ENERGY AND NITROGEN BUDGETS FOR THE ATLANTIC MENHADEN, *BREVOORTIA TYRANNUS* (PISCES: CLUPEIDAE), A FILTER-FEEDING PLANKTIVORE

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ABSTRACT

Experimentally derived energy and nitrogen budgets for the Atlantic menhaden permit a detailed investigation of the food consumption rate, energy expenditures, growth rate, and growth efficiency in this filter-feeding planktivore. The models were developed for adult fish (302 g wet weight, 26 cm fork length) at a temperature of 20°C. Three variables are shown to control the energy and nitrogen budgets: The swimming speed while the fish are feeding, the duration of the daily feeding period, and the concentration of plankton in the water.

Growth rate increased linearly, and growth efficiency increased asymptotically, with an increase in either plankton concentration or the duration of feeding, provided that swimming speed remained constant. However, with increasing swimming speed, growth curvilinearly increased from zero to a maximum value and then declined back to zero. Growth efficiency followed a similar pattern, but reached its maximum value at a slower swimming speed than that which maximized growth. The swimming speeds which maximized growth rate were dependent on plankton concentration, but were independent of the duration of feeding. Conversely, the swimming speeds which maximized gross growth efficiency depended on the duration of feeding, but were independent of food concentration. Laboratory studies demonstrated that menhaden regulate their swimming speeds according to the abundance of plankton in the water. Analysis of the energy budgets revealed that the voluntary swimming speeds of the menhaden were very close to those which maximize growth rate at different concentrations of plankton. We conclude that swimming speed in the menhaden has evolved over time towards maximizing growth rate rather than growth efficiency.

In most circumstances the growth efficiency for calories and nitrogen were significantly different. The observed swimming speeds in the menhaden resulted in higher growth efficiency for nitrogen at low plankton abundance, but higher efficiency for calories at moderate to high plankton abundance. This accounts for the seasonal increase in the fat content of the menhaden during the summer, yet indicates that protein will be conserved when food abundance is low.

The study of fish bioenergetics can provide considerable insight into how different biotic and abiotic factors interact to control food intake and growth in fishes. Here we describe energy and nitrogen budgets for adult Atlantic menhaden, *Brevoortia tyrannus*, a filter-feeding planktivore which ranges in inshore waters along the Atlantic coast from Florida to Maine (Nicholson 1978 and references therein). These budgets are based on experimental investigations of the physiological and behavioral responses of the adult Atlantic menhaden to differing food conditions (Durbin and Durbin 1975, 1981; Durbin et al. 1981).

In the energy budget, the sum of somatic and reproductive growth (G_K) equals the energy content of the ingested ration (R_K), minus the energy losses to respiration (T_K), excretion (E_K), and feces (F_K):

$$G_K = R_K - T_K - E_K - F_K. \quad (1)$$

We have attempted to incorporate into the energy budget the energetic gains and losses which occur during different phases of the normal daily activity of the fish. For example, the energetic expenditures during periods of feeding are considered separately from periods when the fish are not feeding. The energy budget is then used to predict food intake, growth rate, and growth efficiency of Atlantic menhaden under different feeding regimes.

In the nitrogen budget, growth in nitrogen (G_N) equals the nitrogen contained in the daily ration (R_N) minus the daily nitrogen losses to excretion (E_N) and in the feces (F_N):

$$G_N = R_N - E_N - F_N. \quad (2)$$

Food intake, growth rate, and growth efficiency are predicted.

The energy and nitrogen budgets measure different things; the nitrogen budget is mainly for a specific component (protein), while the energy (caloric) budget is more inclusive and attempts to account for

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all changes in body constituents. A comparison of the two budgets will enable us to determine the relative efficiency with which the Atlantic menhaden utilize the total energy content, as distinct from the nitrogen content, of their food for growth. Each of the budgets is presented in two forms, a general model (I) and a special case of this model (II) which incorporates additional details on the behavior of the fish in response to the abundance of food. Symbols used in the budgets are as follows:

R_K, R_N	Total daily food intake ("ration") (kcal/g dry weight per day; mg N/g dry weight per day)
T_K	Total daily oxygen consumption (kcal/g dry weight per day)
$T_{r,K}$	Total daily routine oxygen consumption (kcal/g dry weight per day)
$T_{f,K}$	Total daily oxygen consumption during feeding (kcal/g dry weight per day)
$T_{s,K}$	Oxygen consumption attributable to swimming activity (kcal/g dry weight per day)
$T_{SDA,K}$	Oxygen consumption due to the heat increment from food (kcal/g dry weight per day)
E_K, E_N	Total daily nitrogen excretion (kcal/g dry weight per day; mg N/g dry weight per day)
$E_{b,K}, E_{b,N}$	Total daily endogenous nitrogen excretion (kcal/g dry weight per day; mg N/g dry weight per day)
$E_{f,K}, E_{f,N}$	Total daily exogenous nitrogen excretion (kcal/g dry weight per day; mg N/g dry weight per day)
F_K, F_N	Total daily losses in the feces (kcal/g dry weight per day; mg N/g dry weight per day)
G_K, G_N	Total daily growth (kcal/g dry weight per day; mg N/g dry weight per day)
$K_{1,K}, K_{1,N}$	Gross growth efficiency $= \frac{G_K}{R_K}$ and $\frac{G_N}{R_N}$
p	Assimilation efficiency (dimensionless)
v	Volume searched during feeding (l/fish per hour)
F	Volume swept clear during feeding (l/fish per minute)
L	Food particle length (μm)
e	Filtration efficiency of the gill rakers (dimensionless)
s	Swimming speed during feeding ("foraging speed") (cm/second)
c,n	Concentration of plankton in the water (kcal/l; mg N/l)
h	Duration of the daily feeding period ("foraging time") (hours/day)
$s_{G,OPT}$	Foraging speed which maximizes growth rate at a given concentration of plankton
$s_{K,OPT}$	Foraging speed which maximizes gross growth efficiency for a given foraging time.

Atlantic menhaden are highly specialized planktivores which feed on suspended particulate material (phytoplankton, zooplankton, and detritus). During feeding, an Atlantic menhaden swims with its mouth open and gill opercula flared, causing the comblike gill rakers, which otherwise lie flat inside the mouth, to swing inward and form a fine-meshed screen across the throat (Peck 1894). Water entering the mouth is filtered through the rakers before exiting through the gill arches. Adult Atlantic menhaden do not pursue individual prey (Durbin and Durbin 1975). Instead they filter the column of water that lies directly ahead. Although the menhaden are size-selective, this merely reflects the mesh size of the gill rakers and does not represent active selection for specific types of prey.

Laboratory studies have shown that Atlantic menhaden change their swimming and feeding behavior according to the concentration of food in the water (Durbin et al. 1981). In the absence of food the fish swam at a characteristic speed of 0.47 body lengths/s, with a routine respiration rate of 0.1 mg O_2/g wet weight per h. The menhaden increased their swimming speed and respiration rate severalfold during feeding. Foraging speed increased asymptotically with increasing food concentration, while respiration rate increased exponentially with increasing foraging speed. The fish initiated and terminated feeding at distinct threshold concentrations of plankton that were inversely related to particle size. Exogenous nitrogen excretion in the Atlantic menhaden was proportional to the nitrogen content of the ration (Durbin and Durbin 1981). Digestion rates were rapid, and assimilation efficiency was high. The menhaden were evidently adapted for the efficient processing of large amounts of particulate material which is ingested during prolonged periods of continuous feeding.

These observations provide the basis for the development of the energy and nitrogen budgets and will be discussed in more detail below. In accordance

with the experimental data, the budgets are developed for the case of an adult Atlantic menhaden, 26 cm FL (fork length) and weighing 302 g wet and 101 g dry, which feeds upon the diatom *Ditylum brightwelli*. The temperature is 20°C.

DERIVATION OF ENERGY AND NITROGEN BUDGETS

Energy Budget (Model I)

The general equation for the energy budget is presented in Equation (1).

Energy Intake

TOTAL DAILY RATION, R_K (KCAL/G DRY WEIGHT PER DAY).—The daily ration, R_K (kcal/fish per d) which is obtained by an Atlantic menhaden will be equal to the volume searched (v, l/fish per h), times the efficiency (e, dimensionless) with which particles are removed from the volume searched, times the concentration (c, kcal/l) of food particles in the water, times the duration (h, h/d) of the feeding period.

$$R_K = v\ e\ c\ h \text{ (kcal/fish per d).} \quad (3)$$

Volume searched (v).—During feeding, the mouth is held continuously open and the fish swim in school formation, travelling along a straight or curvilinear path without changing course to pursue individual prey. Thus each fish filters the column of water which lies directly ahead. The volume searched is equal for all prey types, and may be adequately described as a cylinder, or, more accurately, an ellipsoid, with a cross-sectional area equal to that of the fish's open mouth and a length equal to the distance covered by the fish per unit time, i.e., the foraging speed (s, cm/s). For an Atlantic menhaden averaging 26 cm FL, the gape was approximately elliptical, with major and minor axes of 3.91 and 2.90 cm, respectively; the total cross-sectional area of the mouth was therefore 8.93 cm² (Durbin and Durbin 1975). Thus

$$v = 32.148\ s \text{ (l/fish per h).} \quad (4)$$

Filtration efficiency (e).—Filtration efficiency is the efficiency with which the Atlantic menhaden filters particles of a given size from the water and is equal to the observed removal rate or volume swept clear, F (l/fish per min), divided by the total volume searched, v (l/fish per min), i.e.,

$$e = \frac{F}{v}. \quad (5)$$

In feeding experiments (Durbin and Durbin 1975) the mean value of F for *Ditylum brightwelli* was 5.8 l/fish per min, while v was estimated to be 23.3 l/fish per min. This gives a value of $e = 0.25$ for *D. brightwelli*.

Filtration efficiencies for different-sized particles may be calculated from an equation describing the relationship between filtration efficiency and food particle length (Durbin and Durbin 1975):

$$F = 8.290 \log_{10} L - 9.733 \text{ (l/fish per min).} \quad (6)$$

In the experiments the fish were unable to filter particles smaller than about 13 μm.

Incorporating the appropriate values for v and e into Equation (3), the ingested ration, R_K, for *D. brightwelli* would be given by

$$R_K = 8.037\ s\ c\ h \text{ (kcal/fish per d).} \quad (7)$$

In the model the Atlantic menhaden weighed 302 g wet = 101 g dry (Durbin and Durbin 1981). Thus

$$R_K = 0.079574\ s\ c\ h \text{ (kcal/g dry weight per d).} \quad (8)$$

ASSIMILATED RATION, pR_K (KCAL/G DRY WEIGHT PER DAY).—If the fecal losses, F_K, are subtracted from the ingested ration, R_K, a measure of the assimilated ration is obtained. The assimilated ration can also be determined by multiplying R_K by the assimilation efficiency, p, i.e., pR_K, where

$$p = \left(1 - \frac{F_K}{R_K}\right). \quad (9)$$

In our experiments with the Atlantic menhaden, we observed slight changes in the overall assimilation efficiency of a meal, depending on meal size (Durbin and Durbin 1981). However, because the observed differences in overall assimilation efficiency were small and because of the uncertainty about the significance of these differences, we assumed a constant assimilation efficiency for the model and took the means of the experimentally determined values. For Atlantic menhaden feeding on *D. brightwelli*, the mean assimilation efficiency, p, equalled 0.8636 for carbon, 0.9240 for nitrogen, and 0.8954 for calories (Durbin and Durbin 1981).

Substituting Equation (9) into Equation (1) we may rewrite the general equation for the energy budget:

$$G_K = pR_K - T_K - E_K \quad (10)$$

where the assimilated daily ration, pR_K, is given by

$$pR_K = 0.8954\ R_K \text{ (kcal/g dry weight per d)} \quad (11)$$

$$= 0.071250\ s\ c\ h \text{ (kcal/g dry weight per d).} \quad (12)$$

Energy Output

RESPIRATION, T_K (KCAL/G DRY WEIGHT PER DAY).—In the absence of food, the Atlantic menhaden swam at a characteristic speed of 12.2 cm/s (0.47 body lengths/s), with a routine respiration rate of 0.10 mg O_2/g wet weight per h (Durbin et al. 1981).

During feeding the fish increased their swimming speed by a factor of 2.4- to 3.5-fold above the nonfeeding rate, depending on the plankton concentration in the water. Both swimming speed and respiration rate increased abruptly with the onset of feeding, and stabilized within a few minutes. One of the more interesting aspects of the Atlantic menhaden feeding behavior was that they would maintain a virtually constant swimming speed throughout the entire 7-h experimental feeding period, if the input of food remained constant. When the food input was stopped, the fish quickly consumed the remaining plankton in the tank, decreasing their swimming speed as the plankton concentration dropped. Thus the return to the routine swimming speed following feeding was quite rapid. In low-ration experiments, respiration rates declined to the routine, prefeeding rate almost immediately after feeding. In high-ration experiments, respiration rate remained slightly elevated above baseline for 2-5 h after feeding. The amount of energy expended above routine during the postfeeding period was small and did not show any clear relationship with food ration size. It has therefore been omitted for the purpose of the energy budget.

Based on these considerations, the respiratory costs for the energy budget are considered separately for periods of feeding and nonfeeding. Thus

$$T_K = T_{r,K} + T_{f,K} \text{ (kcal/g dry weight per d)} \quad (13)$$

where T_K = total daily expenditure for respiration
$T_{r,K}$ = routine respiration during the nonfeeding period
$T_{f,K}$ = respiration during feeding.

Oxygen consumption rates were converted to caloric equivalents by means of oxycalorific coefficients in Elliott and Davison (1975). The appropriate coefficients were determined from the ratios of oxygen consumed: nitrogen excreted by Atlantic menhaden before, during, and after feeding (Durbin and Durbin 1981). During feeding, Atlantic menhaden swimming at their preferred speed of about 41.3 cm/s appeared to be catabolizing protein. An oxycalorific coefficient of 3.20×10^{-3} kcal/mg O_2 was therefore used during periods when the fish were feeding. Nonfeeding menhaden catabolized about 28% protein and 72% fat (where $Q_{ox} = 3.28 \times 10^{-3}$ kcal/mg O_2), and the combined oxycalorific coefficient was 3.258×10^{-3} kcal/mg O_2.

Routine respiration rate, $T_{r,K}$.—The routine respiration rate of quietly swimming, nonfeeding Atlantic menhaden was 0.10 mg O_2/g wet weight per h = 0.299 mg O_2/g dry weight per h = 0.000974 kcal/g dry weight per h (Durbin et al. 1981). Thus the daily routine respiration during the nonfeeding period is given by

$$T_{r,K} = 0.000974\ (24\text{-}h) \text{ (kcal/g dry weight per d)} \quad (14)$$

where h is the duration of the feeding period (h/d).

Respiration during feeding, $T_{f,K}$.—The respiration rate increased significantly during feeding. This increase could be attributed to three sources: The higher voluntary swimming speed, the possible effect of excitement, and the specific dynamic effect of the food (SDA). The swimming speed was clearly the dominant factor, and accounted for 84.3% of the increased respiratory rate during feeding and 73.3% during the postfeeding period. Excitability was difficult to quantify, but our qualitative observations of the behavior of the fish indicated that they were least excitable during feeding and most excitable during the postfeeding period when they continued to hunt for food after the input to the tank had been stopped. SDA is considered to represent mainly the loss of energy during the deamination of protein, and it appears to constitute a fixed proportion of the energy content of a particular type of food (Muir and Niimi 1972). The energy cost of SDA is usually determined by monitoring the metabolic rate of the fish following a meal. Unfortunately in the present study we were unable to measure SDA separately because of the prolonged feeding period, during which ingestion and digestion occurred simultaneously. However, since about 80% of the ration was digested and assimilated during the 7-h feeding period (Durbin and Durbin 1981), most of the respiratory cost of SDA was included in the measurement of the total respiration rate during feeding.

The total respiration rate during feeding increased exponentially with increasing foraging speed (s, cm/s), where

$$T_{f,K} = 10^{0.02948\,s-1.5342} \text{ (mg } O_2\text{/g wet weight per h)} \quad (15)$$

$$T_{f,K} = 2.994 \quad (10^{0.02948\,s-1.5342}) \quad \text{(mg } O_2\text{/g dry weight per h).} \quad (16)$$

Converting to calories

$$T_{f,K} = 0.00958 \quad (10^{0.02948\,s-1.5342}) \text{ (kcal/g dry weight per h).} \quad (17)$$

The daily energy expenditure for respiration during feeding is therefore

$$T_{f,K} = 0.00958 \quad h \quad 10^{0.02948\,s-1.5342}) \text{ (kcal/g dry weight per d).} \quad (18)$$

Total daily respiration, T_K.—Combining Equations (14) and (18) we obtain an expression for the total respiratory expenditure per day as a function of the foraging speed (s, cm/s) and the foraging time (h, h/d):

$$T_K = h\,[0.00958\,(10^{0.02948\,s-1.5342}) - 0.000974] + 0.02338 \text{ (kcal/g dry weight per d).} \quad (19)$$

NITROGEN EXCRETION, E_K (KCAL/G DRY WEIGHT PER DAY).—Energy is lost through the excretion of nitrogenous compounds. In the absence of food the fish excreted nitrogen at a low rate (basal or endogenous excretion, $E_{b,N}$). Nitrogen excretion increased as a result of feeding (exogenous excretion, $E_{f,N}$). The total daily nitrogen excretion (E_N) is thus:

$$E_N = E_{b,N} + E_{f,N} \text{ (mg N/g dry weight per d).} \quad (20)$$

The energy equivalent of the excreted nitrogen was determined as follows: Of the total nitrogen excreted by menhaden, 69.6% was in the form of ammonia and 30.4% was in the form of dissolved organic nitrogen (DON) (Durbin and Durbin 1981). The caloric equivalent of ammonia nitrogen is 5.94×10^{-3} kcal/mg NH_3– N (Elliott and Davison 1975). The individual compounds comprising the DON excreted by Atlantic menhaden were not determined. For the purpose of the energy budget, the DON was assumed to consist of equal parts of urea, creatine, and trimethylamine, the major organic nitrogen compounds which are known to be excreted by teleosts (Watts and Watts 1974). The caloric equivalents of these compounds are: 5.51×10^{-3} kcal/mg urea-N (Elliott and Davison 1975), 13.32×10^{-3} kcal/mg creatine-N, and 41.3×10^{-3} kcal/mg trimethylamine-N (Weast 1977). The mean value for these compounds was 20.04×10^{-3} kcal/mg DON.

Endogenous nitrogen excretion, $E_{b,K}$.—The endogenous excretion rate equals 10.72 μg N/g dry weight per h (Durbin and Durbin 1981). The daily endogenous nitrogen excretion was therefore

$$E_{b,N} = 0.257 \text{ (mg N/g dry weight per d).} \quad (21)$$

Converting to calories

$$E_{b,K} = 0.0026282 \text{ (kcal/g dry weight per d).} \quad (22)$$

Exogenous nitrogen excretion, $E_{f,K}$.—The exogenous nitrogen excretion of menhaden fed *D. brightwelli* was directly proportional to the total nitrogen content of the ration, R_N (mg N/g dry weight per d) (Durbin and Durbin 1981):

$$E_{f,N} = 0.616\,R_N - 0.020 \text{ (mg N/g dry weight per d).} \quad (23)$$

Converting to calories

$$E_{f,K} = 0.006299\,R_N - 0.0002045 \text{ (kcal/g dry weight per d).} \quad (24)$$

The nitrogen content of a ration of *D. brightwelli*, R_N (mg), may be converted to kilocalories, R_K (kcal), according to the following relationship

$$R_K = 0.06158\,R_N \quad (25)$$

(Durbin and Durbin 1981). Thus if the daily ration is expressed in kilocalories rather than nitrogen, the daily exogenous nitrogen excretion becomes

$$E_{f,K} = 0.1023\,R_K - 0.0002045 \text{ (kcal/g dry weight per d).} \quad (26)$$

Total daily nitrogen excretion, E_K.—Combining Equations (21) and (23) we obtain an expression for the total daily nitrogen excretion rate

$$E_N = 0.616\,R_N + 0.237 \text{ (mg N/g dry weight per d).} \quad (27)$$

Combining Equations (22) and (26), the daily nitrogen excretion rate is expressed in calories

$$E_K = 0.1023\ R_K + 0.002423 \text{ (kcal/g dry weight per d).} \quad (28)$$

Since the total daily ration is given by $R_K = 0.079574\ s\ c\ h$ (kcal/g dry weight per d), we can substitute and obtain an expression for the total energy lost per day through nitrogen excretion, as a function of the foraging speed (s, cm/s) of the Atlantic menhaden, the concentration of food (c, kcal/l) and the foraging time (h, h/d):

$$E_K = 0.008140\ s\ c\ h + 0.002423 \text{ (kcal/g dry weight per d).} \quad (29)$$

Growth Rate, G_K and Gross Growth Efficiency, $K_{1,K}$

Equations (12), (19), and (29) may be combined to provide an estimate of the daily growth rate, G_K (kcal/g dry weight per d), as a function of menhaden foraging speed (s, cm/s), the concentration of plankton in the water (c, kcal/l), and the foraging time (h, h/d), since

$$G_K = pR_K - T_K - E_K \text{ (kcal/g dry weight per d)}$$

$$G_K = h\ [0.06311\ s\ c - 0.00958\ (10^{0.02948\ s - 1.5342}) + 0.000974] - 0.025803 \text{ (kcal/g dry weight per d).} \quad (30)$$

The gross growth efficiency, K_1 is calculated according to

$$K_1 = \frac{G}{R}. \quad (31)$$

Thus K_1 in calories is equal to

$$K_{1,K} = \frac{\text{Equation (30)}}{\text{Equation (8)}}. \quad (32)$$

From Equation (30) we can also determine the foraging speed which maximizes growth rate ($s_{G,\mathrm{OPT}}$), for any given values of c and h. First restating Equation (30) in a more general form, replacing the constants by A, B, C, D, E, J, and M,

$$G_K = h\ [A\ sc - B(10^{(Ds-E)}) + J] - M \text{ (kcal/g dry weight per d).} \quad (33)$$

We then differentiate Equation (30) with respect to s, i.e., set $\frac{dG}{ds} = 0$, and we find

$$s_{G,\mathrm{OPT}} = \frac{\log_{10}K + E}{D} + \frac{1}{D}\log_{10}c \quad (34)$$

where $K = \dfrac{A}{B(\log_e 10)\ I)}$. (35)

In the present study where *D. brightwelli* is the food,

$$s_{G,\mathrm{OPT}} = 119.4433 + 33.9213\ \log_{10}c. \quad (36)$$

To determine the equation for the swimming speed which maximizes gross growth efficiency ($s_{K,\mathrm{OPT}}$), i.e., when $\frac{dK_1}{ds} = 0$, we use the following general equation:

$$K_1 = \frac{\text{Equation (30)}}{\text{Equation (8)}} = \frac{h\ [A\ s\ c - B(10^{(Ds-E)}) + J]}{P\ s\ c\ h} - M \quad (37)$$

where P is the constant in Equation (8), i.e., in the present example, $P = 0.079574$. We next define the new constants

$$A' = \frac{A}{P} \quad (38)$$

$$B' = \frac{B}{P} \quad (39)$$

$$B'' = B'\ (\log_e 10)D \quad (40)$$

$$J' = \frac{J}{P} \quad (41)$$

$$M' = \frac{M}{P}. \quad (42)$$

And thus

$$K_1 = A' - \frac{B'\ 10^{(Ds-E)} - J'}{sc} - \frac{M'}{sc}. \quad (43)$$

For $\frac{dK_1}{ds} = 0$, we find the following identity

$$\frac{M'}{h} - J' = (B''\ s - B')\ 10^{(Ds-E)}. \quad (44)$$

This identity must be solved iteratively for $s_{K,\mathrm{OPT}}$ by using a given value of h and trial values of s.

In the present example using *D. brightwelli*, we find

$$\frac{0.32426}{h} - 0.01224 = (0.0081722\ s - 0.12039) \times 10^{(0.02948\ s - 1.5342)}. \quad (45)$$

Each term in the energy budget has now been defined in the same three variables: The foraging speed (s), the food concentration (c), and the foraging

time (h). Model I describes the potential interactions among these three variables, and their effects on menhaden energy intake, energy expenditure, growth, and growth efficiency.

Energy Budget (Model II)

Model II is a special case of Model I which incorporates information on the swimming and feeding behavior of the Atlantic menhaden in response to plankton concentration. Laboratory observations have shown that Atlantic menhaden adjust their foraging speed according to the concentration of food in the water. When *D. brightwelli* was the food, the threshold concentration for the onset of feeding was about 1 μg chlorophyll a/l. Between about 1 and 4 μg chlorophyll a/l, the menhaden increased their foraging speed roughly in proportion to increasing plankton concentration. Above 4 μg chlorophyll a/l, however, swimming speed remained nearly constant at about 41.3 cm/s (1.6 body lengths/s), independent of further increases in plankton concentration. Thus the relationship between the Atlantic menhaden foraging speed and *Ditylum* chlorophyll a (a, μg/l) was approximately asymptotic, where

$$s = \frac{29.62\ (a - 1)}{0.396 + (a - 1)} + 12.2 \text{ (cm/s)} \quad (46)$$

(Durbin et al. 1981). The equation includes the feeding threshold for *Ditylum* (1 μg chlorophyll a/l) and the routine (nonfeeding) swimming speed of the fish (12.2 cm/s), which represents the lower limit of the foraging speed.

The chlorophyll a content of *D. brightwelli* may be converted to kilocalories according to the following relationship:

$$1\ \mu\text{g chlorophyll a} = 6.06 \times 10^{-4}\ \text{kcal}. \quad (47)$$

Thus Equation (46) becomes

$$s = \frac{48{,}873\ c - 29.62}{1{,}650\ c - 0.604} + 12.2 \text{ (cm/s)} \quad (48)$$

where c (kcal/l) is the plankton concentration.

By substituting Equation (48) for s in Equations (8), (12), (19), (29), (30), and (32) for R_K, pR_K, T_K, E_K, G_K, and $K_{1,K}$, respectively, we are able to eliminate s as a variable and rewrite the menhaden energy budget solely in terms of food concentration (c, kcal/l) and foraging time (h, h/d). This is Model II.

Nitrogen Budget (Model I)

The general equation for the nitrogen budget presented in Equation (2) may be rewritten:

$$G_N = pR_N - E_N \quad (49)$$

where p is the assimilation efficiency for nitrogen = 0.9240 (Durbin and Durbin 1981). The nitrogen budget is controlled by the same three variables as the energy budget: The foraging speed (s), the food concentrations (c or n), and the foraging time (h).

The total dialy ration, R_N (mg N/g dry weight per d), equals

$$R_N = 0.79574\ s\ n\ h \text{ (mg N/g dry weight per d)} \quad (50)$$

where n is the plankton concentration (mg N/l).

The assimilated daily nitrogen ration, pR_N, equals

$$pR_N = 0.073526\ s\ n\ h \text{ (mg N/g dry weight per d)}. \quad (51)$$

The endogenous, exogenous, and total daily nitrogen excretion rates, $E_{b,N}$, $E_{f,N}$, and E_N (mg N/g dry weight per d) are presented in Equations (21), (23), and (27), respectively.

Substituting Equation (27) into Equation (49), we obtain the following expression for the daily growth rate, G_N:

$$G_N = 0.308\ R_N - 0.237 \text{ (mg N/g dry weight per d)}. \quad (52)$$

Gross growth efficiency, $K_{1,N}$, equals

$$K_{1,N} = \frac{0.308\ R_N - 0.237}{R_N} \text{ (mg N/g dry weight per d)} \quad (53)$$

where R_N is calculated according to Equation (50).

If the ration is converted from units of nitrogen to kilocalories (Equation (25)), then Equations (52) and (53) become

$$G_N = 5.0016\ R_K - 0.237 \text{ (mg N/g dry weight per d)} \quad (54)$$

$$K_{1,N} = \frac{5.0016\ R_K - 0.237}{16.239\ R_K} \quad (55)$$

where R_K is calculated according to Equation (8).

Nitrogen Budget (Model II)

The empirical relationship between foraging speed, s (cm/s), and plankton concentration, a(μg/l) (Equa-

tion (46)), is expressed in units of nitrogen through the following relationship:

$$1\,\mu g \text{ chlorophyll a} = 0.00984 \text{ mg N.} \quad (56)$$

$$\text{Thus } s = \frac{3{,}010.2\,n - 29.62}{101.63\,n - 0.604} + 12.2 \text{ cm/s} \quad (57)$$

where n is the plankton concentration in mg N/l.

The nitrogen budget can then be expressed solely in terms of plankton concentration, n (mg N/l), and foraging time, h (h/d), by substituting Equation (57) into Equations (50), (51), (27), (52), and (53) to compute R_N, pR_N, E_N, G_N, and $K_{1,N}$ (mg N/g dry weight per d), respectively

If the food ration or the plankton concentration is expressed in kilocalories rather than units of nitrogen, Equation (48) is substituted into Equation (8), and then Equation (8) into Equations (54) and (55) for the calculations of G_N and $K_{1,N}$, respectively.

The Model II nitrogen budget, like energy budget II, is thus controlled by only two variables, c and h.

RESULTS

Energy Budget

The energy budget is presented in two forms, a general model (Model I) and a special case of this model which incorporates information on the swimming and feeding behavior of the fish in response to plankton concentration (Model II). Model I, which defines the range of values which the energy budget could theoretically assume, is a function of the foraging speed (s), the concentration of plankton in the water (c), and the foraging time (h). In Model II, foraging speed is a dependent function of plankton concentration, and the energy budget is defined simply in terms of the variables c and h. Thus the two models describe the potential, and the actual, bioenergetic ranges within which the menhaden operate.

In the following examples to illustrate the models, the variables s, c, and h assume values from 0 to 50 cm/s, 0 to 0.0090 kcal/l, and 0 to 24 h/d, respectively, which should encompass the range of these variables in nature. In examples where s is assumed to be constant, a value of 41.3 cm/s was selected, because in the experiments this was the average foraging speed of the Atlantic menhaden at moderate to high plankton concentrations, where s was nearly independent of food level. Where c = constant, a value of 0.0030 kcal/l was used, which is slightly above the threshold value of c at which s becomes food-concentration independent. We lack information on the foraging time of adult Atlantic menhaden in the wild. However, since they feed continuously in the laboratory when food is present, when h = constant, we assigned it a value of 14 h, which is approximately equal to the number of daylight hours during the summer at the latitude of Narragansett Bay.

In the experimental studies from which the budgets were derived, the variables s, c, and h took the following values: h = 7 h, c = 0.0010 to 0.0065 kcal/l, and s = 29.3 to 43.3 cm/s (1.1 to 1.7 body lengths/s). Within this relatively narrow range in foraging speed, the respiration rate increased from 2.2- to 5.4-fold over the routine rate. Slower foraging speeds (<29 cm/s) were observed during the transition period of declining phytoplankton concentration, after the input of food was terminated. The minimum foraging speed was greater than the routine swimming speed (12.2 cm/s), but was not closely determined in this study. The total ration ranged from 0.015 to 0.147 kcal/g dry weight, which corresponded to a feeding rate of 0.00217 to 0.02065 kcal/g dry weight per h.

Using Model I we have described how foraging speed, food concentration, and the duration of feeding affect the menhaden energy budget (Fig. 1).

In Figure 1, A1-A4, s increases, while c and h remain constant. The total and the assimilated daily food intake (R_K and pR_K) increase linearly with increasing values of s (Fig. 1, A1). Among the energy expenditure terms, the exogenous nitrogen excretion ($E_{f,K}$) increases linearly, the endogenous nitrogen excretion ($E_{b,K}$) and the routine metabolic rate ($T_{r,K}$) remain constant, and the respiration during feeding ($T_{f,K}$) increases exponentially with increasing s (Fig. 1, A2). Thus the assimilated daily ration increases linearly, whereas the total energy expended increases curvilinearly. If these two curves are drawn on the same axes, we find that they intersect twice, at a low and a high foraging speed (here, about 7 and 51 cm/s) (Fig. 1, A3). These intersections, where the energy intake is balanced by the output and G = 0, define a range of foraging speeds within which the energy intake exceeds expenditure, and positive growth takes place. At foraging speeds outside this range, the energy expenditures exceed the energy intake and the fish must draw upon stored energy reserves, thus undergoing negative growth. Within the defined range of foraging speeds, the growth curve (G_K) is convex upwards, increasing curvilinearly from zero to reach a maximum value at an intermediate swimming speed, then declining back to zero (Fig. 1, A4). The growth efficiency curve ($K_{1,K}$) shows a similar pattern, but reaches its maximum value at a different foraging speed than that for maximum growth.

In Figure 1, B1-B4, c increases, while s and h remain constant. The energy intake (R and pR) increases

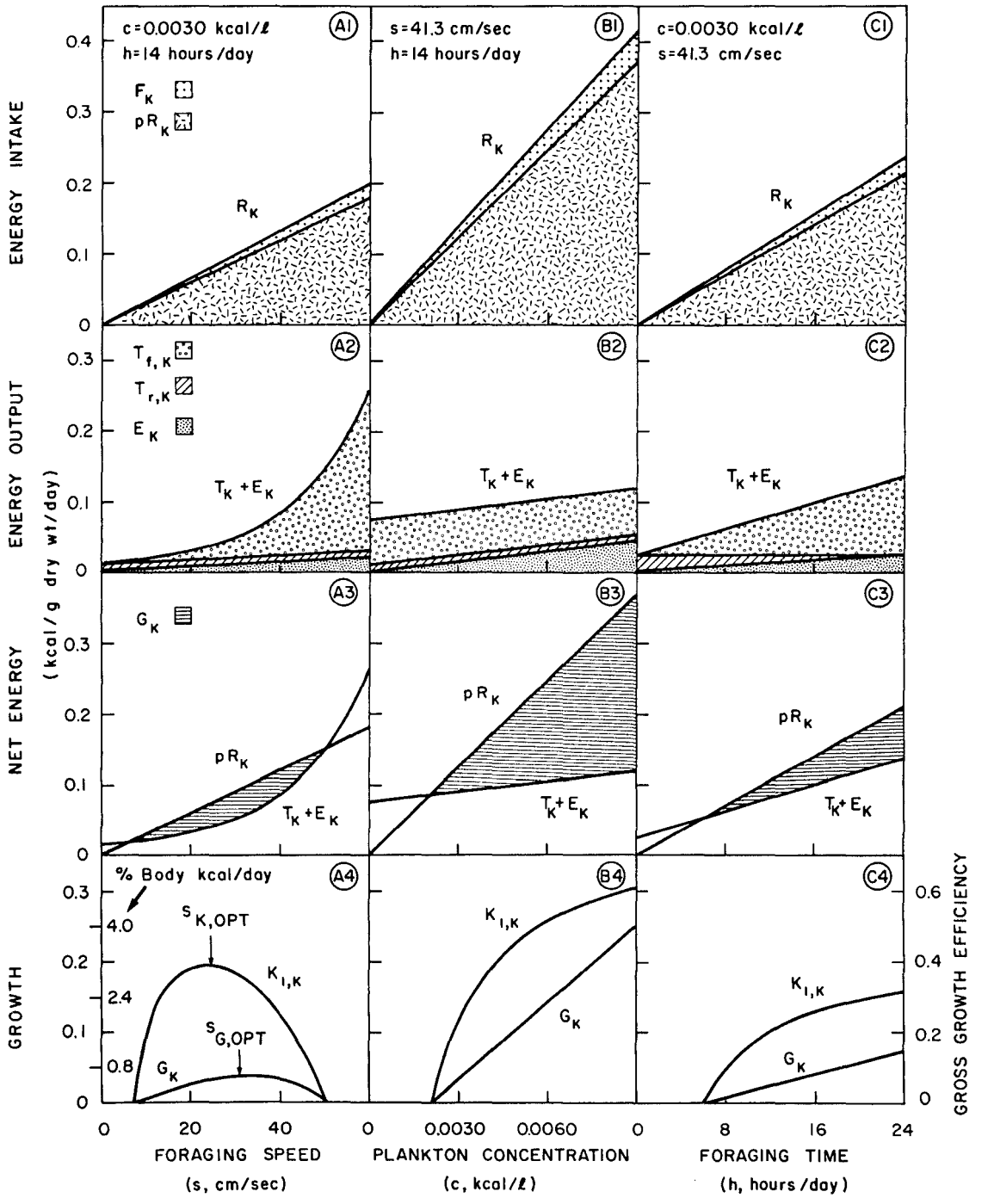

FIGURE 1.—Model I energy budget for the Atlantic menhaden at 20°C, where: A, foraging speed(s) increases, while plankton concentration (c) and foraging time (h) remain constant; B, plankton concentration increases, while foraging speed and foraging time remain constant; and C, foraging time increases, while foraging speed and plankton concentration remain constant. A1, B1, and C1 represent energy intake (R_K and pR_K); A2, B2, and C2, the energy output ($T_{r,K}$, $T_{f,K}$, E_K); A3, B3, and C3 compare the intake and output of energy and show the surplus energy which is available for growth; A4, B4, and C4 illustrate growth and gross growth efficiency.

linearly with increasing c (Fig. 1, B1). The energy expenditure to exogenous nitrogen excretion ($E_{f,K}$) also increases linearly, whereas $E_{b,N}$ and respiration ($T_{r,K}$ and $T_{f,K}$) are constant (Fig. 1, B2). The curves representing energy intake and expenditure both increase linearly with increasing values of c (Fig. 1, B3), and thus growth (G_K) increases linearly and gross growth efficiency increases asymptotically (Fig. 1, B4).

In Figure 1, C1-C4, h increases, while s and c remain constant. Here, also, the energy intake (R and pR) increases linearly with increasing h (Fig. 1, C1). The energy expenditure to endogenous nitrogen excretion ($E_{b,K}$) remains constant, while exogenous nitrogen excretion ($E_{f,K}$) and the respiration during feeding ($T_{f,K}$) increase linearly, and the routine respiration ($T_{r,K}$) declines linearly (Fig. 1, C2). The curves describing the energy intake and expenditure increase linearly with increasing values of h, (Fig. 1, C3), and again we find that growth (G_K) increases linearly, and gross growth efficiency ($K_{1,K}$) increases asymptotically (Fig. 1, C4)

These examples demonstrate that in order for an Atlantic menhaden, which forages at s cm/s for h h/d, to obtain a maintenance ration, the concentration of food must equal a minimum threshold value, c_{min} (i.e., 0.0021 kcal/l in Fig. 1, B3-B4). Similarly, a menhaden foraging at s cm/s when the plankton concentration = c kcal/l, must feed for some minimum period h_{min} (in Fig. 1, C3 and C4; 6.2 h/d) in order to obtain a maintenance ration. There will also be a minimum foraging speed, s_{min}, required to obtain a maintenance ration for each combination of c and h (in Fig. 1, A3 and A4; 7.0 cm/s). If growth is to occur, s, c, and h must exceed s_{min}, c_{min}, and h_{min}. The general rule is that for any swimming speed (s), the more abundant the food, the smaller the maintenance ration, and the shorter the feeding time required to obtain the ration (Fig. 2, A, B). If an Atlantic menhaden forages at 41.3 cm/s, for example, the lowest concentration of *Ditylum* at which it could obtain a maintenance ration would be about 0.0018 kcal/l, assuming that it fed for 24 h/d. The maintenance ration would be about 0.143 kcal/g dry weight per d. With an increase in plankton concentration, the required feeding time and the maintenance ration decline very rapidly, reaching 4 h/d and 0.051 kcal/g dry weight per d at c = 0.0039 kcal/l, and declining more slowly thereafter to 1.3 h/d and 0.038 kcal/g dry weight per d at c = 0.009 kcal/l.

An interesting feature of the energy budget is that for any combination of c and h, there is a single foraging speed which will maximize the growth rate ($s_{G,OPT}$) (Fig. 1, A4). Similarly, growth efficiency reaches its maximum value at a unique foraging speed ($s_{K,OPT}$), which is always less than $s_{G,OPT}$. $s_{G,OPT}$ increases curvilinearly with increasing food concentration (Fig. 3), but is independent of the duration of feeding (Fig. 4, Equation (36)). In contrast, $s_{K,OPT}$ declines as the duration of feeding increases (Fig. 4), but is independent of food concentration (Fig. 3, Equation (45)). It should be remembered however that the values of G_K and $K_{1,K}$ when the fish swim at $s_{G,OPT}$ and $s_{K,OPT}$ are determined by both c and h. For example, if c = 0.0030 kcal/l, a fish will maximize its growth rate if it swims at 33.9 cm/s although the actual rate of growth

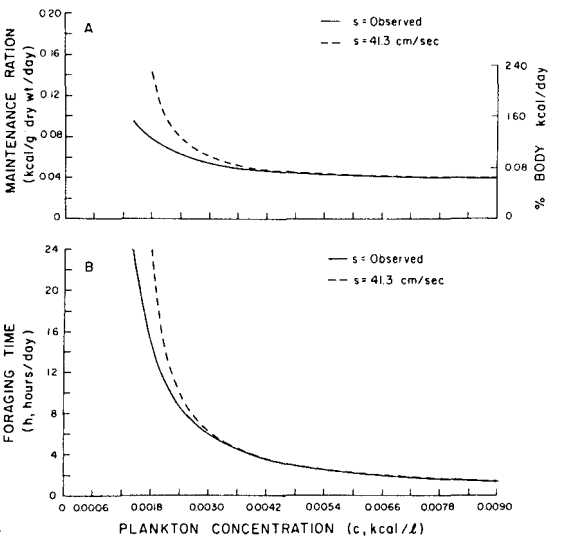

FIGURE 2.—A, relationship between the concentration of plankton and the maintenance ration of Atlantic menhaden which are assumed to swim at a constant speed of 41.3 cm/s (Model I) and at their actual speeds in response to plankton concentration (Model II). B, the foraging time required for the Atlantic menhaden to obtain a maintenance ration at different concentrations of plankton, assuming that they swim at 41.3 cm/s (Model I) or at the actual speed which has been observed in the laboratory (Model II).

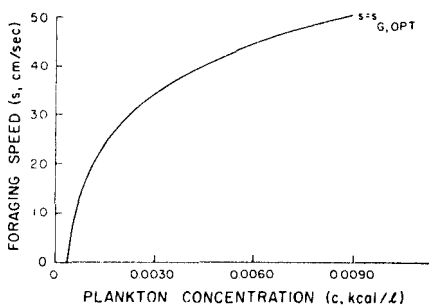

FIGURE 3.—The relationship between plankton concentration and the foraging speed which maximizes the Atlantic menhaden's growth rate ($s_{G,OPT}$). $s_{G,OPT}$ is independent of foraging time (h).

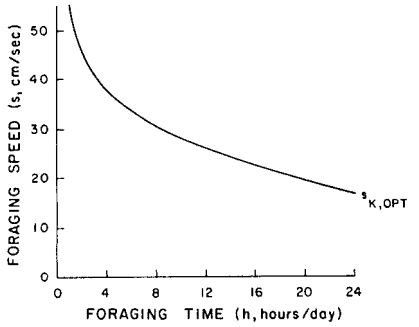

FIGURE 4.—The relationship between foraging time and the foraging speed which maximizes the Atlantic menhaden's gross growth efficiency ($s_{K,OPT}$). $s(s_{K,OPT})$ is independent of plankton concentration (c).

depends on h. Similarly, a fish feeding for 14 h/d will maximize its growth efficiency if it swims at 23.8 cm/s; however the resulting values of K_1 will depend on c.

The foregoing examples demonstrate that the relative size of each component in the energy budget (R_K, pR_K, T_K, E_K, and G_K) will vary according to the values of s, c, and h. Since the different elements retain no fixed proportions within the overall energy balance, there is no single "standard" energy budget which can be described for the Atlantic menhaden.

It can also be seen that in Model I, a change in either food concentration or the duration of feeding has a direct, proportional effect on the growth rate, because total energy intake and expenditure are linear functions of c and h, when s = constant. However, a change in s has a nonlinear impact on the growth rate. This is because the respiration rate is an exponential function of swimming speed, and thus a change in swimming speed causes a proportional change in energy intake but a more-than-proportional change in total energy output.

In the Model II energy budget, s is no longer an independent variable, but is a dependent function of food concentration c, according to the experimentally derived relationship in Equation (48). The foraging speed is nearly constant at moderate to high concentrations, but is reduced at low plankton abundance. The threshold concentration (0.0006 kcal/l) at which the fish stop feeding on *Ditylum* is also included in this model. The effect of reducing the foraging speed, when plankton concentration is low, is illustrated in Figure 5, which provides a comparison of Model II with Model I, where s = constant = 41.3 cm/s. (This foraging speed was chosen for the Model I example because it provides the best overall fit to Model II, facilitating the comparison between the two. The choice of another value for s would cause Model I to depart further from the actual behavior of the fish and would increase the difference between the two models.)

In Model I, we found that when s and h were constant, the curves describing R_K, pR_K, T_K, E_K, and G_K as a function of increasing c were all linear or constant (Fig. 1, B1-B4; Fig. 5, A1-A4). In Model II, these curves are nearly linear or constant at moderate to high plankton concentrations, where $s \sim$ constant. However, they become increasingly curvilinear at lower concentrations, when s is changing rapidly (Fig. 5, B1-B4). Thus we find that Model II is quite similar to Model I where s = 41.3 cm/s, when the food concentration is above c_{min} in the Model I example ($\sim$0.0021 kcal/l for h = 14 h/d). The models diverge significantly as c declines below c_{min}. If the Atlantic menhaden were to continue to swim at their "preferred" speed when the plankton concentration is low, a significant deficit in the energy budget would result (Fig. 5, A3). However, Model II shows that by reducing their foraging speed when food concentration is low, the Atlantic menhaden act to regulate their energy expenditure to remain close to their rate of energy uptake (Fig. 5, B3). Reducing the foraging speed has this effect, because of the exponential relationship between respiration and swimming speed. A reduction in foraging speed causes the respiration term to decline more rapidly than the ingestion term. The resulting change in the energy balance enables the fish to obtain a maintenance ration in less time, and at a lower concentration of food, than would have been possible had they continued to forage at the higher speed. The growth rate and growth efficiency are thereby enhanced at low concentrations (compare Fig. 5, A4 and B4). This effect can also be seen in Figure 2.

At the threshold concentration (0.0006 kcal/l) where Atlantic menhaden cease feeding on *Ditylum*, it can be seen (Fig. 5, B1 and B2) that the routine metabolic costs alone are greater than the energy which could be derived from feeding. The behavior of the fish apparently reflects the fact that it is not bioenergetically profitable to feed at such a low plankton density.

Nitrogen Budget

In the nitrogen budget there are three loss terms: The endogenous excretion, which is a constant, and the exogenous excretion and the fecal losses, which are proportional to the nitrogen content of the daily ration. The remaining nitrogen from the ration is retained as growth. Thus we find that the nitrogen

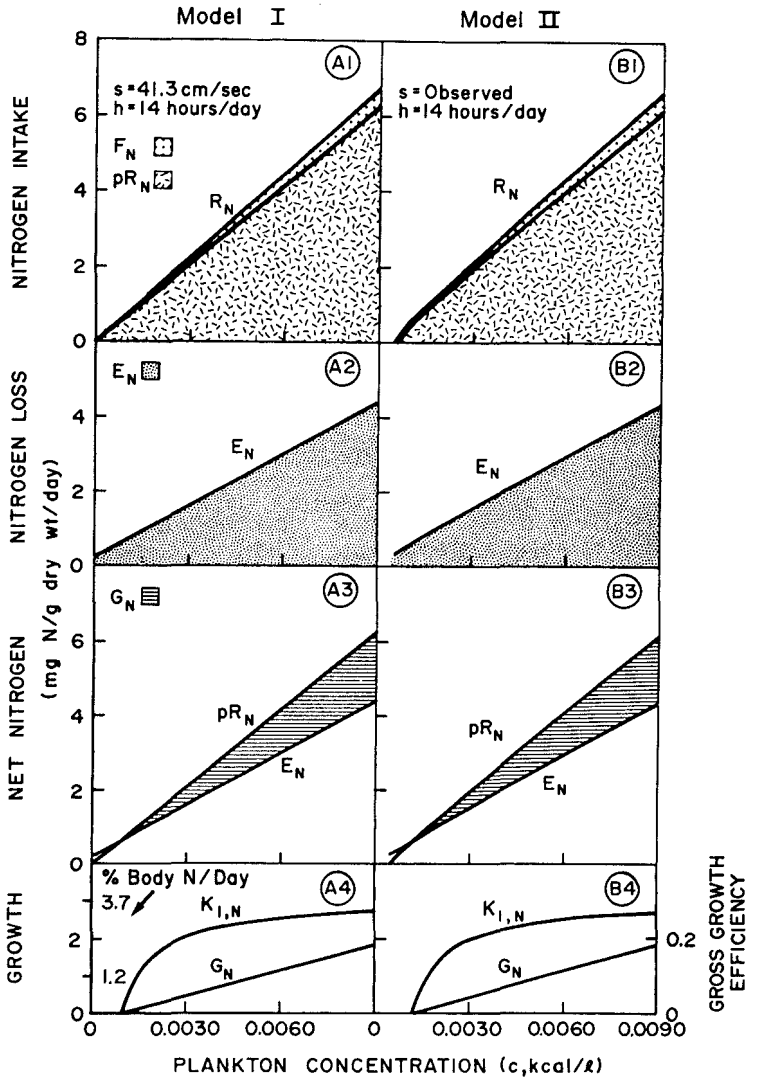

FIGURE 5.—A comparison of the Model I energy budget, where foraging speed and foraging time are constant while plankton concentration increases, with the Model II budget incorporating the actual voluntary swimming speed of the Atlantic menhaden at each concentration of plankton. Panels numbered 1, 2, 3, 4 are as in Figure 1.

budget, though functionally simpler than the energy budget, is controlled by the same three variables: The foraging speed (s, cm/s), the concentration of food (c, kcal or mg N/l), and the foraging time (h, h/d). In the Model I nitrogen budget, R_N, pR_N, $E_{f,N}$, and G_N all increase linearly, $E_{b,N}$ remains constant, and $K_{1,N}$ increases asymptotically with increasing values of s, c, and h (Fig. 6). However, as we found in the energy budget, these curves in the Model II nitrogen budget are nearly linear at plankton concentrations sufficiently high that $s \sim$ constant, but become increasingly curvilinear at low plankton concentrations because of the decline in the foraging speed (Fig. 7). Here, also, the reduction in foraging speed enables the Atlantic menhaden to obtain a maintenance ration in less time and at a lower concentration of plankton, and to increase their growth rate and growth efficiency, relative to the case in Model I where foraging speed was assumed to remain constant at 41.3 cm/s.

The nitrogen and energy budgets differ in some important ways. First, we have seen that in the energy budget, with an increase in swimming speed (s), the growth rate and growth efficiency increase from zero, reach a maximum, then decline back to zero (Fig. 1, A4). However, in the nitrogen budget, growth in nitrogen increases linearly (i.e., indefinitely), and growth efficiency increases asymptotically (Fig. 6, A4) with increasing swimming speed. Second, for any given s, c, and h, the predicted growth efficiency in calories is usually significantly different from that in nitrogen (Fig. 8). Figure 8 shows that differences ex-

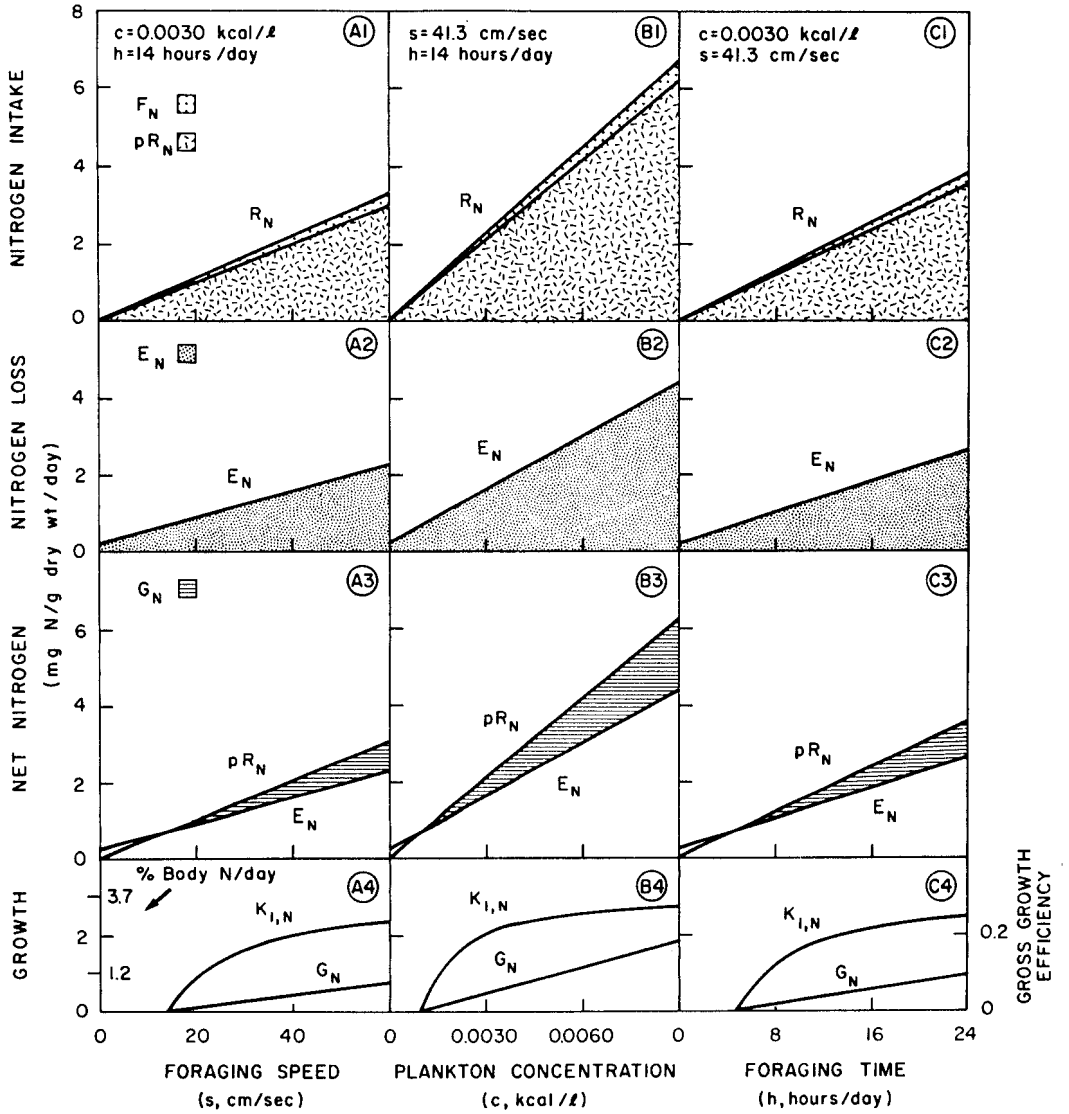

FIGURE 6.—Model I nitrogen budget for the Atlantic menhaden. Panels are as in Figure 1.

ist not only in the maximum or asymptotic values of the two growth efficiencies, but in the x-intercepts of the curves as well. The x-intercepts are of particular interest since they define the minimum requirements ($s_{min}, c_{min}, h_{min}$) for the fish to obtain a maintenance ration in nitrogen or calories. In Figure 8A, for instance, where c = 0.0030 kcal/l and h = 14 h/d, $s_{min,K}$ is $<s_{min,N}$. The Atlantic menhaden would be able to show positive growth in calories at a foraging speed of about 7 cm/s, whereas positive growth in nitrogen would require a higher foraging speed of about 14 cm/s. However, in Figure 8B, C, $c_{min,N}$ is $<c_{min,K}$ and $h_{min,N}$ is $<h_{min,K}$, respectively. Thus in these examples the menhaden would show positive growth in nitrogen at a lower food concentration, and with a shorter foraging time, than they would in calories.

Atlantic menhaden can exercise direct control over the variables s and h, but they may or may not have any impact on the environmental variable c. Thus it is of interest to consider how a change in the values of s and h will affect the minimum plankton concentration required for the Atlantic menhaden to obtain a maintenance ration in calories and nitrogen. The curve in Figure 9, calculated from the Model I budget, shows the combinations of s and h at which $c_{min,K} = c_{min,N}$. For all combinations of s and h, which fall below

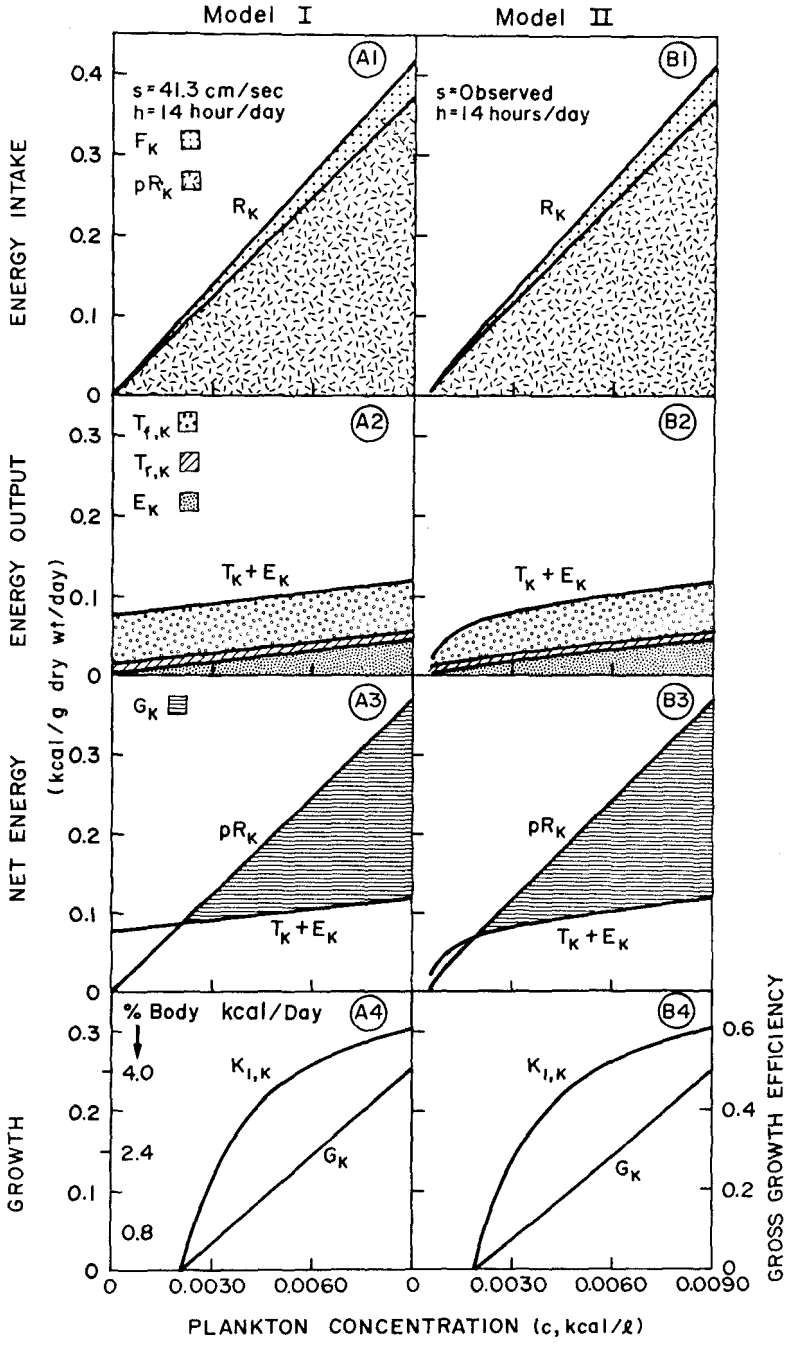

FIGURE 7.—Comparison of the Model I nitrogen budget where foraging speed and foraging time remain constant while plankton concentration increases, with the Model II budget incorporating the observed swimming speeds of the Atlantic menhaden at each plankton concentration.

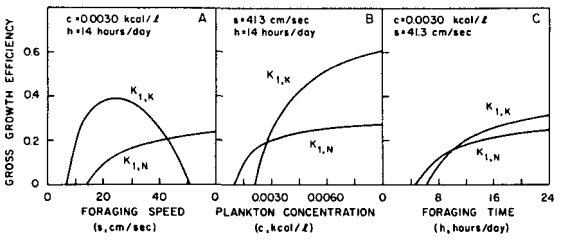

FIGURE 8.—Comparison of the gross growth efficiency of the Atlantic menhaden in calories ($K_{1,K}$) and nitrogen ($K_{1,N}$) where A, foraging speed(s) increases while plankton concentration (c) and foraging time (h) remain constant; B, plankton concentration increases while s and h are constant; and C, foraging time increases while s and c are constant.

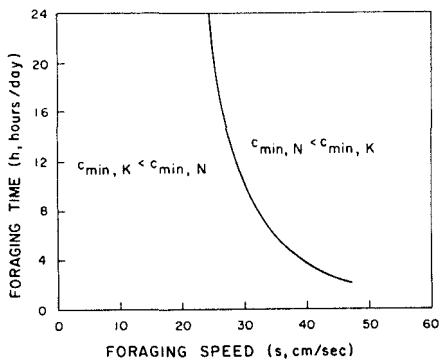

FIGURE 9.—Boundary curve defining the combinations of foraging time and foraging speed at which the minimum plankton concentration required for the Atlantic menhaden's growth in calories ($c_{min,K}$) is less than, and greater than, that required for growth in nitrogen ($c_{min,N}$).

this boundary, $c_{min,K}$ will be lower than $c_{min,N}$. Atlantic menhaden will be able to grow in calories at a lower food concentration than they can in nitrogen. Conversely, where s and h are greater than the boundary values, $c_{min,N}$ will be lower than $c_{min,K}$. Atlantic menhaden can grow in nitrogen at a lower food concentration than they can in calories.

Next we consider how the actual foraging speeds of the Atlantic menhaden compare with the boundary curve in Figure 9. Figure 10A shows the foraging speed in relation to food concentration. Figure 10B shows that for all values of h up to 24 h/d, Atlantic menhaden forage at speeds such that their minimum food requirement for growth in nitrogen is lower than for calories, i.e., $c_{min,N}$ is $< c_{min,K}$. Thus at low plankton concentrations, the growth efficiency in nitrogen is greater than in calories. However, it can be seen from Figure 9 that $K_{1,N}$ remains $> K_{1,K}$ only over a narrow range of food concentrations immediately above $c_{min,N}$. $K_{1,K}$ increases very rapidly above $c_{min,K}$ and soon overtakes $K_{1,N}$. Thus in most circumstances where the fish are growing, growth efficiency in calories will be considerably higher than in nitrogen.

DISCUSSION

Functioning of the Energy and Nitrogen Budgets

These models permit a detailed analysis of the energetics of the Atlantic menhaden, by showing how energy intake (ingestion), as well as energy losses and expenditures (feces, excretion, respiration) vary with the concentration and size of the food particles, the foraging speed of the fish, and the duration of feeding. These different components of the model, and the predicted growth rate and growth efficiency, are discussed in more detail below.

Energy Intake

VOLUME SEARCHED.—The volume searched by the Atlantic menhaden can be described in very

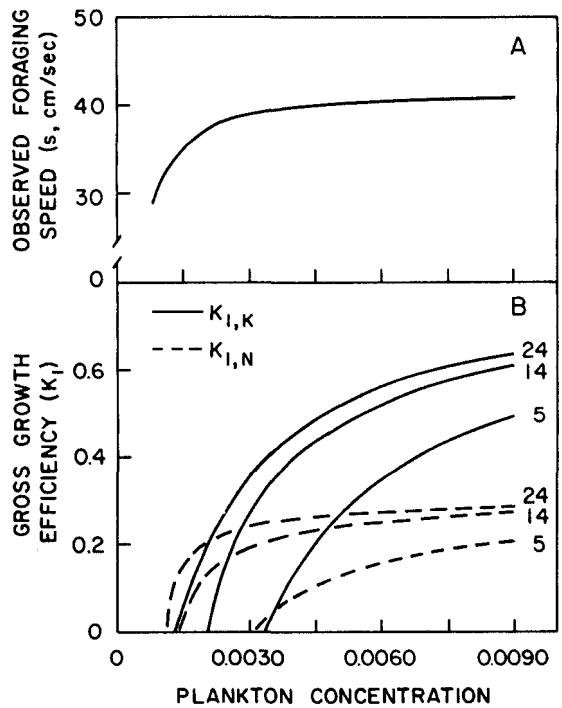

FIGURE 10.—A, laboratory defined relationship between Atlantic menhaden voluntary foraging speed and plankton concentration. B, gross growth efficiency of menhaden which forage at these swimming speeds for different periods of time.

simple terms, i.e., an ellipsoid with cross-sectional area equal to that of the fish's open mouth, and length equal to the distance travelled by the fish per unit time. The volume searched is equal for all types of prey. With other species of filter-feeding fishes, a slight modification of this basic formula may be necessary, according to the mode of feeding. For example, a number of species (northern anchovy, Leong and O'Connell 1969; alewife, Janssen 1978; gizzard shad, Drenner et al. 1978) are described as rhythmically opening and closing the mouth during feeding, apparently producing a suction which draws in particles located outside the perimeter of the mouth. Here, the cross-sectional area of the volume searched is somewhat larger than the mouth area; also, a correction factor is needed to account for the proportion of the time the fish's mouth is closed and not actually filtering. Nevertheless, the basic simplicity of the volume searched by a filter feeder is in marked contrast to the case of a predatory fish or particulate planktivore. Since these fishes visually locate and capture their prey, the volume searched is complex and depends on a variety of factors, including the visual capacity and adaptations of the fish, the inherent visibility and behavioral characteristics of the prey, and the nature of the underwater visual environment (quantity and quality of the illumination, clarity of the water). Thus the volume searched by a particulate feeder is different for different types of prey, and even if a fish were to swim at constant speed and feed on a single prey type, the volume searched will continually change according to variables such as the time of day, and the depth at which the fish swims (Durbin 1979).

FORAGING SPEED.—Foraging speed affects both the energy intake and expenditure terms in the energy budget, but only the energy intake in the nitrogen budget. Foraging speed is the principal determinant of the volume searched for food, since the cross-sectional area of the mouth in an Atlantic menhaden of a given size is constant. Foraging speed in the Atlantic menhaden increases asymptotically with increasing food concentration. Because of this there will be two critical levels of abundance for each prey species: c_t, the threshold concentration at which the menhaden are stimulated to feed, and c_i, the concentration at which foraging speed becomes approximately independent of food concentration. With *Ditylum*, the value of c_t was about 4.5 μg chlorophyll a/l (0.0027 kcal/l), and the fish swam at an average speed of 41.3 cm/s. From Figure 2 it is seen that when $c = 0.0027$ kcal/l, the fish swimming at 41.3 cm/s would obtain a maintenance ration in slightly more than 7 h. At higher food concentrations the required feeding time would be much less, generally <4 h. These results suggest that Atlantic menhaden feeding on *Ditylum* will swim at their "preferred" speed as long as the concentration is sufficiently high to enable the fish to meet their daily energy requirements in <8 h of feeding. At lower food concentrations the fish conserve energy by swimming more slowly during feeding. Whether these results are fortuitous and apply only to *Ditylum*, or instead imply a fundamental relationship between foraging speed and foraging time which is applicable to different food types, cannot be determined from present information.

FILTRATION EFFICIENCY.—The effective volume searched will be determined by the filtration efficiency (e). As described earlier (Equation (6)) filtration efficiency is fairly high for zooplankton-sized particles, but in the range of phytoplankton-sized particles declines sharply to a minimum size threshold of about 13 μm. This means that the Atlantic menhaden cannot directly exploit the <20 μm size fraction of phytoplankton, which forms the greater part of the total phytoplankton biomass on their summer feeding grounds (Durbin et al. 1975). Menhaden exploit this food resource indirectly, however, by feeding upon the zooplankton.

ASSIMILATION EFFICIENCY.—The efficiency with which food is assimilated further modifies the energy intake by the Atlantic menhaden and will affect the predicted growth rate and growth efficiency in the model. If assimilation changes with different meal sizes or rates of feeding, then the proportion of ingested energy which is available for metabolism and growth will also change. Most investigators have found that assimilation efficiency is independent of ration size (Gerking 1955; Menzel 1960; Pandian 1967; Birkett 1969; Iwata 1970; Beamish 1972; Kelso 1972; Staples and Nomura 1976). However, Elliott (1976) and Solomon and Brafield (1972) found a slight decrease in assimilation efficiency as meal size increased. (In the latter study the authors suggest that the change may have been an artifact arising from the incomplete recovery of a small amount of fecal material in the tank.) For the Atlantic menhaden we assumed a constant assimilation efficiency with different ration sizes.

The mean assimilation efficiencies observed for the Atlantic menhaden feeding on phytoplankton were quite high (86.4% for carbon, 92.4% for nitrogen, and 89.5% for calories). For Atlantic menhaden feeding on zooplankton the values were similarly high (86.7,

91.3, and 87.7%, respectively). The high values for zooplankton were consistent with results from other fishes (Gerking 1955; Pandian 1967; Beamish 1972; Kelso 1972). Few measurements of carbon, nitrogen, or caloric assimilation exist for marine herbivorous fishes. Menzel (1959) found that *Holacanthus* assimilated 85% of the nitrogen and 77.7% of the calories from two species of macroalgae. The lower assimilation in *Holacanthus* may have been related to the type of food. However, there do not appear to be any comparable studies with marine phytophageous fishes, which would indicate whether the high assimilation efficiency of the Atlantic menhaden is typical of this trophic group.

Energy Losses

RESPIRATION.—The major energy outputs by the Atlantic menhaden are respiration and excretion. Respiration by the menhaden was divided into feeding ($T_{f,K}$) and nonfeeding components ($T_{r,K}$). SDA was not included as a separate component, but for reasons discussed earlier was included as part of the feeding respiration rate. SDA is thought to be a fixed proportion of the energy content of the food ration, and in carnivorous fishes has been estimated at about 12.7-16% (Muir and Niimi 1972; Beamish 1974; Pierce and Wissing 1974; Schalles and Wissing 1976). Partitioning $T_{f,K}$ into its components, $T_{s,K}$ and $T_{\mathrm{SDA},K}$, would have caused some minor changes within the energy budget, but would not have significantly affected the predictions of growth rate and growth efficiency. The most important change would be in a case analagous to Figure 1B, where food concentration increases while s and h remain constant. Here, the ingested ration automatically increases in proportion to c because Atlantic menhaden filter a constant proportion of particles from the water. $T_{f,K}$ in this illustration is constant, which reflects the fact that its major component $T_{s,K}$ is constant. However, if SDA were included separately we would actually expect to see a small linear increase in $T_{f,K}$ because $T_{\mathrm{SDA},K}$ should presumably increase in proportion to the ration R_K.

For Atlantic menhaden, the metabolic cost of feeding appears to be high (Durbin et al. 1981). This is because of the very rapid increase in respiration rate per unit increase in foraging speed. This rate of increase was about 2.5 times greater than has been observed in other (nonfilter feeding) species during forced long-term swimming (Beamish 1978). Thus even minor changes in the foraging speed can have a significant impact on metabolic expenditures and the overall energy balance.

The energy budget demonstrates that for an active species such as the menhaden, it is not possible to use a constant multiplier of the standard metabolism, as recommended by Winberg (1956), to estimate metabolic expenditures in the field. Not only is the suggested multiplier of 2 times the standard rate too low (in our studies the routine rate was 3.4 times the estimated standard rate, and the average feeding rate 2.3-4.8 times routine, or about 8-17 times standard), but also the relative size of the respiration component within the overall energy budget is also a variable, changing according to the values of s, c, and h.

EXCRETION.—Excretion, the other major energy output, is similarly a variable. In contrast to respiration which depends on swimming speed and foraging time, excretion depends on the amount of food eaten. Excretion, therefore, will follow no constant relationship to respiration in the energy budget (Model I). The linear relationship between ration size and exogenous nitrogen excretion is similar to results in other studies (Gerking 1971; Savitz et al. 1977), although the proportion of nitrogen excreted will depend on the balance of amino acids in the food relative to the requirements of the fish.

Growth Rate and Growth Efficiency

The rates of energy intake and expenditure determine the amount of energy which is available for growth. Atlantic menhaden must invest considerable time and energy in feeding. The Model I energy and nitrogen budgets show that if foraging speed remains constant, then growth will increase linearly with increasing ration size, regardless of whether this is brought about by an increase in food concentration or foraging time. Consequently, gross growth efficiency increases asymptotically with increasing ration size. Model II demonstrates that given the actual swimming behavior of the menhaden, the relationship between ration size and growth is in fact very nearly linear at moderate-high plankton densities were s ~ constant, but becomes significantly curvilinear at lower plankton levels because of the decreasing foraging speed. With the reduction in foraging speed, the energy balance changes because proportionally less of the ingested ration is used to support metabolism, which leaves more energy available for growth.

Ivlev's (1960) bioenergetic model of the bleak, *Alburnus alburnus*, showed that in this particulate-feeding planktivore, growth increased asymptotically, rather than linearly, with increasing food concen-

tration. These results reflect basic differences in the ingestion process between filter- and particulate-feeding planktivores. Since a filter feeder like the Atlantic menhaden removes a constant proportion of the particles in the water per unit of time, without the necessity to capture and handle each item of prey individually, the ingestion rate increases linearly with increasing food concentration and swimming speed. In contrast, with the particulate planktivore, feeding is a series of discrete events and there will be a maximum ingestion rate set by the time required to capture and handle each prey. Thus, as Ivlev has shown experimentally (Ivlev 1960, 1961), ingestion rate increases asymptotically with increasing food concentration. This causes an asymptotic growth curve. There does not appear to be any information available to describe the ingestion pattern of a particulate feeder as a function of swimming speed. However, based on Holling's predation model (Holling 1966), an increase in the swimming speed of a particulate planktivore will increase the encounter frequency and hence the feeding rate. Based on this model we could expect that with increasing swimming speed, the ingestion rate will increase asymptotically towards a maximum rate set by the handling time.

In most laboratory studies of the relation between feeding and growth, the fish are given a fixed ration for a specified period, after which the amount of growth is determined. The food is made readily available to the fish, and hence the time and energy expended for feeding is presumably small. In the majority of these studies, growth was linearly related to ration size, which implies that assimilation efficiency and the increment in metabolism and growth per unit of ration remained constant at all ration levels (Pandian 1967; Birkett 1969; Gerking 1971; Jones and Hislop 1972, 1978; Niimi and Beamish 1974; Staples and Nomura 1976; Stirling 1977). Where reported, growth efficiency increased asymptotically with increasing ration size; this is a consequence of the observed linear growth-ration relation.

In several studies the relationship between growth and meal size appeared to be slightly curvilinear, however, with the growth rate somewhat depressed at high rations (Carline and Hall 1973; Elliott 1975; Wurtsbaugh and Davis 1977). Under these conditions, growth efficiency increased curvilinearly from zero at the maintenance ration to a maximum value, and thereafter declined curvilinearly. Warren and Doudoroff (1971) suggested that such a phenomenon could be caused either by a reduction in assimilation efficiency at high rations, or by a change in the energy balance within the fish, in which the metabolic component increased (higher SDA, or greater spontaneous activity) at the expense of the energy available for growth. Another possible cause of departure from linearity could arise from changes in the wet weight:dry weight ratios (Staples and Nomura 1976). These investigators found that fish at high ration levels increased in percent of dry weight relative to fish on low rations. Thus measurements of growth based on wet weight will overestimate the true growth of fish at low rations, and underestimate growth at high rations, which can lead to an apparent curvilinearity in the growth-ration relationship.

The growth of sockeye salmon on fixed rations increased nearly linearly with increasing ration size, in keeping with results from other similar studies (Brett et al. 1969; Brett and Shelbourn 1975). However the latter investigators found that if they included growth data from fish fed "excess rations," where voluntary food intake continually declined as the fish grew, the overall relationship between growth and increasing ration size was asymptotic, making the growth efficiency curve convex upwards.

The Model I prediction of a linear relation between ration size and growth in the Atlantic menhaden, when swimming speed is constant (i.e., activity = constant), and the slight departure from linearity by Model II, is therefore supported by most experimental studies of feeding and growth in other fish species. It should be noted that if assimilation efficiency in Atlantic menhaden were to decline at high feeding rates beyond the range of the experimental data, we would expect that growth rate will approach an asymptote, and growth efficiency will decline with further increases in ration size. However since the experiments covered the range of plankton concentrations which the fish might be expected to encounter in nature (Durbin and Durbin 1981), the possible decline in assimilation at very high feeding rates would not appear to be meaningful for Atlantic menhaden under most circumstances in the wild.

It should also be noted that since the foraging costs of obtaining a ration of a particular size will vary according to s, c, and h, there will not be a single (unique) relationship between ration size, growth rate, and growth efficiency in Atlantic menhaden.

The models predict that over most of the range of plankton concentrations where growth is possible, growth efficiency will be higher for calories than for nitrogen. These findings are consistent with field observations that the fat and caloric composition of the menhaden increases relative to protein during its season of growth (Dahlberg 1969; Dubrow et al. 1976). At low plankton concentrations the fish forage at speeds such that growth in nitrogen is possible even when there is an overall net energy deficit. This

suggests that protein is conserved when food levels are low.

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Optimal Foraging by Planktivores

In a landmark study, Ware (1975) combined Ivlev's (1960) data on *Alburnus* with Holling's (1966) predation model to develop a bioenergetic model of this particulate planktivore, which could be used to test different theories of optimal foraging. Ware was the first to demonstrate the existence of $s_{G,\mathrm{OPT}}$ and $s_{K,\mathrm{OPT}}$, and showed the importance of swimming speed in determining the energy balance within the fish. His analysis demonstrated that the swimming speeds of fish in nature can be extremely useful and sensitive indicators of how different species respond to and exploit changes in their food resource. An interesting feature of Ware's (1975) model of a particulate planktivore was that as c increased, $s_{G,\mathrm{OPT}}$ curvilinearly increased to a maximum at a single food concentration, and thereafter declined, whereas $s_{K,\mathrm{OPT}}$ declined monotonically with increasing values of c. These changes in $s_{G,\mathrm{OPT}}$ and $s_{K,\mathrm{OPT}}$ were due to the effect of handling time on the rate of ingestion in the Holling (1966) model. In contrast the present study, which extends Ware's concepts of $s_{G,\mathrm{OPT}}$ and $s_{K,\mathrm{OPT}}$ to a filter feeder, shows that since handling time is negligible in a filter feeder, $s_{G,\mathrm{OPT}}$ increases asymptotically with increasing values of c, whereas $s_{K,\mathrm{OPT}}$ is solely a function of h and independent of c. It is interesting that for both particulate and filter-feeding planktivores, distinct foraging strategies are required in order to achieve maximal growth rate or growth efficiency.

The experimental data from the Atlantic menhaden make it possible to determine whether the foraging behavior of this species is directed towards enhancing some measure of ecological fitness such as growth rate or growth efficiency. This may be done by comparing the growth rates and growth efficiencies calculated for the observed swimming speeds of the menhaden with those that would result if the fish were to swim at speeds equivalent to either $s_{G,\mathrm{OPT}}$ or $s_{K,\mathrm{OPT}}$. The comparison is made with $s_{G,\mathrm{OPT}}$ in Figure 11 for the case where $h = 14$ h/d and with $s_{K,\mathrm{OPT}}$ in Figure 12 for the case where $c = 0.0030$ kcal/l.

Figure 11 demonstrates that the growth of Atlantic menhaden which swim according to the laboratory derived relationship in Equation (48) is very close to the maximum possible growth at each concentration of plankton. This suggests that foraging speed in the adult Atlantic menhaden is a behavioral adaptation to maximize growth rate.

In contrast, at any given concentration of food the observed foraging speed was always $>s_{K,\mathrm{OPT}}$, which resulted in submaximal values of $K_{1,K}$ (Fig. 12). This is evidence that the fish were not acting to maximize growth efficiency. To maximize growth efficiency the fish would have had to regulate their foraging speed according to the duration of feeding. This was not observed in Atlantic menhaden in the laboratory, where foraging speed at a given concentration of food remained constant for periods of up to 7 h. Further, we have shown that foraging strategies which regulate swimming speed in order to maximize growth rate and growth efficiency are mutually exclusive.

Figures 4 and 11 provide an explanation for the hyperbolic nature of the plankton concentration-foraging speed relationships in Equation (48). $s_{G,\mathrm{OPT}}$ changes most rapidly at low concentrations of plankton, and it is in this region where Atlantic menhaden most strongly regulate their foraging speed, $s_{G,\mathrm{OPT}}$

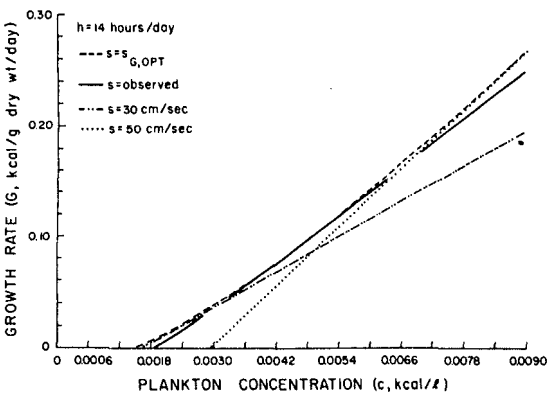

FIGURE 11.—A comparison of the growth of the Atlantic menhaden at different concentrations of plankton, when the fish swim according to $s_{G,\mathrm{OPT}}$; their actual voluntary speeds; and constant speeds of 30 and 50 cm/s. Foraging time is 14 h/d.

changes less rapidly at moderate-high plankton abundance, and in fact the constant preferred speed of the Atlantic menhaden (41.3 cm/s) is sufficiently close to $s_{G,\,OPT}$ that growth remains nearly maximal over a very broad range of plankton abundance. Thus there is no great "penalty" if the fish swim at constant speed rather than exactly at $s_{G,\,OPT}$ within this region of the curve. The choice of this preferred speed is fairly exacting, however. As can be seen in Figure 11, at speeds not greatly different from 41 cm/s (30 and 50 cm/s), growth will be suboptimal over much of the plankton concentration range.

How much of a sacrifice in growth efficiency is implied if the fish swim at $s_{G,OPT}$? Figure 12 indicates that $K_{1,\,K}$, though suboptimal, is still reasonably high when the fish swim at $s_{G,OPT}$. However, as the foraging speed increases above $s_{G,OPT}$, there is an increasingly rapid decline in $K_{1,\,K}$, as can be seen in Figure 12 where s = constant = 50 cm/s.

In conclusion, the present results, which demonstrate a very close agreement between the predicted relationship between $s_{G,OPT}$ and food concentration, and the observed relationship between foraging speed and c, indicate that the foraging speeds of the adult Atlantic menhaden have evolved over time towards maximizing growth rate. This optimization of growth rate has necessarily resulted in a submaximal growth efficiency. In his analysis of data for the bleak, Ware (1975) showed that the observed foraging speed when $c \sim 0.000808$ kcal/l was also quite close to the value of $s_{G,OPT}$ predicted from his model. However, there was insufficient information in Ivlev's (1960) original study to indicate whether the bleak adjusts its foraging speed to remain near $s_{G,OPT}$ at different plankton concentrations. Studies demonstrating selective feeding in planktivores (e.g., Brooks 1968; Leong and O'Connell 1969; O'Connell 1972; Werner 1974; Werner and Hall 1974; O'Brien et al. 1976; Eggers 1977; Confer et al. 1978) indicate that foraging strategies, which result in the maximization of energy intake, may be a more general phenomenon among these fishes. However, it should be pointed out that these feeding studies only consider energy intake and not energy expenditures, so that the extent to which these fishes are following optimal strategies for growth or growth efficiency cannot really be determined.

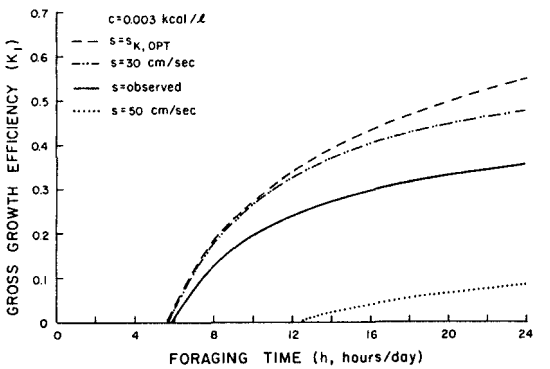

FIGURE 12.—A comparison of the gross growth efficiency of the Atlantic menhaden as a function of foraging time, when the fish swim according to $s_{K,OPT}$; their actual voluntary speeds; and constant speeds of 30 and 50 cm/s. Plankton concentration is 0.0030 kcal/1.

Extension of the Model to Particles of Different Size

Observations using several phytoplankton species as food (Durbin and Durbin 1975) indicated that the preferred (concentration independent) foraging speeds were similar for these species. However these estimates of swimming speed, made with a stopwatch, were not sufficiently accurate to distinguish the small changes in foraging speed that have been found to be significant in the energy budget. Thus it would be desirable to verify this observation using a more precise method, such as video or cinematography, to determine the swimming speeds.

In the same study it was, however, clear that the threshold concentration for the onset of feeding (c_t) and the concentration at which foraging speed became approximately independent of food concentration (c_i) were quite different for plankton particles of different size. The inverse nature of this relationship is consistent with the fact that when an Atlantic menhaden forages at a given speed, its energy expenditure is the same for all food types, yet its energy intake declines with decreasing food particle size because of the declining efficiency of the gill rakers. This means that a higher concentration of small particles is needed in order for a fish to satisfy its minimum energy requirement, and thus we would expect an increase in c_t and c_i as particle size declines.

The constants in the equations presented here have been specified for *Ditylum brightwelli*, which is about 80 μm long. A change in particle size will change the filtration efficiency (e), which will necessitate recalculation of some of the constants in the equations for $R, E, G, s_{G,OPT}$, and $s_{K,OPT}$. This is a simple matter except for the last two quantities, and for these we have presented the steps in the integration of the equations in sufficient detail (Equations (33) to (45)) to permit recomputation for different particle sizes.

It is of particular interest to consider how $s_{G,OPT}$ changes with a change in food particle size. It has

been shown (Fig. 4) that $s_{G,OPT}$ increases with increasing food concentration. This is because with increasing c, the rate of energy intake increases per unit of energy expenditure. An increase in food particle size affects the ingestion rate in a manner analagous to an increase in particle abundance, and thus we find that $s_{G,OPT}$ increases with increasing particle size as well (Fig. 13). $s_{G,OPT}$ is most strongly affected by food particle size in the range of 20-60 μm, moderately affected within the range of 60-300 μm, and relatively unaffected by further increases in particle size above about 300 μm. In other words, $s_{G,OPT}$ is strongly size-dependent in the range of phytoplankton particles, less so in the range of microzooplankton, and is for practical purposes independent of particle size in the range of copepodites and late-stage nauplii. This pattern, of course, reflects the filtration efficiency curve of the gill rakers (Equation (6)).

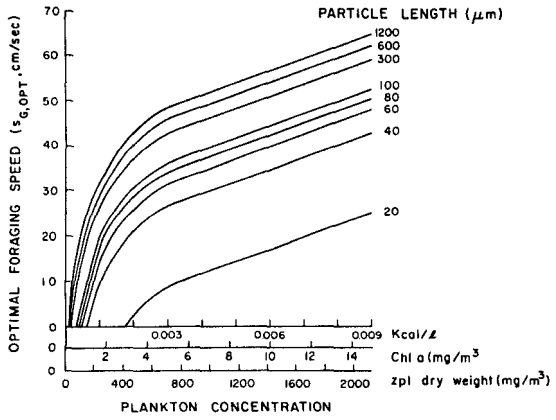

FIGURE 13.—The effect of particle size on the relationship between the foraging speed which maximizes the Atlantic menhaden's growth rate ($s_{G,OPT}$) and plankton concentration.

Figure 13 illustrates the need for information on how the Atlantic menhaden responds to mixtures of different-sized particles. For example, do the menhaden respond to the total biomass of particles, or do they key in on certain size classes, ignoring the remainder even though they may filter these particles simultaneously with the larger prey? We have seen that Atlantic menhaden feeding on a single food type will alter their energy expenditures according to the abundance of food, such that they maximize their growth rate at each level of food abundance. However there is a need for further investigation of their feeding behavior on different sizes and mixtures of particles to determine the degree to which they act as "optimal foragers" in a mixture of plankton species.

Application of the Atlantic Menhaden Models to the Field

The energy and nitrogen budgets have been derived in terms of three controlling variables, each of which can be determined from direct field measurements: The foraging speed (s), the concentration of plankton (c), and the foraging time (h). Foraging speed can be measured in the field using acoustic techniques, and this procedure can be used to verify our predictions of swimming speed based on laboratory investigations of the relationship between s and c. If confirmed in the field, these laboratory studies will enable us to eliminate s as an independent variable and define the budgets simply in terms of c and h. However, as mentioned previously, before we can use this approach in the field, where the fish feed on a variety of particle sizes, additional laboratory work is needed to quantify the foraging speed-food-concentration relationships for different types and sizes of plankton. The foraging time (h) could be determined from diel surveys of stomach contents to determine gut fullness and the state of digestion of the food (the latter is an indicator of how recently the food was ingested). If h proves to be relatively invariant, or under simple control of an external variable such as day length, it may ultimately become possible to describe the energy and nitrogen budgets of the Atlantic menhaden solely as a function of the average concentration of different-sized plankton in the water.

The effects of body size and temperature also need to be considered in applying the models to the field. Hettler (1976) has investigated the effects of body size, temperature, and salinity on routine metabolism in juvenile Atlantic menhaden. The influence of these variables on the swimming and feeding behavior of the Atlantic menhaden, and on the other components of the energy budget, must be investigated as well, before a general energy and nitrogen budget for the Atlantic menhaden can be described.

Another point to consider in applying the present energy budget to the field is that Atlantic menhaden in nature may have additional energy expenditures beyond those of the laboratory fish, principally the costs of predator avoidance, spawning activity, and the energy cost of migration. The first two activities would increase respiratory expenditure, and correspondingly reduce the amount of surplus energy that is available for growth. It is not clear to what extent seasonal migrations of the Atlantic menhaden (Nicholson 1971, 1978) represent an additional energy cost, however, since it is possible that the Atlantic menhaden continue feeding as they move along their migratory routes. In addition, the seasonal migration

does not require elevated swimming speed since Atlantic menhaden swimming at a routine speed of 12.2 cm/s could accomplish the distance between Rhode Island and Cape Hatteras, N.C., well within the 3-4 mo duration of the spring and fall migrations.

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LITERATURE CITED

BEAMISH, F. W. H.
1972. Ration size and digestion in largemouth bass, *Micropterus salmoides* Lacepède. Can. J. Zool. 50:153-164.
1974. Apparent specific dynamic action of largemouth bass *Micropterus salmoides*. J. Fish. Res. Board Can. 31:1763-1769.
1978. Swimming capacity. *In* W. S. Hoar and D. J. Randall (editors), Fish physiology, Vol. VII, p. 101-189. Acad. Press, N.Y.

BIRKETT, L.
1969. The nitrogen balance in plaice, sole and perch. J. Exp. Biol. 50:375-386.

BRETT, J. R., AND J. E. SHELBOURN.
1975. Growth rate of young sockeye salmon, *Oncorhynchus nerka*, in relation to fish size and ration level. J. Fish. Res. Board Can. 32:2103-2110.

BRETT, J. R., J. E. SHELBOURN, AND C. T. SHOOP.
1969. Growth rate and body composition of fingering sockeye salmon, *Oncorhynchus nerka*, in relation to temperature and ration size. J. Fish. Res. Board Can. 26:2363-2394.

BROOKS, J. L.
1968. The effects of prey size selection by lake planktivores. Syst. Zool. 17:272-291.

CARLINE, R. F., AND J. D. HALL.
1973. Evaluation of a method for estimating food consumption rates of fish. J. Fish. Res. Board Can. 30:623-629.

CONFER, J. L., G. L. HOWICK, M. H. CORZETTE, S. L. KRAMER, S. FITZGIBBON, AND R. LANDESBERG.
1978. Visual predation by planktivores. Oikos 31:27-37.

DAHLBERG, M. D.
1969. Fat cycles and condition factors of two species of menhaden, *Brevoortia* (Clupeidae), and natural hybrids from the Indian River of Florida. Am. Midl. Nat. 82:117-126.

DRENNER, R. W., J. R. STRICKLER, AND W. J. O'BRIEN.
1978. Capture probability: the role of zooplankter escape in the selective feedings of planktivorous fish. J. Fish. Res. Board Can. 35:1370-1373.

DUBROW, D., M. HALE, AND A. BIMBO.
1976. Seasonal variations in chemical composition and protein quality of menhaden. Mar. Fish. Rev. 38(9):12-16.

DURBIN, A. G.
1979. A review of the principles of food selection by plankton-feeding fishes. *In* R. Stroud (editor), Symposium on predator-prey systems in fish communities and their implications in fisheries management, p. 203-218. Sport Fishing 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.

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., AND A. G. DURBIN.
1981. Assimilation efficiency and nitrogen excretion of a filter-feeding planktivore, the Atlantic menhaden, *Brevoortia tyrannus* (Pisces: Clupeidae). Fish. Bull., U.S. 79:601-616.

DURBIN, E. G., R. W. KRAWIEC, AND T. J. SMAYDA.
1975. Seasonal studies on the relative importance of different size fractions of phytoplankton in Narragansett Bay (USA). Mar. Biol. (Berl.) 32:271-287.

EGGERS, D. M.
1977. The nature of prey selection by planktivorous fish. Ecology 58:46-59.

ELLIOTT, J. M.
1975. The growth rate of brown trout (*Salmo trutta* L.) fed on reduced rations. J. Anim. Ecol. 44:823-842.
1976. The energetics of feeding, metabolism and growth of brown trout (*Salmo trutta* L.) in relation to body weight, water temperature and ration size. J. Anim. Ecol. 45:923-948.

ELLIOTT, J. M., AND W. DAVISON.
1975. Energy equivalents of oxygen consumption in animal energetics. Oecologia (Berl.) 19:195-201.

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.

HETTLER, W. F.
1976. Influence of temperature and salinity on routine metabolic rate and growth of young Atlantic menhaden. J. Fish Biol. 8:55-65.

HOLLING, C. S.
1966. The functional response of invertebrate predators to prey density. Mem. Entomol. Soc. Can. 48:1-86.

IVLEV, V. S.
1960. On the utilization of food by planktophage fishes. Bull. Math. Biophys. 22:371-389.
1961. Experimental ecology of the feeding of fishes. Yale Univ. Press, New Haven, 302 p.

IWATA, K.
1970. Relationship between food and growth in young Crucian carps, *Carassius auratus cuvieri*, as determined by the nitrogen balance. Jpn. J. Limnol. 31:129-151.

JANSSEN, J.
1978. Feeding-behavior repertoire of the alewife, *Alosa pseudoharengus*, and the ciscoes *Coregonus hoyi* and *C. artedii*. J. Fish. Res. Board Can. 35:249-253.

JONES, R., AND J. R. G. HISLOP.
1972. Investigations into the growth of haddock, *Melanogrammus aeglefinus* (L) and whiting, *Merlangius merlangus* (L) in aquaria. J. Cons. Int. Explor. Mer 34:174-189.
1978. Further observations on the relation between food intake and growth of gadoids in captivity. J. Cons. Int. Explor. Mer 38:244-251.

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.

LEONG, R. J. H., AND C. P. O'CONNELL.
1969. A laboratory study of particulate and filter feeding of the northern anchovy (*Engraulis mordax*). J. Fish. Res. Board Can. 26:557-582.

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

MUIR, B. S., AND A. J. NIIMI.
1972. Oxygen consumption of the euryhaline fish aholehole (*Kuhlia sandvicensis*) with reference to salinity, swimming, and food consumption. J. Fish. Res. Board Can. 29:67-77.

NICHOLSON, W. R.
1971. Changes in catch and effort in the Atlantic menhaden purse-seine fishery 1940-68. Fish. Bull., U.S. 69:765-781.
1978. Movements and population structure of Atlantic menhaden indicated by tag returns. Estuaries 1:141-150.

NIIMI, A. J., AND F. W. H. BEAMISH.
1974. Bioenergetics and growth of largemouth bass (*Micropterus salmoides*) in relation to body weight and temperature. Can. J. Zool. 52:447-456.

O'BRIEN, W. J., N. A. SLADE, AND G. L. VINYARD.
1976. Apparent size as the determinant of prey selection by bluegill sunfish (*Lepomis macrochirus*). Ecology 57:1304-1310.

O'CONNELL, C. P.
1972. The interrelation of biting and filtering in the feeding activity of the northern anchovy (*Engraulis mordax*). J. Fish. Res. Board Can. 29:285-293.

PANDIAN, T. J.
1967. Transformation of food in the fish *Megalops cyprinoides* II. Influence of quantity of food. Mar. Biol. (Berl.) 1:107-109.

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

PIERCE, R. J., AND T. E. WISSING.
1974. Energy cost of food utilization in the bluegill (*Lepomis macrochirus*). Trans. Am. Fish. Soc. 103:38-45.

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.

SCHALLES, J. R., AND T. E. WISSING.
1976. Effects of dry pellet diets on the metabolic rates of bluegill (*Lepomis macrochirus*). J. Fish. Res. Board Can. 33:2443-2449.

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.

STAPLES, D. J., AND M. NOMURA.
1976. Influence of body size and food ration on the energy budget of rainbow trout *Salmo gairdneri* Richardson. J. Fish Biol. 9:29-43.

STIRLING, H. P.
1977. Growth, food utilization and effect of social interaction in the European bass *Dicentrarchus labrax*. Mar. Biol. (Berl.) 40:173-184.

WARE, D. M.
1975. Growth, metabolism, and optimal swimming speed of a pelagic fish. J. Fish. Res. Board Can. 32:33-41.

WARREN, C. E., AND P. DOUDOROFF.
1971. Biology and water pollution control. W. B. Saunders Co., Phila., 434 p.

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

WEAST, R. C. (editor).
1977. CRC handbook of chemistry and physics. 58th ed. CRC Press, Inc., Cleveland.

WERNER, E. E.
1974. The fish size, prey size, handling time relation in several sunfishes and some implications. J. Fish. Res. Board Can. 31:1531-1536.

WERNER, E. E., AND D. J. HALL.
1974. Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). Ecology 55:1042-1052.

WINBERG, G. G.
1956. [Rate of metabolism and food requirements of fishes.] Nauchnye Tr. Belorussk. Gos. Univ. Minsk, 253 p. (Transl. 1960. Fish. Res. Board Can. Transl. Ser. 194.)

WURTSBAUGH, W. A., AND G. E. DAVIS.
1977. Effects of temperature and ration level on the growth and food conversion efficiency of *Salmo gairdneri*, Richardson. J. Fish Biol. 11:87-98.