Metabolic rate in relation to temperature and swimming speed, and the cost of filter feeding in Atlantic menhaden, *Brevoortia tyrannus*

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Abstract.—Respiration rates of non-feeding adult menhaden induced to swim against currents of various speeds in a large circular flume at 10°, 15°, and 20°C were measured in order to quantify the cost of swimming separately from total metabolic expenditure during filter feeding. Standard metabolic rates of 0.040, 0.073, and 0.087 mg O_2 / (g wet wt · h) at 10°C, 15°C, and 20°C were estimated by extrapolation of the relationship of swimming speed and metabolic rate to zero swimming speed. We determined that when menhaden filter-feed at 20°C, at the preferred swimming speed of 41.3 cm/s, filtering and specific dynamic action (SDA) account for 59% of total energetic expenditures. The cost of locomotion was only about 23% of the total expenditure. Our results are compared with routine oxygen consumption rates of larval and juvenile menhaden as a function of temperature and with extensive metabolic data for sockeye salmon.

The Atlantic menhaden, *Brevoortia tyrannus,* is a pelagic filter-feeding clupeoid inhabiting coastal waters of North America from Maine to Florida. Menhaden adopt filter feeding in early juvenile life (Peck, 1893; June and Carlson, 1971; Friedland et al., 1984). Adults are obligate filter feeders and consume phytoplankton, zooplankton, and detritus larger than about 13 µm (Durbin and Durbin, 1975). Menhaden are size selective in their feeding, but the basis of selection is passive, reflecting the size distribution of particulate material in the water relative to the "pore size" of the gill rakers; they do not actively pursue individual prey. Energy expenditures during "ram" filter feeding (analogous to towing a plankton net) are high (Durbin et al., 1981; Sanderson and Cech, 1992), probably due to the hydrodynamic drag of the filtering apparatus. However, menhaden compensate for the high cost of filter feeding by regulating their swimming speed to maximize the ratio of net energy gain to expenditure (Durbin and Durbin, 1983), as predicted by Ware (1975). Our study was undertaken to partition the previously determined energetic cost of filter feeding (Durbin and Durbin, 1983) into two components: the cost of locomotion alone and the cost of filter feeding. This division was accomplished by measuring respiration rates of nonfeeding fish forced to swim against currents of known speed and by comparing these respiration rates with those of feeding fish.

Materials and methods

Live Atlantic menhaden, *Brevoortia tyrannis*, were collected from a commercial fish trap located in the lower West Passage of Narragansett Bay on 22 and 25 September 1989. The fish were removed from the trap with dip nets and placed in 114-L seawater-filled polyethylene garbage cans for transport to the Narragansett Bay Campus. Menhaden were randomly divided and placed with three open-flow circular fiberglass tanks, 1.7 m in diameter and 0.5 m deep, supplied with sand-filtered seawater. Acclimation to the three test temperatures (10°, 15°, and 20°C) began 5 October 1989, starting from the ambient temperature, 18°C, with a rate of change of about 1°C/d. Ambient salinities varied between 28 and 30 ppt. The fish were considered acclimated after maintenance for 30 days at the target temperature. Menhaden were fed salmon starter mash (Ziegler Bros., Inc.) at a rate of about 4.5% of dry food:live

Table 1

Vital statistics for the experimental fish are given in the upper panel. Relationships between respiration rate (R, mg O_2/(g wet wt · h)) and swimming speed (S, cm/s or body lengths [BL/s]) are given in the lower panel. T = temperature and FL = fork length, NF = not fed for 24 h, and FF = filter feeding.

T (°C)	No. of fish in sample	FL (cm)	Wet wt (g)	Dry wt (g)
10	13	26.0 ± 0.9	327 ± 45	99.2 ± 15.6
15	13	25.5 ± 0.6	303 ± 38	92.1 ± 15.2
20	10	25.5 ± 1.2	283 ± 40	86.4 ± 12.3

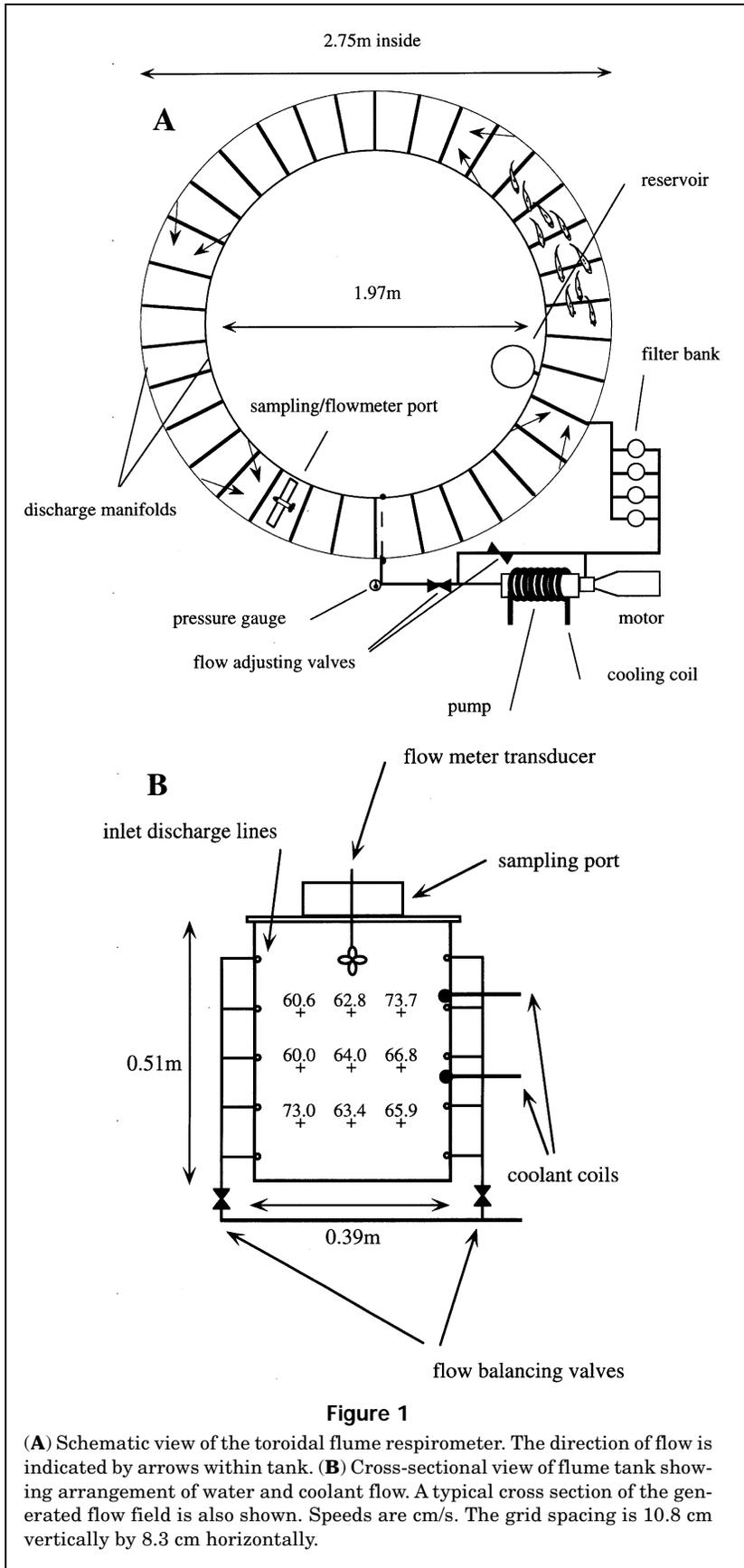| T (°C)	Behavior	Regression equation	r^2	Source
10	NF	$\log_{10} R = 0.0141\, S\,(\text{cm/s}) - 1.402$ $\log_{10} R = 0.3655\, S\,(\text{BL/s}) - 1.598$	0.99	This study
15	NF	$\log_{10} R = 0.0095\, S\,(\text{cm/s}) - 1.139$ $\log_{10} R = 0.2419\, S\,(\text{BL/s}) - 1.861$	0.90	
20	NF	$\log_{10} R = 0.0086\, S\,(\text{cm/s}) - 1.061$ $\log_{10} R = 0.2187\, S\,(\text{BL/s}) - 1.939$	0.96	
20	FF	$\log_{10} R = 0.0271\, S\,(\text{cm/s}) - 1.446$	0.84	Durbin et al. (1981)

weight/d. The acclimation tanks were cleaned daily. During the holding and experimental periods, a 12 h:12 h light:dark photoperiod was provided by overhead fluorescent lights, and sufficient current was provided to cause the fish to orient head into the current. Experiments took place 3–14 December 1989. Vital statistics for the fish are given in the top section of Table 1.

Respiration measurements were made on a small school of menhaden because studies of schooling fishes have shown that respiration rates are higher and growth rates lower in isolated fish than in those kept in groups (Skazhina, 1975; Kanda and Itazawa, 1978; see also Ross and Backman, 1992). Experiments were begun with the 15°C trials on 3 and 4 Dec., followed by the 10°C trials on 7 and 8 Dec. The 20°C trials were conducted on 14 Dec. Thirteen fish were used for the 10°C and 15°C experiments. For the 20°C trials only 10 fish were used. Digestion is rapid in menhaden (Durbin and Durbin, 1981), and metabolism quickly returns to preceding levels after a meal (Durbin et al., 1981). Thus a starvation period of 24 h was considered sufficient to remove the effect of the previous meal on metabolic-rate measurements. Handling and transfer protocols were similarly chosen to reduce bias due to stress-induced factors, such as those identified by Waring et al. (1992) in flounder and salmon.

A sealed, toroidal fiberglass flume tank (Fig. 1A), modified from Hettler (1976), was used as a respirometer. The flume (2.75 m inside diameter, 0.51 m depth, and 0.39 m wide annular swimming channel) was large enough to hold a small school of adult menhaden. The flume was painted with a white, nontoxic, polyester gel coat. Black radial stripes 5.1 cm wide, spaced 21.8 cm apart (at the inside diameter of the flume), were painted on the walls and bottom of the flume, to provide reference marks for later determination of swimming speeds and to provide visual cues for the fish to sense displacement by the flow. To produce the desired flow rates, a high-pressure, 3.7-kW, multi-stage electric pump (Fig. 1A) was connected to coils of polyethylene tubing (6 mm inside diameter) arrayed along the walls of the flume (Fig. 1B). Discharge holes were punched at an angle of about 45° downstream and 20° downward from the horizontal with a hypodermic needle along the length of tubing to form small jets creating a counterclockwise flow in the flume. A valve placed at the pump outlet (Fig. 1A) controlled the speed of water in the flume. Return water to the pump flowed through a drain line located at the bottom of the tank and thence through a bank of 4 fiber-wound cartridge filters (3 μm). An integral reservoir (12.9-L capacity) was used to replenish sample water removed during experiments. Cooling coils were installed along the inner wall of the flume and around the pump housing (Fig. 1B) to remove heat generated by the pump and to maintain a constant temperature during trials. Water temperature was monitored with a YSI Model 2100 Tele-thermometer.

Flow rates within the flume were measured with a General Oceanics Inc. flowmeter connected to a proprietary digital display. The transducer head was

A

2.75m inside

1.97m

reservoir

filter bank

sampling/flowmeter port

discharge manifolds

pressure gauge

flow adjusting valves

pump

motor

cooling coil

B

flow meter transducer

inlet discharge lines

sampling port

0.51m

60.6	62.8	73.7
60.0	64.0	66.8
73.0	63.4	65.9

coolant coils

0.39m

flow balancing valves

Figure 1

(**A**) Schematic view of the toroidal flume respirometer. The direction of flow is indicated by arrows within tank. (**B**) Cross-sectional view of flume tank showing arrangement of water and coolant flow. A typical cross section of the generated flow field is also shown. Speeds are cm/s. The grid spacing is 10.8 cm vertically by 8.3 cm horizontally.

suspended in the flume by a stainless steel rod (Fig. 1B). During experiments the flowmeter head was fixed radially in the middle of the flume, near the top of the water column. However, sensor depth and radial position could be varied to measure flow rate in different regions of the flume. By varying the number of discharge holes across the vertical array of inlet coils and by regulating the flow to the inner and outer inlet coils, it was possible to produce a relatively uniform cross-sectional flow field. Typical flow rates (cm/s) determined at maximum pump pressure (1.38×10^3 kPa), on a grid 10.8 cm vertically by 8.3 cm horizontally measured vertically from the flume bottom, are shown in Figure 1B. Preliminary trials established that the relationship between pressure of the inflowing water from the pump and the flow rate generated inside the flume was linear up to the maximum pump pressure, 1.38×10^3 kPa, corresponding to a flume speed of 64 cm/s. Blank trials without fish demonstrated that the system was airtight and that changes in oxygen concentration due to microbial respiration were negligible over periods comparable to those in the experiments.
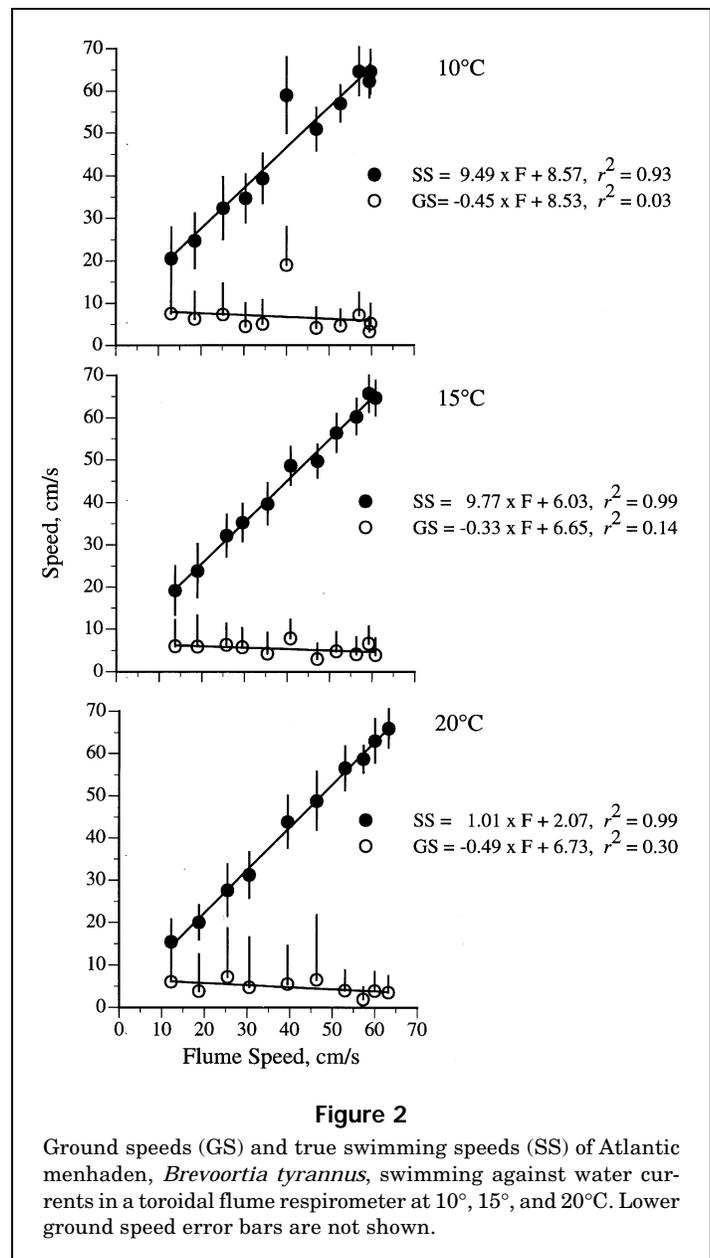
Each experiment comprised a series of trials over a 2-d period. Menhaden were anesthetized with MS-222 and transferred to the flume 24 h before an experiment to permit recovery from handling stress (Barton and Schreck, 1987; Waring et al., 1992). The menhaden remained in the flume until the conclusion of the experiment and were fed in the late afternoon of each day. In the morning, fecal material and debris was siphoned off the bottom of the flume, the bottom and interior walls of the flume were scrubbed with a polyethylene scouring pad, and the flume was flushed with filtered seawater. All experiments were conducted during daylight in the afternoon, 24 h after the last feeding. The fish were accustomed to this procedure and quietly circuited the flume. A clear

Plexiglas lid, composed of interlocking sections, was then carefully fitted over the surface of the tank to provide an airtight seal. During respiration trials, the flume was operated as a closed system; between trials and at night, however, the flume received a continuous inflow of temperature-controlled filtered seawater, with a flow rate of about 6 cm/s to orient the fish.

During each 2-d experiment a series of trials was carried out at flume speeds ranging from 12–13 (minimum) to 60–63 (maximum) cm/s. Between four and six trials were conducted per day, with each trial lasting 1 h. Test speeds were selected randomly, and at the completion of a trial the next test speed was set, followed by a 30-min interval during which flow rate became stable again and fish were able to adjust to the new speed. An interval of about 1 h was used to reoxygenate the flume when necessary. Test current speeds were set by regulating the discharge pressure of the circulating pump (Fig. 1A) by using the predetermined pressure to flow-rate calibration curve. Although we attempted to use the same test current speeds at all three temperatures, minor inaccuracies in the calibration curve and gauge readings resulted in only approximately equal test speeds (Fig. 2).

Fish behavior was observed continuously during experiments and recorded with a monochrome MTI Dage M65 video camera suspended directly above the center of the flume and connected to a VHS format video recorder. Swimming speed in relation to the bottom (ground speed, GS) was determined from the video recordings at 3-min intervals, by marking the position of each fish on the video monitor screen with a grease pencil and noting its subsequent location 10 s later. The number of reference marks crossed by each fish during this interval was then multiplied by the distance between marks (21.8 cm) to obtain ground speed. Fish moving upstream were assigned positive values, whereas those swimming downstream were scored negatively. Actual swimming speed (SS) through the water was then computed as the algebraic sum of the ground speed (speed of fish in relation to the bottom) and the flow rate in the flume. Mean swimming speed during a trial was computed from the individual swimming speeds, irrespective of direction.

During experiments a YSI Model 51B dissolved oxygen meter was used to monitor oxygen levels in real time; oxygen content of the water was not permitted to decline below 60% of saturation. At 15-min intervals during a trial, duplicate water samples were siphoned from the collection port into 300-mL biological oxygen

Figure 2

Ground speeds (GS) and true swimming speeds (SS) of Atlantic menhaden, *Brevoortia tyrannus*, swimming against water currents in a toroidal flume respirometer at 10°, 15°, and 20°C. Lower ground speed error bars are not shown.

demand (BOD) bottles that were allowed to overflow twice their volume and that were then fixed for determination of oxygen content by Winkler titration (Carritt and Carpenter, 1966; Strickland and Parsons, 1972). Analyses were performed on 5–6 50 mL subsamples withdrawn from the bottles with a volumetric pipette. Dissolved oxygen declined linearly over time (overall mean $r^2 \pm 1$ SD for all regressions=0.987 ±0.018). Metabolic rates were therefore assumed to be unaffected by declining oxygen content during the trials. Menhaden respiration rates were computed from the change in dissolved oxygen content over time as determined by least squares linear regression, corrected for the wet weight of the fish and volume of the flume.

Results

The menhaden formed a loose school in the upper central portion of the flume. The fish usually oriented head into the current and moved slowly upstream (positive ground speed). Occasionally a fish would break away and swim downstream with the flow, but within a few seconds reoriented itself to swim against the flow. These brief periods of downstream swimming occurred most frequently at slow current speeds and at the warmest temperature, 20°C. The frequency of occurrence of downstream coasting or swimming during respiration trials was as follows: 0 of 11 trials at 10°C; 2 of 11 at 15°C (2.2% of observations during those 2 trials); and 6 of 10 at 20°C (6.4% of observations in those 6 trials). When corrected for current speed, swimming speeds of fish moving downstream were comparable to those of fish moving upstream. Overall, the incidence of downstream swimming did not significantly affect the results.

In our study, menhaden swimming into a water current maintained a nearly constant ground speed at 10°, 15°, and 20°C (6.8, 5.3, and 4.7 cm/s respectively, or about 0.2 BL/s) (Fig. 2), whereas their true swimming speeds ranged from 20.5 to 64.6 cm/s (10°C), 19.2 to 65.7 cm/s (15°C), and 15.5 to 66.0 cm/s (20°C). The mean ground speed was not significantly different at the three temperatures ($\bar{x} \pm$ SD=6.8 ±5.8 cm/s at 10°C; 5.3 ±4.8 cm/s at 15°C; and 4.7 ±8.2 cm/s at 20°C). Because ground speed remained nearly constant, actual swimming speed increased linearly with increasing current speed in the flume (Fig. 2).

The distribution of individual swimming velocities within the school was unimodal but was skewed towards a speed slightly faster than the flow rate in the flume (Fig. 3). The coefficient of variation in swimming speed declined curvilinearly as velocity increased, indicating that fish behavior grew less variable at higher speeds (Fig. 4). The pattern of decreasing variability with increasing swimming speed was similar at all three temperatures.

Respiration rates increased exponentially with increasing swimming speed (Fig. 5, Table 1). Analysis of covariance revealed that the relationships between respiration rate and swimming speed differed significantly at the three temperatures. The regression slope, or the rate of increase in oxygen consumption per unit swimming speed, was greatest at 10°C, significantly higher than at 15° or 20° (Fig. 6). The 15° and 20°C curves differed in elevation but not in slope, indicating that the overall level of metabolism was higher at 20°C than at 15°C, but the rate of increase in metabolic rate with increasing swimming speed was similar at the two temperatures. The cost of swimming was therefore higher at 10°C (metabolism increased by a factor of 2.32 per 1 BL increment in swimming speed) than at 15° or 20°C (metabolism increased by 1.75 and 1.65, respectively) (Table 2). At the higher test speeds, metabolic rates at 10°C were equal to or greater than those at 15°and 20° (Fig. 6).

Standard metabolism, as indicated by the *y*-intercepts of the equations given in Table 1, increased with temperature. At 10°, 15°, and 20°C, standard metabolism was equal to 0.040, 0.073, and 0.087 mg O_2/(g wet wt · h) respectively, or 0.131, 0.238, and 0.284 mg O_2/(g dry wt · h). The Q_{10} for standard metabolism (Prosser, 1973) was higher over the interval 10–15°C (3.3) than for 15–20°C (1.4). The Q_{10} over the interval 10–20°C was intermediate (2.2) (Table 3).

Discussion

Previous work has shown that menhaden swimming behavior reflects environmental conditions and food availability. At 20°C, adult menhaden of about 300 g swim at a characteristic speed of about 12.2 cm/s (0.5 BL/s) in still water in the absence of food (Durbin et al., 1981). During feeding, swimming speed and metabolic rate increase hyperbolically with increasing food concentration (Durbin et al., 1981). Hettler (1976) found that routine swimming speed in larval and juvenile menhaden (up to 80 g) increased with temperature but decreased with increasing salinity, starvation, and in the dark.

Ground speeds in the present experiments were remarkably stable considering the tested temperature range and the different energy expenditures at the different current speeds. The decline in individual variability in swimming speed as mean swimming speed increased (Fig. 4) was very similar to that observed by Durbin et al. (1981). This decline in variability may reflect decreased excitability as fish swim faster as well as a transition to steadier swimming with lower energy costs (reviewed in Brett and Groves, 1979; Boisclair and Tang, 1993).

The nearly constant ground speed in all trials indicated that menhaden did not approach their maximum swimming capacity at any of the tested speeds and, as a result, were probably not fatigued at the end of a day's trials despite the lack of rest between trials. The maximum observed metabolic rate of fish in our study, 0.356 mg O_2/(g wet wt · h) at 20°C, while fish were swimming at 63.2 cm/s, was considerably lower than that associated with filter feeding at a slower speed (0.538 mg O_2/(g wet wt · h) at 20°C and 43.4 cm/s: Durbin et al., 1981), further indicating that the fish were not performing near their physiologi-
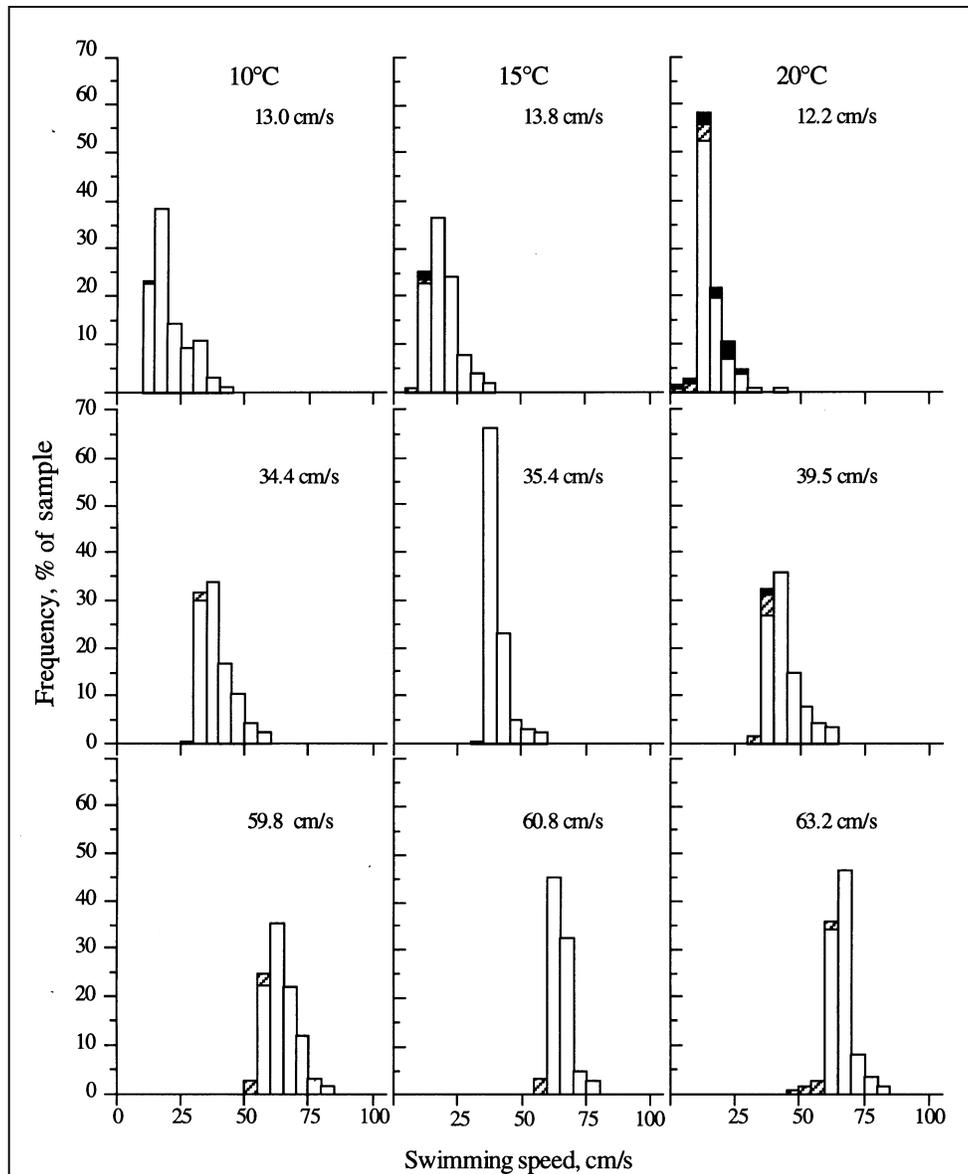
Figure 3

Frequency distribution of swimming speeds within a menhaden school swimming against typical slow, intermediate, and fast flows, at 10°, 15°, and 20°C. The flow rate inside the flume is indicated in each graph. Open bars indicate fish swimming against the current faster than the flume speed; diagonally hatched bars indicate fish swimming against the current, but slower than the flume; solid bars indicate fish actively swimming down current (i.e. with the current).

cal limit in the present experiments. Hettler (1976) measured a high oxygen consumption rate of 0.82 mg O_2/(g wet wt · h) during feeding by juvenile menhaden at 27°C, but the full metabolic scope (Fry, 1957) of menhaden remains unknown. Metabolic scope is related to the surface area of the gills and to the capacity of fish to take up oxygen from the surrounding medium. The unusually large gill area in men-

haden (Gray, 1954) suggests that metabolic scope is also large.

We were unable to determine either maximum or critical swimming speeds for adult menhaden (Brett and Glass, 1973) because sufficiently high currents could not be produced in the flume respirometer. Current speeds ranged from 12 to 63 cm/s (0.5 to 2.5 BL/s), which spans the reported range of voluntary

swimming speeds during routine activity and feeding (Durbin and Durbin, 1975; Hettler 1976; Durbin et al., 1981). Swimming capacity is unusually high in Atlantic menhaden; Hartwell and Otto (1978) reported that 5.8-cm-SL juvenile menhaden sustained a critical swimming speed of 15.8 BL/s for 64 min at 20°C. The critical swimming speed of similarly sized sockeye salmon at 15°C is about 7 BL/s (Brett and Glass, 1973).

Standard metabolism (Fry, 1957) is a measure of basic maintenance costs and as such may be a useful reference level for interspecific comparisons. The magnitude of standard metabolism also seems to reflect species life styles with respect to their general activity levels. Standard metabolic rates for menhaden (Table 3) were lower than those for active predators like the bluefish, *Pomatomus saltatrix* (0.156 mg O_2/(g wet wt · h), for 217-g fish at 15°C (Freadman, 1979), but higher than those for the sedentary flatfish *Limanda limanda* (0.015, 0.029, and 0.042 mg O_2/(g wet wt · h) at 5°, 10°, and 15°C for 236–400 g fish (Duthie, 1982)). Standard metabolism in menhaden was similar to that of sockeye salmon (Brett, 1964) at 15°C, but lower at 10° and 20°C (Table 3). Durbin et al. (1981) previously estimated standard metabolism for menhaden at 20°C to be only 0.036 mg O_2 /(g wet wt · h), from the regression of feeding metabolism as a function of swimming speed. However we believe that the present higher estimates are more reliable because the data include a broader range of swimming speeds and require less extrapolation to zero swimming speed than the earlier estimate.

The Q_{10} values (Prosser, 1973) provide a measure of the effect of environmental temperature on metabolic rates. The Q_{10} for standard metabolic rate in our study was very close to that of Hettler for routine metabolism in juvenile menhaden (Table 3). The decline in Q_{10} between 10°–15°C and 15°–20°C thus appears to be real. A similar pattern was observed in dab, *Limanda limanda*, where the Q_{10} over 5°–10°C was higher than over 10°–15°C (3.7 and 2.1 respectively (Duthie, 1982). The more extensive data of Hettler (1976) and Brett (1964) indicate that over a wide temperature range (Hettler: 14–24°C; Brett: 5–24°C), the Q_{10} for metabolic rate is close to 2.0, but within this range the Q_{10} declines as the thermal optimum is approached and increases towards the thermal extremes for the species.

Hettler's data on routine metabolic rate in juvenile menhaden, when extrapolated to 300-g fish (Table 3), yield relatively high routine metabolic rates compared with those observed by Durbin et al. (1981)
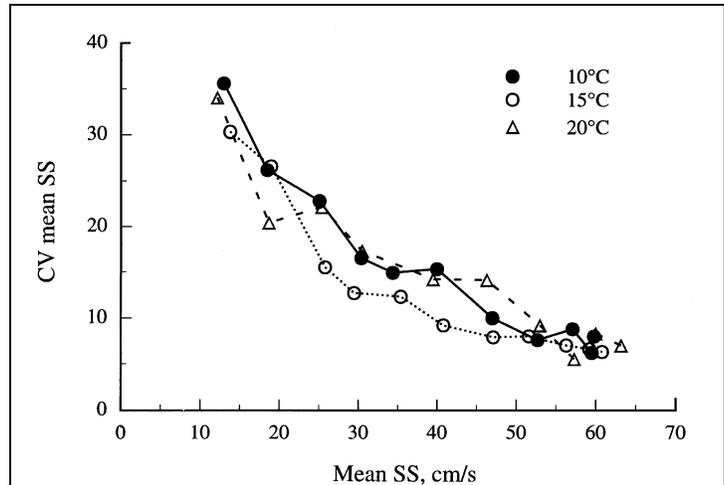

Figure 4

The coefficient of variation (CV) in relation to mean swimming speed (SS) of a menhaden school in the respirometer at 10°, 15°, and 20°C.
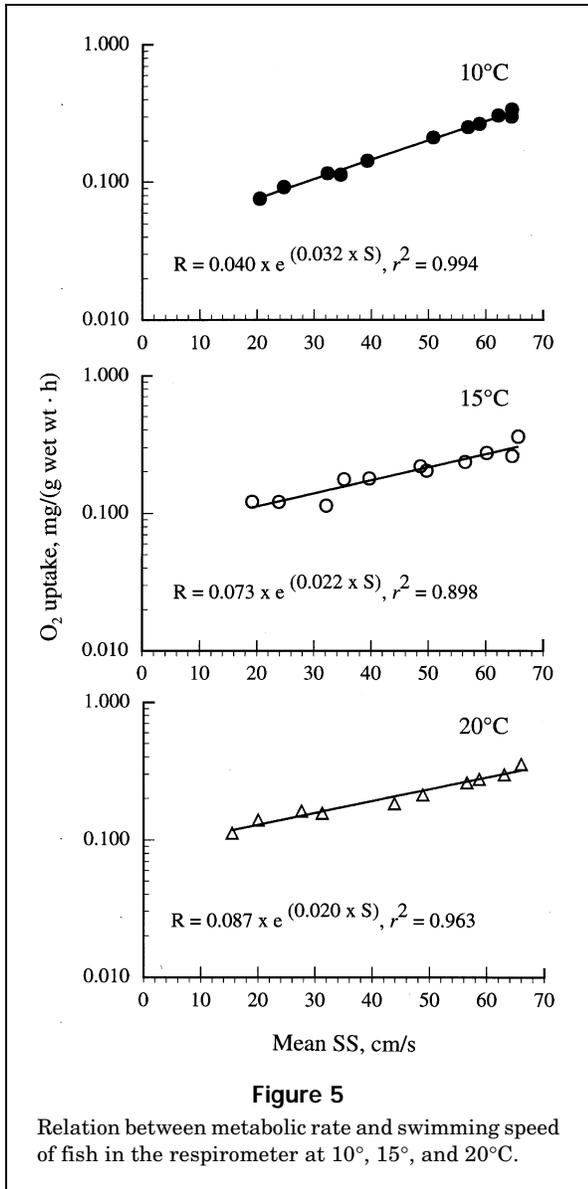
Table 2

Comparison of the metabolic cost of increasing swimming speed by 1 BL/sec (ratio of respiration rate at 2BL:1 BL/s) in Atlantic menhaden, *Brevoortia tyrannus* (Table 1, this study), with that in sockeye salmon, *Oncorhynchus nerka* (Table II in Brett, 1964). Fish were not fed for 24 h.
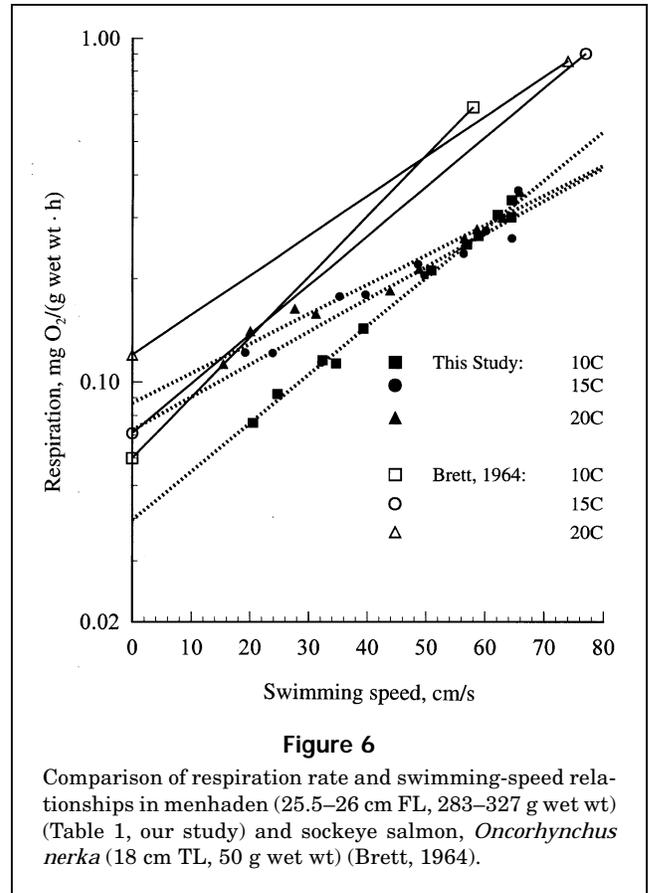
Temp. (°C)	Menhaden (this study)			Sockeye (Brett, 1964)		
	Length (cm)	Wt (g)	Cost	Length (cm)	Wt (g)	Cost
5				18.0	50	2.19
10	26.0	327	2.32	18.0	50	1.91
15	25.5	303	1.75	18.0	50	1.86
20	25.5	283	1.65	18.0	50	1.66
24				18.0	50	1.48

(0.10 mg O_2/(g wet wt · h) at 20°C). Because the maximum weight of Hettler's fish was only 74.3 g, the extrapolated values for 300-g fish are most likely overestimates. The calculated routine rates in Table 3 correspond to swimming speeds of 18.8, 25.7, and 27.4 cm/s at 10°, 15°, and 20°C, respectively, which were faster than the routine speed of 12.2 cm/s at 20°C reported by Durbin et al. (1981).

Routine metabolic rates are measured directly at spontaneous activity levels. Thus routine rates reflect real world activity levels, because few fish actually sleep or totally cease movement that would depress metabolic rates to basal or standard levels. Our present observations do seem to be comparable

Figure 5

Relation between metabolic rate and swimming speed
of fish in the respirometer at 10°, 15°, and 20°C.

Figure 6

Comparison of respiration rate and swimming-speed rela-
tionships in menhaden (25.5–26 cm FL, 283–327 g wet wt)
(Table 1, our study) and sockeye salmon, *Oncorhynchus
nerka* (18 cm TL, 50 g wet wt) (Brett, 1964).

to routine rates calculated from Hettler's data (Table
3) that indicate that a 300-g menhaden at 10°C would
have a routine metabolic rate of 0.073 mg O_2/(g wet
wt·h) and to previously cited observations by Durbin
et al. (1981) on routine swimming and metabolic rates
in menhaden at 20°C. Johnstone et al. (1993) re-
ported routine metabolic rates of 0.118 mg O_2/(g wet
wt · h) for 290–380 mm Atlantic mackerel, *Scomber
scombrus*, swimming at 0.6 BL/s at 11.1°C, and 0.093
mg O_2/(g wet wt · h) for 255–310 mm Atlantic her-
ring, *Clupea harengus*, swimming at 0.3 BL/s at
9.3°C. Because these routine swimming speeds were
lower than previously reported by these investiga-
tors (0.9–1.2 BL/s for mackerel, and 2 BL/s for her-
ring) and because the fish were maintained for a pro-
longed period in the respirometer without feeding

(5–16 d for mackerel, 13 d for herring), these may be
under-estimates. Routine activity and metabolic
rates in menhaden thus may be lower than in her-
ring and mackerel.

Durbin et al. (1981) noted that the actual measured
routine metabolic rate in menhaden was higher than
that predicted for the same swimming speed by us-
ing the swimming-speed and metabolic-rate relation-
ship during feeding. This higher routine rate was as-
sumed to reflect increased excitability in fish when
not occupied by feeding and also the more variable
and energetically less efficient mode of swimming
associated with routine activity. Routine swimming
also appears to be energetically more expensive than
forced swimming (as shown in our study) and directed
swimming, where the optomotor response is used to
induce fish to swim at a steady, but possibly more
variable, speed than in forced swimming. In a re-
view of ten species, three marine and seven fresh-
water, Boisclair and Tang (1993) found that routine
swimming was energetically the most expensive and,
on average, was 9.4 times higher (range: 6.4 to 14.0)
than forced swimming at the same speed. Directed
swimming ranged from 1.0 to 2.8 times as expen-
sive. Applying a similar analysis to menhaden at

Table 3

Comparison of Q_{10} for standard (R_{Std}) and routine (R_{rout}) metabolism in Atlantic menhaden, *Brevoortia tyrannus* (this study and Hettler, 1976, respectively), with standard metabolism in sockeye salmon, *Oncorhynchus nerka* (Table II in Brett, 1964). Hettler's data were extrapolated to a 300-g menhaden by using regressions in his Table I.

	Menhaden (this study)		Menhaden (Hettler, 1976)		Sockeye (Brett, 1964)			Menhaden (this study)	Menhaden (Hettler, 1976)	Sockeye (Brett, 1964)
Temp °C	Wt (g)	R_{Std} (mg O$_2$/(g · h))	Wt (g)	R_{Rout} (mg O$_2$/(g · h))	Wt °C	R_{Std} (mg O$_2$/(g · h))	Temp °C	Q_{10}	Q_{10}	Q_{10}
5					50	0.041				
10	327	0.040	300	0.073	50	0.060	5–10			2.2
15	303	0.073	300	0.127	50	0.071	10–15	3.3	3.0	1.4
20	283	0.087	300	0.149	50	0.120	15–20	1.4	1.4	2.9
24					50	0.195	20–24			3.4
25			300	0.231			20–25		2.4	
							5–24			2.2
							10–20	2.2	2.0	
							10–25		2.1	

20°C, we first calculated from Table 1 the metabolic rate for forced swimming at the routine speed (12.2 cm/s) = 0.111 mg O$_2$/(g wet wt · h) and subtracted the standard metabolic rate from Table 3 (0.087 mg O$_2$/(g wet w · h) to obtain the net cost of swimming = 0.024 mg O$_2$/(g wet wt · h). The net cost of routine swimming (Durbin et al., 1981) is 0.1 − 0.087 = 0.013 mg O$_2$/(g wet wt · h). The ratio of the two (= swimming cost ratio [SCR] of Boisclair and Tang, 1993) = 0.024/0.013 = 1.8. This value is much lower than Boisclair and Tang's (1993) average SCR value of 9.4 for the ratio of routine to forced swimming costs and is more comparable to their average SCR value of 1.6 for the ratio of directed to forced swimming costs. This suggests that routine activity in menhaden, although energetically more expensive than sustained swimming, is relatively economical. Metabolism associated with routine activity is, in fact, only slightly elevated above standard metabolism in menhaden. Menhaden thus may be an exception to the rule (Webb, 1991) which states that routine metabolic rates of swimming menhaden are not quasi-steady but are substantially higher than forced-swimming rates.

The cost of swimming in menhaden increases exponentially with a linear increase in swimming speed (Fig. 5, this study; Durbin et al., 1981), a pattern characteristic of fish in general (reviewed by Brett and Groves, 1979). The relation between the metabolic cost of swimming and temperature is similar for unfed Atlantic menhaden and sockeye salmon (*Oncorhynchus nerka*) (Fig. 6; Table 2). In both species, the rate of increase in respiration rate per increment of swimming speed is highest at the lowest temperature. With increasing temperature the slopes of the relationships decrease, indicating that the metabolic cost of swimming declines. The cost of swimming to unfed Atlantic menhaden is close to Beamish's (1978) mean value for eight species, where metabolism increased by 2.3-fold for a 1 BL/s increase in swimming speed. Thus we conclude that the metabolic cost of swimming in nonfeeding menhaden is similar to that of other pelagic fish species.

Conversely, the cost of swimming to menhaden while filter-feeding is much higher, where the metabolic rate rose five-fold per BL/s increase in swimming speed (Eq. 2 in Table 2, Durbin et al., 1981), compared with a 1.65-fold increase in unfed fish at 20°C (Table 2, our study). Durbin et al. (1981) speculated that the very high cost of swimming during filter feeding was related to the increased hydrodynamic drag of the expanded gill opercula and the long gill rakers that strain plankton from the water. Present results permit the separation of metabolic rate during feeding into its component parts at 20°C (Table 4; Fig. 7). We observed that during filter feeding, menhaden swam at a preferred speed of about 41.3 cm/s over a wide range of plankton concentrations. However, after prey concentrations had been reduced to subthreshold levels, feeding ceased and activity and respiration both returned to routine levels where there was no postfeeding respiration peak (Durbin et al., 1981). Standard metabolism accounted for only 18.1% of the total metabolism, and the energy demand for swimming was about 22.9%. The remaining 59% of metabolism was associated with the energy cost of feeding, which includes the in-
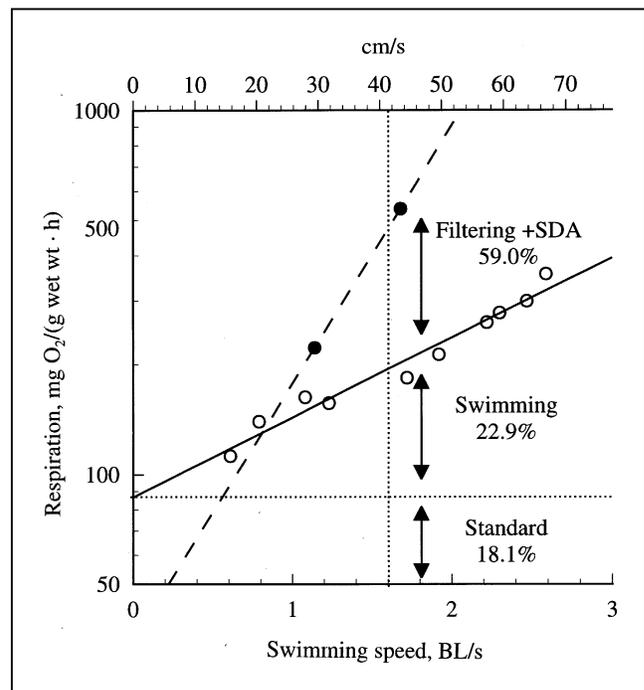
creased drag of the filtration apparatus, and the metabolic cost of processing the food (specific dynamic action [SDA]). SDA could not be distinguished from total metabolism during feeding (Durbin et al., 1981) because food is processed very rapidly as was shown by the fact that 50% of nitrogen was excreted 1.4 h after ingestion (Durbin and Durbin, 1981) and by the lack of a postfeeding respiration peak. The high cost of filter feeding in the menhaden provides an interesting contrast with a sedentary, ambush predator such as the Northern pike, where the energy required for prey capture is relatively small and where most of the cost of feeding is associated with SDA during an extended postfeeding period of digestion (Lucas et al., 1991).

The bioenergetics of feeding differ between filter feeders, such as menhaden, and particulate feeders that consume zooplankton by individual capture. Prey consumption increases linearly with prey concentration and predator swimming speed for filter feeders but increases hyperbolically (Durbin, 1979) for particulate feeders because of the limitations of handling time. The energy cost is higher for filter feeding than for particulate feeding. Both feeding modes are energetically more expensive than routine swimming (James and Probyn, 1989). The optimal swimming patterns in relation to food concentration and foraging time therefore differ between filter and particulate feeders (Ware, 1975; Durbin and Durbin, 1983). Many planktivorous fishes switch between filter and particulate feeding, according to the size and concentration of prey in the water (northern anchovy: Leong and O'Connell, 1969; O'Connell, 1972; Hunter and Dorr, 1982; cape anchovy: James and Probyn, 1989; pilchard: van der Lingen, 1994; Pacific mackerel: O'Connell and Zweifel, 1972; Atlantic herring: Gibson and Ezzi, 1985, 1990, 1992). The switch between filter and particulate feeding can be predicted from the relationship between energy gain and expenditure as the plankton size spectrum changes (Crowder, 1985; James et al., 1989; Gibson and Ezzi, 1992). In contrast, Atlantic menhaden are less flexible in their feeding behavior and consequently may be restricted to coastal and estuarine waters of high production because energetic costs of filter feeding are high and because a relatively small volume of water is searched with mode of feeding (Durbin and Durbin, 1983).

Table 4

Partitioning of metabolism during filter feeding in Atlantic menhaden *Brevoortia tyrannus*, swimming at their preferred speed of 41.3 cm/s at 20°C. Components of the energy budget: total metabolism during feeding (R_{Feed}); total metabolism nonfeeding but swimming at the same speed ($R_{Nonfeed}$); standard metabolism (R_{Std}); metabolism associated with swimming (R_{Swim}); metabolism associated with filter feeding (R_{Filter}); metabolism associated with digestion and transformation of the food (R_{SDA}). R_{Feed} from Durbin et al. (1981); remaining data from this study.

Metabolic budget	mg O_2/(g wet wt · h)	Percent of total
$R_{Feed} = R_{Std} + R_{Swim} + R_{Filter} + R_{SDA}$	0.480	100
$R_{Nonfeed} = R_{Std} + R_{Swim}$	0.197	
R_{Std}	0.087	18.1
$R_{Swim} = R_{Nonfeed} - R_{Std}$	0.110	22.9
$R_{Filter} + R_{SDA} = R_{Feed} - R_{Std} - R_{Swim}$	0.283	59.0

Figure 7

The energy budget of Atlantic menhaden during foraging at the preferred swimming speed, 41.3 cm/s (Durbin et al., 1981) partitioned by the vertical dotted line into the energy required for standard metabolism (horizontal dotted line), swimming (solid line), and feeding (dashed line) = filtering + SDA.

However, menhaden flourish in their chosen habitat, and as omnivores specializing in the smaller size spectrum of particulate material, they have no important competitors among the fishes. Herring and mackerel eat larger zooplankton and live further offshore. The small anchovies that live in the men-

haden's range are exclusively zooplanktivores (Bigelow and Schroeder, 1953). Mesozooplankton are competitors for both food and prey of the menhaden (Peck, 1893; Durbin and Durbin, 1975). Menhaden are important in nearshore food webs as primary herbivores and are a major prey species for predatory fishes (Bigelow and Schroeder, 1953; Friedland et al., 1989; Baird and Ulanowicz, 1989); because of their great abundance, they support one of the largest domestic finfisheries in the United States (Ahrenholz et al., 1987).

Acknowledgments

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