13), and the maximum fecal elimination rates should occur during the postfeeding period (because of the time required for material to travel through the intestine). However, in Experiment 6, the elimination rates quickly rose to high levels, but then declined and leveled off during the postfeeding period without reaching the maximum rates predicted by the model (Figure 1). This implies that stomach evacuation was also lower than the model would predict during the last 2 or 3 h of feeding. A possible explanation is that after the Atlantic menhaden had fed for several hours at this high rate, the amount of food may have accumulated in the stomach to an extent which exceeded the maximum physical capacity of the fish to process the material, which caused the gastric evacuation rate to level off. It was interesting that

assimilation efficiency in this experiment was also somewhat reduced. However, even with this high feeding rate, the behavior of the Atlantic menhaden did not change significantly during the course of the feeding period, and the fish gave no indication of approaching satiation (Durbin et al. 1981).

In summary we conclude that the calculated gastric evacuation by Atlantic menhaden calculated from Elliott and Persson's (1978) model agrees well with our experimental measurements of elimination rates following a meal. The calculated lag between the gastric evacuation of a particle and its elimination in the feces was similar for all ration sizes and also agreed well with the estimates of the time of the beginning of fecal elimination (Table 3, column 2). These results indicate that R' should be a good estimator of R. However, the stomach evacuation rates of Atlantic menhaden need to be determined directly, both in order to verify the model predictions, and to explore the reasons for the systematic deviations of the observed elimination from that predicted as food ration size changes.

Finally, with regard to methods employed for the study of fish digestion, present results with Atlantic menhaden indicate that when digestion is an exponential process, measurements of the time to "100% evacuation" are of limited value. This is because they cannot be used to determine the exponential evacuation rate R. The evacuation of the final portion of a meal is extremely protracted and may even be nonexponential. With Atlantic menhaden, for example, the food eliminated between 8 and 41 h after the end of feeding corresponded on average to the food ingested during the final 35 min of feeding; feces eliminated during hours 14-41 corresponded to the final 10 min of feeding. This makes selection of an end point, to be taken as 100%, quite difficult and arbitrary. If the final stages are nonexponential, then obviously the estimate of R would be biased. The final problem is computational: in an exponential process, the stage of 100% digestion is mathematically never reached, and it is necessary to approximate 100% with another value, such as 98, 99, or 99.9%. Although the choice of any of these values would be purely arbitrary, each provides a very different estimate of the value of R.

Assimilation Efficiency

The Atlantic menhaden was very efficient at absorbing N, C, and calories from both phytoplankton and zooplankton food. These high assimilation efficiencies are in general agreement with those reported for carnivorous fish (Gerking 1955; Menzel 1960; Pandian 1967; Beamish 1972; Kelso 1972). Few studies have examined the assimilation efficiency of herbivorous fishes. C. M. Moriarty and D. J. W. Moriarty (1973) and D. J. W. Moriarty and C. M. Moriarty (1973) found that the maximum mean C assimilation of *Tilapia nilotica* varied according to food type, being highest for the diatom *Nitzschia* (79%), somewhat lower for two bluegreen algae, *Microcystis* (70%) and *Anabaena* (75%), and least for the green alga *Chlorella* (49%). The average maximum C assimilation of *Haplochromis nigripinnis* for *Microcystis* was 71%. Menzel (1959) reported that *Holacanthus bermudensis* assimilated 85% (range 82-91%) of the N and 77.7% (range 72-84%) of the calories from two macroalgae, *Monostroma* and *Enteromorpha*. Plant materials described from the gut contents of Atlantic menhaden are planktonic and resuspended benthic diatoms, and detrital particles presumably derived from marsh grasses (Peck 1894; Darnell 1958; Peters and Kjelson 1975; Jeffries 1975). The high assimilation efficiency for *D. brightwelli* indicates that Atlantic menhaden should have high assimilation efficiency for other diatoms also. The ability of Atlantic menhaden to assimilate detrital material has not been experimentally determined. Planktonic green and bluegreen algae are much less important in the marine environment than in freshwater; moreover they are generally too small to be filtered by Atlantic menhaden (Durbin and Durbin 1975) and are not a significant food. Thus the comparatively low assimilation efficiency which has been reported for some freshwater herbivores fed green and bluegreen algae is not relevant to Atlantic menhaden or to most other marine phytoplankton-feeding fishes, which eat mainly diatoms and dinoflagellates (i.e., see Durbin 1979 and references therein).

Ration size has generally been shown to have little or no effect on assimilation efficiency (Gerking 1955; Pandian 1967; Beamish 1972; Kelso 1972; Solomon and Brafield 1972), although Elliott (1976) found that assimilation in brown trout, *Salmo trutta*, decreased as ration level increased.

Our results show a slight increase in assimilation efficiency with increasing meal size. This effect, as well as the changes in assimilation efficiency during the course of a feeding period, may have two possible causes: 1) the addition to the fecal pellets of significant quantities of materials

secreted by the gut, resulting in lower apparent assimilation efficiencies; and 2) a possible lag in the secretion of digestive enzymes after a period of fasting, which would cause assimilation to be initially low. The latter effect was observed by D. J. W. Moriarty and C. M. Moriarty (1973), who found that in *Tilapia* a period of about 4 h was required for the secretion of stomach enzymes, and hence assimilation efficiency, to reach high values. We have no measures of temporal changes in stomach enzymes for the Atlantic menhaden. While explanation 2 may have contributed to the initial low assimilation efficiency at the beginning of feeding, it would not explain the decline in assimilation towards the end of feces elimination, since this food was presumably digested at the end of the feeding period when stomach enzymes should have been maximal. Visual observations of the organic material surrounding the feces at low fecal production rates provided support for the first explanation, and would be consistent with the reduced assimilation efficiency observed at both the beginning and end of feces production.

The reason for the reduced assimilation efficiency at the highest ration level is unclear. If the maximum capacity of the digestive tract was reached, the assimilatory processes may have become saturated, causing a reduction in assimilation efficiency.

However, the supply rate of plankton in the highest ration experiment exceeded the concentration of diatoms which Atlantic menhaden would normally be expected to encounter on its summer feeding grounds in Narragansett Bay (Durbin and Durbin 1981). Thus Atlantic menhaden probably does not ordinarily feed at such high rates for prolonged periods in nature. Therefore, the slight decline in assimilation efficiency at the high feeding rate of Experiment 6 may not have much ecological significance. We conclude that overall, the effect of meal size on the assimilation efficiency of Atlantic menhaden is small. Because of the very rapid digestion rates and high assimilation efficiencies of Atlantic menhaden, this planktivore appears to be adapted to process efficiently large amounts of food continuously.

Nitrogen Excretion

In most teleosts ammonia is the principal end product of protein catabolism, and is the major component of N excretion; other N compounds excreted include urea, creatine, creatinine, and trimethylamine oxide (Watts and Watts 1974). In Atlantic menhaden the percent of total N excreted as ammonia (69.6%) appears to be similar to that observed in other species (Smith 1929; Atherton and Aitken 1970; McCarthy and Whitledge 1972).

Nitrogen excretion by Atlantic menhaden changed according to whether or not the fish were feeding, the rate at which they fed, and the time since the last meal. Previous studies have also found that N excretion increases as a result of feeding (Brett and Zala 1975; Elliott 1976; Savitz et al. 1977). These studies differed from the present study, however, in the timing of the peak of N excretion and the subsequent return to endogenous rates. Fingerling sockeye salmon, *Oncorhynchus nerka*, at 15° C showed a peak ammonia excretion rate about 4 h after a meal and did not return to a basal rate until about 16 h after feeding (Brett and Zala 1975). Similarly, N excretion rates of brown trout at 17° C did not return to baseline until about 12-20 h after feeding (Elliott 1976) and largemouth bass, *Micropterus salmoides*, at 21°-23° C took 1 or 2 d (Savitz et al. 1977). In contrast, when Atlantic menhaden fed continuously for 7 h, the excretion rate remained high throughout the feeding period and lagged only 1 or 2 h behind ingestion of the food. The return to baseline was also rapid, with 90% of the exogenous N excretion occurring within a mean of 2.4 h following the end of feeding.

The Atlantic menhaden excreted a constant proportion of N in its ration (61.6% of the ingested and 65.5% of the assimilated ration). Savitz et al. (1977) also found a linear relationship between ingestion and N excretion in largemouth bass, although in that case only 40% of the ingested N was excreted. Gerking (1971) reported that in bluegill there was a linear relationship between the amount of N consumed and the amount retained for growth, which implied that the relationship between the amount of N ingested and that excreted was also linear. Additional studies are needed to determine the extent to which the proportion of N excreted by different species varies. Factors which may be expected to affect this proportion are the nutritional requirements of the fish, which may change seasonally, relative to the chemical composition of the food.

Oxygen:Nitrogen Ratios

The chemical composition of Atlantic menhaden compared with that of plankton indicates that the

fish conserve C and calories relative to N and ash from its food. Exogenous N in excess of body requirements is excreted. The O:N ratios indicate that proteins are used as a metabolic fuel by both feeding and nonfeeding Atlantic menhaden with subsequent excretion of N. This is consistent with results from other teleosts (Watts and Watts 1974). If an O:N ratio of 7.4 indicates that pure protein is being burned, then the mean value of 28.2 in fish unfed for 36 h indicates that 7.4/28.2 = 26.2% of the O_2 consumed is being used for protein catabolism. The increase in O:N ratios immediately after the beginning of feeding indicates that the fish are metabolizing proportionally more carbohydrate or lipid to support the increased swimming speed until significant quantities of food have been assimilated and become available as an energy source. During the feeding period of the three high ration experiments, the O:N ratios declined to or below that associated with the combustion of pure protein. The decline in the O:N ratios during feeding can be caused by two processes, which can act simultaneously: the fish are obtaining a large proportion of their energy directly from the breakdown of the C skeletons of amino acids absorbed from the food, with subsequent excretion of the N; and the proportions of the various amino acids taken in the food are being balanced to meet the requirements of protein synthesis; excess α-amino acids are excreted (Watts and Watts 1974). While it is impossible to separate the two processes in the present experiments, O:N ratios below 7.4 are an indication that both are occurring.

Kutty (1978) has calculated the ammonia quotient (AQ = NH_3 excreted/O_2 consumed) from the data of Brett and Zala (1975), from which O:N ratios can be determined. In that study the fish were fed a single meal over a brief time interval, and the peaks in O_2 consumption and N excretion were separated by several hours. However, the trend in the O:N ratios was similar to the present study, in that they declined from high values ($\approx$ 40.0) in the unfed fish to a minimum of about 8.3 during the digestion and assimilation of the food, then gradually increased to the prefeeding level.

ACKNOWLEDGMENT

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LITERATURE CITED

ATHERTON, W. D., AND A. AITKEN.
1970. Growth, nitrogen metabolism and fat metabolism in *Salmo gairdneri*, Rich. Comp. Biochem. Physiol. 36:719-747.

BAGGE, O.
1977. Meal size and digestion in cod (*Gadus morrhua* L.) and sea scorpion (*Myoxocephalus scorpius* L.). Medd. Dan. Fish. Havunders. N.S. 7:437-446.

BEAMISH, F. W. H.
1972. Ration size and digestion in largemouth bass, *Micropterus salmoides* Lacépède. Can. J. Zool. 50:153-164.

BRETT, J. R., AND D. A. HIGGS.
1970. Effect of temperature on the rate of gastric digestion in fingerling sockeye salmon, *Oncorhynchus nerka*. J. Fish. Res. Board Can. 27:1767-1779.

BRETT, J. R., AND C. A. ZALA.
1975. Daily pattern of nitrogen excretion and oxygen consumption of sockeye salmon (*Oncorhynchus nerka*) under controlled conditions. J. Fish. Res. Board Can. 32:2479-2486.

DARNELL, R. M.
1958. Food habits of fishes and larger invertebrates of Lake Pontchartrain, Louisiana, an estuarine community. Publ. Inst. Mar. Sci. Univ. Tex. 5:353-416.

D'ELIA, C. F., P. A. STEUDLER, AND N. CORWIN.
1977. Determination of total nitrogen in aqueous samples using persulfate digestion. Limnol. Oceanogr. 22:760-764.

DURBIN, A. G.
1979. Food selection by plankton feeding fishes. *In* H. Clepper (editor), Predator-prey systems in fisheries management, p. 203-218. Sport Fish. Inst., Wash., D.C.

DURBIN, A. G., AND E. G. DURBIN.
1975. Grazing rates of the Atlantic menhaden *Brevoortia tyrannus* as a function of particle size and concentration. Mar. Biol. (Berl.) 33:265-277.
1981. Standing stock and estimated production rates of phytoplankton and zooplankton in Narragansett Bay, Rhode Island. Estuaries 4:24-41.

DURBIN, A. G., E. G. DURBIN, P. G. VERITY, AND T. J. SMAYDA.
1981. Voluntary swimming speeds and respiration rates of a filter-feeding planktivore, the Atlantic menhaden *Brevoortia tyrannus* (Pisces: Clupeidae). Fish. Bull., U.S. 78:877-886.

DURBIN, E. G.
1977. Studies on the autecology of the marine diatom *Thalassiosira nordenskioeldii*. II. The influence of cell size on growth rate, and carbon, nitrogen, chlorophyll *a* and silica content. J. Phycol. 13:150-155.

EDWARDS, D. J.
1971. Effect of temperature on rate of passage of food through the alimentary canal of the plaice *Pleuronectes platessa* L. J. Fish Biol. 3:433-439.

ELLIOTT, J. M.
1972. Rates of gastric evacuation in brown trout, *Salmo trutta* L. Freshwater Biol. 2:1-18.
1976. Energy losses in the waste products of brown trout (*Salmo trutta* L.). J. Anim. Ecol. 45:561-580.

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

FÄNGE, R., AND D. GROVE.
1979. Digestion. *In* W. S. Hoar, D. J. Randall, and J. R. Brett (editors), Fish physiology, Vol. VIII, p. 161-260. Acad. Press, N.Y.

GERKING, S. D.
1955. Influence of rate of feeding on body composition and protein metabolism of bluegill sunfish. Physiol. Zool. 28:267-282.
1971. Influence of rate of feeding and body weight on protein metabolism of bluegill sunfish. Physiol. Zool. 44:9-19.

HUNT, B. P.
1960. Digestion rate and food consumption of Florida gar, warmouth, and largemouth bass. Trans. Am. Fish. Soc. 89:206-211.

IKEDA, T.
1977. The effect of laboratory conditions on the extrapolation of experimental measurements to the ecology of marine zooplankton. IV. Changes in respiration and excretion rates of boreal zooplankton species maintained under fed and starved conditions. Mar. Biol. (Berl.) 41:241-252.

JEFFRIES, H. P.
1975. Diets of juvenile menhaden (*Brevoortia tyrannus*) in three estuarine habitats as determined from fatty acid composition of gut contents. J. Fish. Res. Board Can. 32:587-592.

JOBLING, M., D. GWYTHER, AND D. J. GROVE.
1977. Some effects of temperature, meal size and body weight on gastric evacuation time in the dab *Limanda limanda* (L). J. Fish Biol. 10:291-298.

KELSO, J. R. M.
1972. Conversion, maintenance, and assimilation for walleye, *Stizostedion vitreum vitreum*, as affected by size, diet, and temperature. J. Fish. Res. Board Can. 29:1181-1192.

KUTTY, M. N.
1972. Respiratory quotient and ammonia excretion in *Tilapia mossambica*. Mar. Biol. (Berl.) 16:126-133.
1978. Ammonia quotient in sockeye salmon (*Oncorhynchus nerka*). J. Fish. Res. Board Can. 35:1003-1005.

LAURENCE, G. C.
1971. Feeding and bioenergetics of largemouth bass larvae (*Micropterus salmoides*). Ph.D. Thesis, Cornell Univ., Ithaca, 139 p.

MCCARTHY, J. J., AND T. E. WHITLEDGE.
1972. Nitrogen excretion by anchovy (*Engraulis mordax* and *E. ringens*) and jack mackerel (*Trachurus symmetricus*). Fish. Bull., U.S. 70:395-401.

MENZEL, D. W.
1959. Utilization of algae for growth by the angelfish, *Holacanthus bermudensis*. J. Cons. 24:308-313.
1960. Utilization of food by a Bermuda reef fish, *Epinephelus guttatus*. J. Cons. 25:216-222.

MOLNÁR, G., AND I. TÖLG.
1962. Relation between water temperature and gastric digestion of largemouth bass (*Micropterus salmoides* Lacépède). J. Fish. Res. Board Can. 19:1005-1012.

MORIARTY, C. M., AND D. J. W. MORIARTY.
1973. Quantitative estimation of the daily ingestion of phytoplankton by *Tilapia nilotica* and *Haplochromis nigripinnis* in Lake George, Uganda. J. Zool. (Lond.) 171:15-23.

MORIARTY, D. J. W., AND C. M. MORIARTY.
1973. The assimilation of carbon from phytoplankton by two herbivorous fishes: *Tilapia nilotica* and *Haplochromis nigripinnis*. J. Zool. (Lond.) 171:41-55.

NOBLE, R. L.
1973. Evacuation rates of young yellow perch, *Perca flavescens* (Mitchill). Trans. Am. Fish. Soc. 102:759-763.

PANDIAN, T. J.
1967. Intake, digestion, absorption and conversion of food in the fishes *Megalops cyprinoides* and *Ophiocephalus striatus*. Mar. Biol. (Berl.) 1:16-32.

PECK, J. I.
1894. On the food of the menhaden. Bull. U.S. Fish. Comm. 13:113-126.

PETERS, D. S., AND M. A. KJELSON.
1975. Consumption and utilization of food by various postlarval and juvenile fishes of North Carolina estuaries. *In* L. E. Cronin (editor), Estuarine research, Vol. I, p. 448-472. Acad. Press, N.Y.

SAVITZ, J., E. ALBANESE, M. J. EVINGER, AND P. KOLASINSKI.
1977. Effect of ration level on nitrogen excretion, nitrogen retention and efficiency of nitrogen utilization for growth in largemouth bass (*Micropterus salmoides*). J. Fish Biol. 11:185-192.

SMITH, H. W.
1929. The excretion of ammonia and urea by the gills of fish. J. Biol. Chem. 81:727-742.

SOLOMON, D. J., AND A. E. BRAFIELD.
1972. The energetics of feeding, metabolism and growth of perch (*Perca fluviatilis* L.). J. Anim. Ecol. 41:699-718.

SOLÓRZANO, L.
1969. Determination of ammonia in natural waters by the phenolhypochlorite method. Limnol. Oceanogr. 14:799-801.

STRICKLAND, J. D. H., AND T. R. PARSONS.
1972. A practical handbook of seawater analysis. 2d ed. Fish. Res. Board Can., Bull. 167, 310 p.

SWENSON, W. A., AND L. L. SMITH, JR.
1973. Gastric digestion, food consumption, feeding periodicity, and food conversion efficiency in walleye (*Stizostedion vitreum vitreum*). J. Fish. Res. Board Can. 30:1327-1336.

TYLER, A. V.
1970. Rates of gastric emptying in young cod. J. Fish. Res. Board Can. 27:1177-1189.

WATTS, R. L., AND D. C. WATTS.
1974. Nitrogen metabolism in fishes. *In* M. Florkin and B. Scheer (editors), Chemical zoology, Vol. VIII, p. 369-446. Acad. Press, N.Y.

WINDELL, J. T.
1966. Rate of digestion in the bluegill sunfish. Invest. Indiana Lakes Streams 7:185-214.