VOLUNTARY SWIMMING SPEEDS AND RESPIRATION RATES OF A FILTER-FEEDING PLANKTIVORE, THE ATLANTIC MENHADEN, *BREVOORTIA TYRANNUS* (PISCES: CLUPEIDAE)

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ABSTRACT

Voluntary swimming speeds and respiration rates of a group of adult Atlantic menhaden (mean wet weight = 302 g) were measured before, during, and after a 7-hour feeding period, during which the diatom *Ditylum brightwelli* was made available at a constant rate. Total ration for the 12 fish ranged between 9.60 and 94.79 g dry weight. Temperature was $20°\pm1°$ C. In the absence of food, the routine swimming speeds and respiration rates of the menhaden were: mean $\pm$ 95% confidence limits = 12.2 ± 1.6 cm per second (0.47 ± 0.06 body lengths per second), and 0.10 ± 0.009 mg O_2 per gram per hour. During feeding the fish increased their voluntary swimming speed 2.4- to 3.5-fold, and their respiration rates 2.2- to 5.4-fold above the routine rates, depending on the concentration of plankton in the water. There was a linear relationship between $\log_{10}$ respiration rate and mean swimming speed during the feeding and the postfeeding periods. During feeding, the metabolic cost per increment in swimming speed was about 2.5 times higher than the cost of swimming in other species; this is believed to reflect a high energetic cost of filter feeding. There was an approximately hyperbolic relationship between the voluntary swimming speed of the Atlantic menhaden, and the phytoplankton chlorophyll *a* concentration in the water. The swimming speed and respiration rate of the fish remained constant as long as the input of phytoplankton into the tank continued at a constant rate. After feeding, the activity levels and respiration rates of the menhaden quickly returned to prefeeding routine rates.

The Atlantic menhaden, *Brevoortia tyrannus*, is a schooling, filter-feeding planktivore (Peck 1894; Durbin and Durbin 1975) which supports a major commercial fishery along the Atlantic coast of the United States.

The present study investigates voluntary swimming speeds and oxygen consumption rates of Atlantic menhaden before, during, and after a 7-h period during which the fish were fed a ration of the diatom *Ditylum brightwelli*. During this period the plankton was made available at a constant rate, so that feeding was continuous and the ingestion rate was constant. The prolonged feeding was designed to reproduce, as much as possible, natural feeding conditions for menhaden. During these experiments ammonia and dissolved organic nitrogen excretion rates, feces production rates, and assimilation efficiencies were also measured and will be reported in a second paper. These studies are part of a larger effort to determine the energy budget of Atlantic menhaden in Narragansett Bay, R.I.

METHODS

Adult Atlantic menhaden were dipnetted from a commercial purse seine, 2-3 min after it had been set around a school. These fish were transferred to a round, 1.2 m diameter tank and brought in good condition to the laboratory. There the fish were maintained outdoors, in a circular fiber glass tank 1.85 m in diameter and 0.76 m deep, supplied with flowing unfiltered seawater. The tank was protected by a large fiber glass canopy.

Five days after capture, the number of fish in the tank was reduced to 25. Once a day the fish were fed a ration of Rangen's[3] salmon feed, size 00 powder, equivalent to 3% of their dry body weight per day. Within 3 wk all fish fed readily in the tank. The fish were held for 6 wk before use in experiments. During this period, the tank was cleaned every day, and preliminary trials were carried out. This enabled the fish to become accustomed to routine sampling procedures, to the presence of observers near the tank, and also to the presence of a clear Plexiglas cover, which was lowered onto the surface of the tank water during respiration mea-

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surements. The experiments were conducted in the same tank in which the fish were maintained. This removed two potential problems: first, the possibility of injury to the fish as a result of frequent handling; and second, the possibility of stress resulting from recent handling and transfer of the fish to an unfamiliar tank. Stress has been shown to affect the respiration rate and swimming performance of schooling fishes (i.e., Skazhina 1975; Hartwell and Otto 1978).

One week before the experiments were begun, one-half of the fish were removed for length and weight determination, leaving 12 Atlantic menhaden in the tank. We have found that 12-15 adult fish is an optimum number for a tank of this size; fewer fish begin to show signs of stress, whereas more fish begin to interfere with each other during feeding. Experiments were carried out between 26 July and 9 September 1977. At the end of this period the fish were sacrificed for length and weight determination. All fish appeared to be in excellent condition thoughout the experimental period, and showed no evidence of injury or disease.

Experimental Procedure

The experiments were carried out at $20° \pm 1.0°$ C and a salinity of 31‰. Prior to each experiment, the bottom and walls of the tank were thoroughly cleaned with a wire brush. The fish were fed their normal ration, and then deprived of food for 36 h until the beginning of the experiment to permit evacuation of the intestine and to avoid any effect of the previous meal on the metabolism of the fish. During this 36-h period, the seawater inflow was filtered through a GAF polypropylene bag filter of 5 μm nominal pore size. Feces from the last meal were periodically siphoned from the tank. On the evening before the experiment, the tank walls were again scrubbed and the tank rapidly flushed several times with filtered seawater.

Each experiment was begun at approximately 0630 h, with an initial baseline measurement of respiration rate and voluntary swimming speed of the unfed fish. Plankton was then added to the tank at a constant rate during a 7-h period from approximately 0800 to 1500 h. During each experiment, respiration rates and voluntary swimming speeds were measured on 10 occasions, termed "measurements," which lasted for about 1 h when the fish were feeding, and 1½-2 h when they were not. These measurements correspond to the fol-

lowing periods: no. 1, initial (unfed for 36 h); no. 2-4, feeding during the 7-h period of food input; no. 5, the transition from feeding to postfeeding; no. 6-8, during the first 10 h following feeding; and no. 9 and 10, the next morning, 15-20 h after feeding.

To prevent an excessive accumulation of ammonia in the tank when the fish were fed the larger rations, the tank was flushed briefly with filtered water at the conclusion of feeding.

Food

The solitary diatom *Ditylum brightwelli* was used as food in the experiments. These large cells ($\sim$80 μm long) are readily eaten by menhaden. Phytoplankton was raised in outdoor batch cultures. Narragansett Bay water was filtered into 400 l fiber glass tanks, using a series of four cartridge filters culminating in a Gelman 0.45 μm membrane filter, and then enriched to the level of Guillard's F/2 (Guillard and Ryther 1962).

Large volumes (up to 2,500 l) of culture were raised for each experiment, and it was necessary to concentrate the cells before feeding them to the fish. Since the duration of the feeding period was 7 h, the culture was divided into seven batches of equal volume. Each batch was concentrated by gentle back filtration into a volume of 18 l, which was then subsampled by filtering onto a precombusted glass fiber filter for determination of the C and N concentration (Hewlett Packard Model 185B CHN Analyzer). On several occasions additional subsamples were centrifuged to form a pellet, from which the water was aspirated off, and the C, N, ash (combustion at 475°C for 4 h), caloric (Parr adiabatic bomb calorimeter), and Si (Durbin 1977) contents were determined. Each 18 l batch of food was slowly siphoned into the tank over a 1-h period, to provide an approximately constant rate of input of food. By changing the concentration of plankton in these batches, different concentrations of food in the tank and different ration sizes could be obtained. The volume of water added with the food was balanced by the volume removed during sampling, and thus the volume in the tank (1,400 l) remained approximately constant. The chlorophyll *a* concentration in the tank was also periodically determined by fluorometry (Yentsch and Menzel 1963; Lorenzen 1966).

Turbulence produced by the fish stirred the tank and kept the plankton in suspension. The Atlantic menhaden were estimated to filter 13-20% of the tank volume per minute, removing the *D.*

brightwelli with an efficiency of about 25% (Durbin and Durbin 1975).

Respiration Rate

Oxygen consumption by the fish was determined by closed system respirometry. The water in the tank was sealed from contact with the atmosphere by means of a circular cover made of clear 1.2 cm Plexiglas, suspended on pulleys over the tank, which could be gently lowered onto the water surface. Replicate water samples for oxygen determinations (Strickland and Parsons 1972) were siphoned from the tank through a sampling port every 12 min during feeding measurements, and every 20 min during nonfeeding measurements. The precision of the method was ± 0.019 mg O_2/l. Measurements of oxygen from different locations in the tank demonstrated that the movement of the fish kept it well mixed at all times. Control measurements on the tank, filtered seawater, and tank water after the addition of phytoplankton demonstrated that these did not contribute significantly to the change in oxygen content of the water during respiration measurements. The oxygen level in the tank was not allowed to drop by more than 2 mg/l during any measurement; between measurements, the lid was raised off the surface of the water, and air was bubbled through the airstones along the tank walls. The decline of oxygen in the tank with time was linear, with a correlation coefficient of 0.98 or better in all cases; the mean respiration rate of the fish was calculated from the slope of this regression. Ninety-five percent confidence limits (CL) were computed for the slope and used to calculate the 95% CL for the respiraton rate in each measurement. Respiration rates are reported as milligrams oxygen consumption per gram wet weight of fish per hour (mg O_2/g per h).

Swimming Speed

During the respiration measurements the swimming behavior of the fish was recorded with a Sankyo ES-44XL 8 mm movie camera, equipped with a wide angle lens and a remote control and mounted above the tank. The fish were photographed with Kodak Ektachrome 160 film, exposed at 9 frames/s. Paired 10 s shots, 1 min apart, were taken every 6-10 min while the fish were feeding, and every 15-20 min when they were not feeding. Films were later analyzed using a Kodak

Model MPG-TH microfilm reader at a magnification of 34×. A sheet of clear acetate was placed over the viewing screen, and the location of each fish was plotted at every fifth frame (the corresponding time interval at 9 frames/s = 5/9 s) when the fish were feeding and swimming rapidly, and every 10th frame (or, every 10/9 s) when the fish were not feeding and swimming slowly. These measurements were then converted to swimming speed in centimeters per second and body lengths (BL) per second. Vertical travel by the fish, which was not corrected for in this method, was negligible since the fish tended to maintain themselves at middepth in the water column.

During each measurement of oxygen consumption, an average of 680 observations of swimming speed were obtained. The average swimming speed during each measurement was determined from the mean of all observations $\pm 95\%$ CL. The distribution of swimming speeds within each measurement was compared with a normal curve. Measurements were compared by first testing for homogeneity of variance, and when appropriate the significance of the difference between means was tested using analysis of variance. When variances were nonhomogeneous, differences between means were tested according to a nonparametric test.

The mean values of each measurement were used to determine the relationship between swimming speed and respiration rate. Measurements were grouped into three categories: initial and final (unfed), feeding, and postfeeding. In the latter two categories there was a linear relationship between swimming speed and log oxygen consumption. Predictive regressions of Y on X are presented to permit the comparison of present results with those in earlier studies. However, we also present the functional regressions (GM) (Ricker 1973), which represent the geometric mean of the regression of Y on X and the reciprocal of the regression of X on Y. Although there has been some controversy on the subject (Jolicoeur 1975; Ricker 1975) the functional regression nevertheless appears to be the preferable method of describing the data. Differences in the slopes and elevations of the regressions were tested for significance by covariance analysis.

RESULTS

The menhaden were 3 yr old, with a mean fork length of 25.8 cm (range 23.0-27.9 cm), a mean wet

TABLE 1.—Basic data on feeding experiments with a school of 12 Atlantic menhaden, total wet weight = 3,624 g. Oxycalorific coefficient used was 4.7 cal/ml of oxygen consumed (Kleiber 1961). Column numbers, in brackets, are for text reference.

Experiment no. (1)	Total ration		Total respiration in excess of routine during the 7-h feeding period			Total respiration in excess of routine during the postfeeding period		
	G dry wt (2)	Kcal (3)	MgO_2 (4)	Kcal (5)	% of ration kcal (6)	MgO_2 (7)	Kcal (8)	% of ration kcal (9)
6	94.79	177.4	10,220	33.62	19.0	1,812	5.96	3.36
4	86.93	162.7	10,075	33.15	20.4	2,040	6.71	4.13
5	67.46	126.3	9,640	31.72	25.1	1,634	5.38	4.26
9	27.64	51.7	5,871	19.32	37.4	286	0.94	1.82
7	20.76	38.9	4,711	15.50	39.8	315	1.04	2.66
8	15.43	28.9	3,914	12.88	44.6	496	1.63	5.65
10	9.60	18.0	2,979	9.80	54.4	573	1.89	10.47

weight of 302 g (range 248-346 g), and a mean dry weight of 104 g.

The food rations ranged from 0.79 to 7.8% of the dry weight of the fish, and thus during the 7-h feeding period the fish fed at rates equivalent to 0.11-1.11% of their dry weight per hour (Table 1).

In a filter feeder such as the Atlantic menhaden, the food ration obtained depends on the volume of water filtered, corrected for the filtration efficiency of the gill rakers. The volume filtered is essentially cylindrical, with cross-sectional area equal to the area of the fish's open mouth, and length equal to the distance swum by the fish in a unit of time. It is shown below that the fish swam at about the same average speed during feeding,

and since all fish were of similar size, each fish filtered an approximately equal volume of water during the 7-h feeding period. Thus we assume that each fish obtained the same proportion (1/12) of the plankton added to the tank.

The behavior of the fish followed the same general pattern in all experiments (Figures 1, 2). The voluntary swimming speeds and respiration rates of the fish were low during the initial measurement and then abruptly increased severalfold over the initial rates during feeding. When the input of food was stopped, the fish rapidly filtered the remaining plankton from the water, decreasing their swimming speed and respiration rate as the plankton levels dropped. During the postfeeding period there was a gradual return to prefeeding activity levels and respiration rates, a transition which was completed before the final two measurements on the following morning.
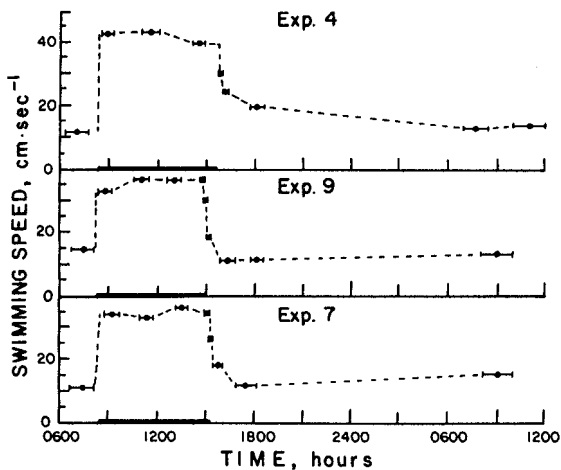

FIGURE 1.—Mean voluntary swimming speed of a school of 12 Atlantic menhaden before, during, and after a 7-h period (indicated by the heavy line on the x-axis) during which they were fed, at a constant rate, a ration of the diatom *Ditylum brightwelli*. Three representative experiments are shown, in which total rations were: no. 4, 162.7 kcal; no. 9, 51.7 kcal; no. 7, 38.9 kcal. The 95% confidence limits were enclosed by the symbols; horizontal bars indicate the duration of each experiment.
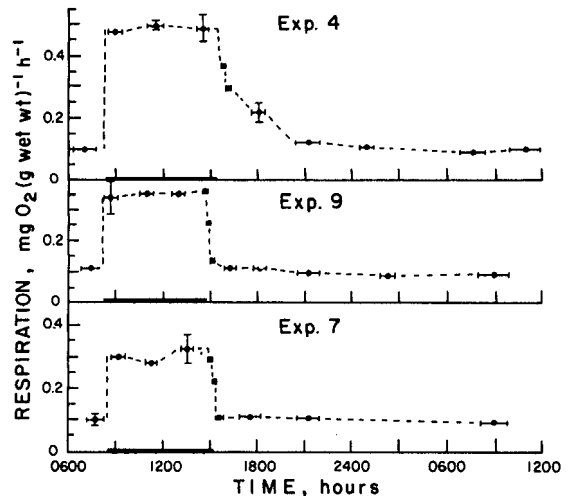

FIGURE 2.—Mean respiration rate for Atlantic menhaden in the measurements presented in Figure 1. The 95% confidence limits are shown by vertical bars when they exceed the size of the symbol.

In most measurements the distribution of swimming speed observations showed small but statistically significant ($\chi^2 < 0.01$) departures from normality. These usually took the form of a slight positive skewness, and leptokurtosis (data values concentrated in the region of the mean).

The variance of the swimming speed, which included the variability shown by each individual fish, as well as differences among fish, was positively correlated with the mean. However, the coefficient of variation revealed that the fish were relatively more variable in their swimming behavior when they were not feeding (Figure 3). These results confirmed qualitative observations during the experiments that the fish were least excitable, and most consistent in their swimming behavior, when they were engaged in feeding.

With the exception of measurement no. 5, which bracketed the transition from feeding to postfeeding, the fish were very consistent in their swimming behavior and respiration rate during individual measurements. Thus the 95% CL about the
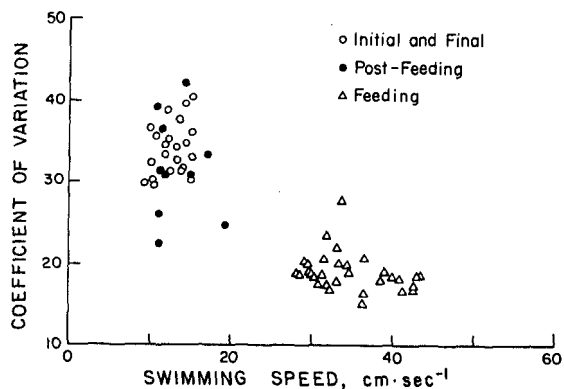
estimates of mean respiration rate and swimming speed during each of the measurements were small, averaging ±8.9% of the mean respiration rate and ±2.3% of the mean swimming speed.

Initial and Final Measurements (No. 1, 9, 10)

These may be termed "routine" (Fry 1957) since the fish were unfed and spontaneously active. During these measurements the fish swam slowly about the tank without showing any strong schooling patterns. The mean swimming speeds and respiration rates were very similar during the initial and final measurements (Table 2). The range among the mean voluntary swimming speeds of the measurements was also fairly small, 10.5-15.2 cm/s (0.41-0.59 BL/s) (Figure 4). The range among

FIGURE 3.—Relationship between mean and coefficient of variation ($\sigma/\bar{x}$ [100%]) in the swimming speeds of a school of 12 Atlantic menhaden during the initial and final, feeding, and postfeeding measurements.

$$(S-12.2) = \frac{29.62 (A-1)}{0.396 + (A-1)}$$

Where S = Swimming speed, cm·sec^{-1}
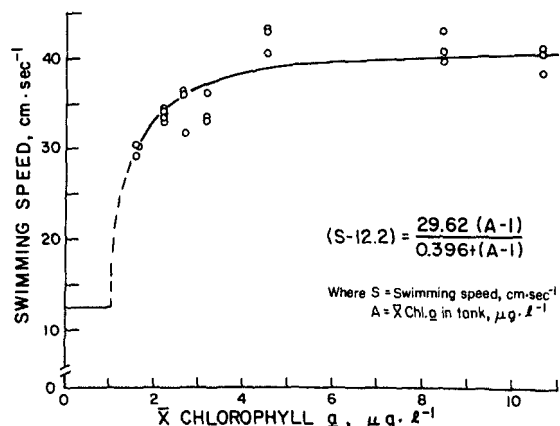A = $\bar{x}$ Chl.$\underline{a}$ in tank, $\mu g \cdot \ell^{-1}$

FIGURE 4.—Hyperbolic relationship between voluntary swimming speed (S) of a school of 12 Atlantic menhaden feeding on *Ditylum brightwelli*, and chlorophyll *a* concentration in the water (A). The three measurements of mean swimming speed obtained during the 7-h feeding period of each experiment are plotted as a function of the mean chlorophyll *a* concentration during each experimental feeding period.

TABLE 2.—Swimming speeds (S) and respiration rates (R) of Atlantic menhaden in the feeding experiments and their regression equations.

Measurements (periods)	Mean ± 95% confidence limits	
	Swimming speed cm/s	Respiration rate mg O₂/g per h
Initial (no. 1)	12.2±1.6	0.10 ±0.009
Final (no. 9, 10)	13.4±1.2	0.093±0.007

	Derived regressions		
	Predictive		Functional (GM)
Feeding (no. 2, 3, 4)	$\log_{10}R = 0.0271 (S) - 1.446$ Equation (2) $r = 0.918$, SE slope = 0.0026		$\log_{10}R = 0.0295 (S) - 1.534$ Equation (3)
Postfeeding (no. 6, 7)	$\log_{10}R = 0.0293 (S) - 1.276$ Equation (4) $r = 0.856$, SE slope = 0.0062		$\log_{10}R = 0.0342 (S) - 1.342$ Equation (5)

the respiration rates was similarly narrow and did not show any clear relationship with swimming speed (Figure 4).

Feeding Measurements (No. 2, 3, 4)

As soon as food was added, the fish began "tasting" the water by flaring their opercula and swimming rapidly forward for a few seconds. After 1-2 min they began to feed, circuiting the tank and swimming in the same direction at about the same speed. Within each experiment, the mean voluntary swimming speed and the associated respiration rate remained nearly constant throughout the entire 7-h feeding period (Figures 1, 2). The mean swimming speed was established during the first 15 min of feeding and was related to the amount of plankton in the water (Figure 4). Within a range of about 1.5-4 μg chlorophyll a/l the voluntary swimming speed and respiration rate of the fish were roughly proportional to the chlorophyll a content of the water. Above about 4 μg chlorophyll a/l however, the swimming speed was independent of plankton concentration. In the three high-ration experiments during feeding, the mean speed ±95% was 41.3±1.5 cm/s and the corresponding mean respiration rate was 0.48±0.029 mg O_2/g per h. The relationship between chlorophyll a concentration and the voluntary

swimming speed can be described by a rectangular hyperbola [Equation (1), see Figure 4]. The zero point for the curve was taken as the mean swimming speed of unfed fish (12.2 cm/s) and the approximate concentration threshold (1 μg chlorophyll a/l) (Durbin and Durbin 1975) of $D.$ $brightwelli$ at which Atlantic menhaden will begin to feed.

In these experiments the mean voluntary swimming speed of the Atlantic menhaden during feeding ranged between 29.3 and 43.4 cm/s (1.14-1.68 BL/s). This represented a 2.2-3.3 fold increase over the mean prefeeding routine swimming speed (12.2 cm/s). Respiration rates during feeding ranged between 0.221 and 0.538 mg O_2/g per h and were thus elevated 2.2-5.4 fold over the mean initial routine respiration rate (0.10 mg O_2/g per h). There was a good linear relationship between the mean swimming speed during feeding and the log_{10} transformed mean respiration rate (Figure 5, Table 2).

Postfeeding Measurements (No. 6, 7, 8)

When the input of food was stopped at the end of 7 h, the fish rapidly depleted the plankton remaining in the tank. Within 5 min the swimming speed of the fish decreased noticeably, and as plankton levels continued to decline, the fish progressively reduced their swimming speed (Figure 1, measurement 5). Respiration rates also declined (Figure 2). Feeding usually became intermittent within 15-20 min, and ceased entirely during the next one-half hour, at which time the plankton in the tank had been reduced to a negligible level.

After the Atlantic menhaden had removed the last of the plankton, they continued to "taste" the water fairly frequently and were somewhat restless, as though searching for additional food. During this postfeeding period, however, there was a gradual return toward the prefeeding behavior. Dusk arrived during or shortly after the second postfeeding measurement. Although it was not possible to photograph the fish during the third postfeeding measurement at midnight, their activity levels appeared to be very low as indicated by their low respiration rates, and qualitative observations of their swimming behavior in the dim light.

The postfeeding measurements were spaced too far apart to precisely define the time by which the fish returned to their routine activity and metabolic levels. In general the duration of this
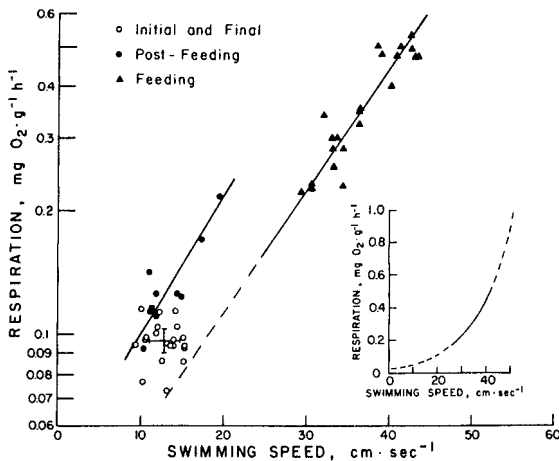

FIGURE 5.—Relationships between mean voluntary swimming speed and mean respiration rate of a school of 12 Atlantic menhaden. The $\bar{x}$ and 95% confidence limits of the initial and final measurements are shown; functional regressions shown for the feeding and postfeeding measurements are presented in Table 2. Inset is an arithmetic plot of Equation (3); extrapolations beyond observed data are dashed.

period was greater with larger ration sizes (~4.5 h, experiment 4); at low food levels (e.g., experiments 7, 9) the respiration rate had essentially returned to baseline in <2 h (Figure 2).

The mean swimming speed of the first two postfeeding measurements (no. 6, 7) usually fell within the range of the routine swimming speeds; however, the respiration rates tended to be elevated above the routine rates (Figure 5). There was a linear relationship between mean swimming speed and $\log_{10}$ respiration rate in these postfeeding measurements (Figure 5, Table 2).

DISCUSSION

These results demonstrate that the voluntary swimming speed of adult Atlantic menhaden is related to the availability of plankton food in the water. If food is not present, the voluntary swimming speed and respiratory rate of Atlantic menhaden are low. Swimming speed increases during feeding, following an approximately hyperbolic relationship with increasing plankton density in the water. Over a wide range of plankton concentrations the characteristic swimming speed of the menhaden is about 1.60 BL/s, with a respiratory rate of about 0.48 mg O_2/g per h. This approximately 5-fold increase in respiratory rate above the routine implies that the energy expenditures during feeding will be a major element in the energy budget of menhaden.

Previous descriptions of menhaden feeding behavior (Durbin and Durbin 1975), based on short-term experiments in which the plankton concentration decreased during the course of each experiment, were generally confirmed by the present study. However, respiration rates measured in the present study indicate that the feeding frenzy, which was observed in the earlier study after a large amount of zooplankton was added to the tank, is not likely to persist during prolonged feeding in nature. Swimming speeds during the frenzy were estimated to be about 2-2.5 BL/s. The energy cost of swimming at these speeds, as estimated from Equation 3 (Table 2), would be high (10-23 times the routine metabolic rate) and would not appear to be bioenergetically profitable over prolonged periods.

The same general behavior patterns have been observed in five groups of Atlantic menhaden collected during three summers. Such consistency indicates that the behavior of the Atlantic menha-

den in the laboratory can provide insight into their behavior in the field. However, these laboratory based predictions of menhaden swimming speeds need to be tested in the field.

Satiation has often been observed to be an important feature which affects the feeding behavior of fishes (i.e., Ivlev 1961). This is most evident for "macrophageous" fishes (those which take their food in large particles). In the present study, however, there was no evidence of satiation even with the largest ration, when the fish consumed the equivalent of 8% of their body weight during a 7-h period. Evidence of satiation would include a decrease in their swimming speed during the experiments or a switch to intermittent feeding. In contrast, the fish fed continuously at a constant rate as long as food was available, and they continued to search for food after it stopped coming into the tank. Plankton densities sufficient to saturate the physical capacity of menhaden to handle and process food may not be of much ecological significance. This is because natural plankton populations in the size range which can be filtered by menhaden are seldom found in concentrations greater than those used in the present experiments. The high concentrations of chlorophyll a which occur in coastal and estuarine waters during the summer are primarily small flagellates (e.g., Durbin et al. 1975), which are too small to be retained on the gill rakers of the menhaden (Durbin and Durbin 1975).

There are comparatively few studies which have simultaneously measured routine respiration rate and activity. At very low swimming speeds, respiration rate has been found to be linearly (Spoor 1946) and log linearly (Smit 1965; Muir et al. 1965) related to activity. In the present study, the routine swimming speeds were clustered within a narrow range (0.36-0.59 BL/s), and there was no detectable relationship between respiration rate and swimming speed.

In all of the nonfeeding (initial, final, postfeeding) measurements, the respiration rates were higher than those which would have been predicted from the observed swimming speeds and an extrapolation of Equation (3) (Table 2, Figure 5). Thus the respiration rates of the fish when they were not feeding, and therefore swimming slowly, were higher per unit swimming speed than when the fish were feeding and swimming more rapidly. These results were consistent with previous studies, in which routine metabolic rates also tended to be variable, and elevated above those

predicted from respiration rate-swimming speed relationships during long-term swimming at constant speed (Brett 1964; Smit 1965; Muir and Niimi 1972). Explanations for this phenomenon include: 1) stress, which elevates the metabolic rate, is reduced when the fish are occupied by some activity such as swimming against a water current (Brett 1964), or feeding, if the fish are nonaggressive (this study); 2) the intermittent swimming of spontaneously active fish, accompanied by frequent accelerations and changes in direction, is hydrodynamically less efficient than the smooth caudal locomotion of continuous swimming and thus exacts a relatively higher metabolic cost (Smit 1965).

The increased respiration rates during feeding consumed a significant fraction of the energy obtained from the ration (Table 1, column 6). Energy expenditures above routine during the postfeeding period averaged 4.61% of the energy contained in the food ration (Table 1, column 9). The increased metabolic rate during and soon after feeding appeared to be primarily due to the increased voluntary swimming speed. Swimming speed accounted for 84.3% of the variability in metabolic rate during feeding and 73.3% during the postfeeding period (Table 2). Other factors which may affect the metabolic rate as a result of feeding include changes in excitability of the fish, and the calorigenic effect of the food ration (SDA, the "specific dynamic affect").

The excitability of the fish is in practice difficult to measure. Qualitative observations of the behavior of the fish and the degree of variability in their swimming behavior (Figure 3) indicated that excitability was not a significant factor contributing to the elevated respiration during feeding, but could be important during the postfeeding period of restlessness. The latter evidently resulted from the abrupt termination of the input of food when the fish were not satiated.

The cost of digestion and transformation of the food, or SDA, has generally been measured as an increase in oxygen consumption following feeding (Kleiber 1961; Warren and Davis 1967). In several earlier studies, in which fish were fed a single meal over a brief period, the increase in oxygen consumption peaked several hours after the meal, then gradually subsided over a prolonged period (as long as 2-3 d) to the prefeeding level (Muir and Niimi 1972; Pierce and Wissing 1974; Beamish 1974). In these species, digestion of the food also occurs over an extended period. The energy loss to

SDA was generally estimated to represent about 12-16% of the energy content of the ration.

The Atlantic menhaden results differed considerably from these earlier studies. There was no peak in oxygen consumption during the postfeeding period, but instead a rapid and continuous return of the metabolic rate to the prefeeding level. This rapid return is consistent with the rapid digestion rates observed for menhaden.[4] Food was assimilated within 1-2 h after ingestion, and approximately 80% of the food ingested during the 7-h feeding period was digested and assimilated within the same period. The amount of energy expended above the routine during the postfeeding period was larger in the larger ration experiments (Table 1, columns 7, 8), which may appear to indicate some effect of SDA. However, voluntary activity levels were also higher in these experiments. SDA is believed to be proportional to ration size, but if the oxygen consumption attributable to swimming activity, Equation (3) (Table 2) is subtracted from the total respiration rate during the postfeeding period, there was no relationship between ration size and the amount of elevated respiration which can be ascribed to SDA.

Thus, while Atlantic menhaden may be assumed to experience some respiratory costs related to SDA, the major part of these will be included as a part of the total respiratory increase during feeding. In practice it would be very difficult to distinguish SDA in the total metabolism because of the overwhelming effect of swimming speed on the metabolic rate.

Equations (2) and (3) (Table 2) may be extrapolated to zero activity to obtain an estimate of standard metabolism. These estimates, 0.036 mg O_2/g per h from Equation (2) and 0.029 mg O_2/g per h from Equation (3) are generally lower than those reported from most other fishes which have been studied (Table 3). Respiration rates which menhaden sustained during feeding were also high relative to those which can be sustained by other species, and actually exceeded the active rate (the maximum which can be maintained for 1 h) (Brett 1964) of a number of species, including the aholehole, largemouth bass, rainbow trout, and tilapia (Table 3). Since the present study measured only voluntary respiration rates, the active

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[4]Durbin, E. G., and A. G. Durbin. Assimilation efficiency and nitrogen excretion of a filter-feeding planktivore, the Atlantic menhaden *Brevoortia tyrannus*. Unpubl. manuscr.

TABLE 3.—Metabolic rates among 10 fish species. Except where noted, rates were extrapolated to a 300 g fish, using the appropriate weight-swimming speed-respiration relationships.

Species	Temperature (°C)	Standard mg O_2/g per h	Active mg O_2/g per h	Author
Brook trout, Salvelinus fontinalis	20	0.153		Beamish (1964)
White sucker, Catostomus commersonii	20	0.086		Beamish (1964)
Brown bullhead, Ictalurus nebulosus	20	0.093		Beamish (1964)
Carp, Cyprinus carpio	20	0.043		Beamish (1964)
Tilapia, Tilapia nilotica	25	0.086	0.378	Farmer and Beamish (1969)
Largemouth bass, Micropterus salmoides	20	~0.10	0.302	Beamish (1970)
Rainbow trout, Salmo gairdneri[1]	15	0.073	0.48	Webb (1971)
Aholehole, Kuhlia sandvicensis	23	0.043	0.387	Muir and Niimi (1972)
Sockeye salmon, Oncorhynchus nerka	20	0.103	0.799	Brett and Glass (1973)
Atlantic menhaden, Brevoortia tyrannus[1]	20	0.029	(0.538)[2]	This study

[1]Actual measured values; $\bar{x}$ wet weight of rainbow trout = 272 g, and Atlantic menhaden = 302 g.
[2]Maximum voluntary metabolic rate in this study; presumably less than active rate.

rate in menhaden remains unknown, though presumably higher than those reported here. Thus the metabolic "scope" (Fry 1947) in menhaden appears to be significantly larger than that of many species. A large metabolic scope is consistent with Hartwell and Otto's (1978) finding that the critical swimming speeds in juvenile Atlantic menhaden far exceed those reported from other species: at 20° C nonfeeding fish averaging 5.8 cm standard length were able to maintain a speed of 15.8 BL/s for 64 min and a speed of 20.8 BL/s for 2 min. In contrast, at 20° C the critical speed of a 6 cm sockeye salmon, for example, is only about 6.5 BL/s (Brett and Glass 1973).

The respiration during feeding increased significantly faster per increment in swimming speed in menhaden than in other species which have been studied. In Atlantic menhaden an increase in swimming speed of 1 BL/s caused a 5.8-fold increase in the respiration rate (Table 2, Equation (3)); while for eight species reviewed by Beamish (1978) (Oncorhynchus nerka, Lepomis gibbosus, Melanogrammus aeglefinus, Tilapia nilotica, Micropterus salmoides, Liza macrolepis, Cyprinus carpio, Salmo gairdneri), a similar increase in speed caused a roughly 2.3-fold elevation in the metabolic rate. Thus the cost of increasing the swimming speed is 2.5 times higher in Atlantic menhaden during feeding than in these eight species (which were not feeding).

The very steep slope of the swimming speed-respiration relation for the Atlantic menhaden indicates that during feeding, the loss in streamlining caused by the expanded opercula and the resistance of the closely spaced gill rakers substantially increase the hydrodynamic drag of the fish. It is likely that the respiratory cost for nonfeeding Atlantic menhaden swimming at equivalent speeds would be much lower. It would be of

interest to determine the maximum swimming performance of nonfeeding adult fish, for comparison with Hartwell and Otto's (1978) data from juveniles.

The rapidly increasing respiratory cost of swimming during feeding is perhaps more clearly illustrated when the relationship is plotted arithmetically (Figure 5, inset). The highest mean voluntary swimming speed in the present experiments, 43.4 cm/s or 1.68 BL/s, is very close to the inflection of the curve in Figure 5 (inset), beyond which an increase in swimming speed drastically increases the metabolic rate. Because of the high energy cost it is likely that in nature the voluntary swimming speeds of adult Atlantic menhaden during feeding will be <2 BL/s for most of the time.

In conclusion, the Atlantic menhaden, a filter-feeding planktivore, offers an interesting contrast to pelagic predaceous fishes, which have been more widely studied (Durbin 1979). These predators typically consume their daily ration in a few large meals (they are "macrophagists"). The time and energy costs of feeding varies in different species, and the energy lost to SDA is a conspicuous component of their daily metabolism. In contrast, a "microphagist," such as the Atlantic menhaden, consumes its food as a continuous stream of very small food particles. While the energy cost associated with feeding is consistently high, in menhaden there is no extended period of elevated respiration following feeding, as observed in macrophagists, but rather a continuous and rapid return to prefeeding rates.

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