A BIOENERGETIC MODEL FOR THE ANALYSIS OF FEEDING AND SURVIVAL POTENTIAL OF WINTER FLOUNDER, *PSEUDOPLEURONECTES AMERICANUS*, LARVAE DURING THE PERIOD FROM HATCHING TO METAMORPHOSIS

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ABSTRACT

A bioenergetic model was developed which simulated effects of temperature, prey density, and larval size on ability of winter flounder, *Pseudopleuronectes americanus*, larvae to obtain food energy to provide for experimentally determined growth and metabolism. Larval feeding at constant temperature and as a function of prey concentration was exponential and more sharply asymptotic in younger fish than in those near metamorphosis. Specific growth rates were exponentially related to prey concentrations and ranged from 5.72 to 8.70%/day at survival prey concentrations of 3.7 to 21.7 cal/liter. Daily required feeding time was directly related to prey availability. Critical plankton densities below which larvae did not have enough time during the day to obtain adequate food for growth and metabolism varied with age and ranged from 2.1 to 5.7 cal/liter. Simulated physiological energy utilization and required caloric food intake were inversely related to prey concentration and varied with larval stage of development. Food requirements expressed as numbers of copepod nauplii consumed per day ranged from 19 for first feeding larvae to 235 for metamorphosed juveniles. Predicted gross growth efficiencies were directly related to prey concentration and increased with age from 5 to 33%. All indications pointed to a "critical period" of larval survival during the period of exogenous feeding initiation and immediately after.

One of the important problems in fishery research and management is identifying and understanding the functional mechanisms of the stock–recruitment relationship. It is becoming more apparent that focusing attention on studies of mortality in the early life stages, particularly the larval stage, may help in this understanding. Mortality rates are usually the highest and most variable from year to year during the early life stages. Because of this, even small changes in mortality during this period can produce a magnified effect on the eventual numbers of recruits to sport or commercial fisheries.

Other than predation, the most important probable factors influencing larval mortality are food and feeding relationships and the influence of environmental parameters on these processes. The acquisition of the required food ration by fish larvae is of prime importance in survival and successful development. Without the proper quantity and quality of food, larvae will be adversely affected and survival will be influenced. Bioenergetic relationships have been studied extensively for adult fishes, and the works of Ivlev (1939a, b, c), Winburg (1956), Paloheimo and Dickie (1966a, b), and Warren and Davis (1967) are among the most complete. However, the use of energy resources in physiological mechanisms and the relationships of feeding, growth, and survival in the early life stages of fishes have only recently been studied (Ivlev 1961a, b; Lasker 1962; Laurence 1969, 1973).

It is the object of this research to examine the effects of food and feeding on winter flounder, *Pseudopleuronectes americanus*, survival from the period of hatching to metamorphosis and to develop a model of these critical processes. The model includes the forcing variables of temperature, prey density, and larval size or age and their effects on the ability of winter flounder larvae to successfully acquire energy rations necessary for experimentally determined growth and metabolic parameters. The energy rations are quantified as to caloric value of ration, numbers of specific prey organisms consumed, time for required intake, and metabolic parameters dealing with conversion into fish flesh.

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MATERIALS AND METHODS

Adult winter flounder were captured by trawl net from Narragansett Bay, R.I., and maintained in 1,900-liter experimental aquaria. Embryos were obtained by allowing the fish to ripen naturally under optimum temperature and photoperiod conditions or causing ovulation with hormones according to the techniques of Smigielski (1975). Embryos were incubated with methods developed at the Narragansett Laboratory (Smigielski and Arnold 1972).

All experiments and rearing were done at 8°C during these studies since this temperature is the approximate mean temperature for the entire period from hatching to metamorphosis for winter flounder in the Narragansett Bay area. Stock cultures of larvae were reared in series of black 64-liter experimental aquaria. The aquaria were placed in an environmental room or in water baths where the temperatures were maintained by program recorders controlling heating and cooling coils. All experimental aquaria were aerated with air stones and were semiclosed systems with a portion of the seawater being replenished every 1 or 2 days. Illumination was controlled by timers which provided a 12:12 day–night photoperiod corresponding to the mean photoperiod during the normal winter flounder spawning time.

Zooplankton fed during all experiments consisted mainly of the nauplii, copepodites, and adults of the copepods *Acartia clausi, Centropages hamatus,* and a few *Temora longicornis* and *Eurytemora affinis* collected from the Narragansett Bay area with 0.5-m plankton nets fitted with 64- and 116-μm mesh. Collections were sieved through 200- or 500-μm mesh strainers, depending on the size of larvae to be fed. Plankton densities in experimental aquaria were monitored by taking two to four 5-ml aliquots from the aquaria and counting the number of plankters under a dissecting microscope.

The relationship between larval size (body dry weight) and stomach contents was studied from hatching to metamorphosis. Larvae were reared in a 64-liter black aquarium and were fed high prey concentrations of 13.6–20.5 cal/liter or approximately 2 or 3 nauplii/ml. Samples of 25 larvae were taken each week until metamorphosis for stomach analyses and dry body weight determinations.

Experiments determining the influence of prey concentration on daily feeding intensity expressed as stomach contents were conducted at 0.68, 3.41, 6.80, 20.5, 34.1, and 47.8 cal/liter (corresponding to 0.1, 0.5, 1.0, 3.0, 5.0, and 7.0 nauplii/ml). Larvae aged 2, 5, and 7 wk after hatching were used. Approximately 25 larvae were placed in all black 4-liter aquaria containing the desired prey densities. The larvae were allowed to feed for 1 day's photoperiod (12 h) after which they were pipetted onto a 100-μm mesh screen and allowed to suffocate to prevent regurgitation of food before being preserved in 5% Formalin.[2] Ten larvae from each prey concentration were used for stomach analyses and 10 were used for mean dry body weight determinations. Stomach analyses were done with a dissecting microscope. Larval stomachs and intestines were teased apart with fine needles, and contents were identified to genus and species if possible.

Digestion rate measured by gut clearance time of larval winter flounder at 8°C was determined by feeding dyed zooplankton according to the techniques of Laurence (1971a). Transparency of the larvae permitted visual observation of dyed plankters in stomachs of living larvae. To determine the evacuation time of the stomach and intestine under active feeding conditions, larvae feeding on dyed plankters at concentrations of 1 or 2 nauplii/ml were removed and placed in duplicate aquaria with similar concentrations of nondyed plankton, and the gut clearance times of the dyed plankters from individual larvae were recorded.

Experiments determining the influence of temperature on growth of winter flounder larvae were conducted in 38-liter experimental aquaria. Feeding, monitoring, and sampling techniques and results for these experiments are described in detail by Laurence (1975).

The influence of planktonic prey concentration on growth and survival at 8°C from the period hatching to metamorphosis was studied at prey concentrations of 0.068, 0.68, 3.41, 6.80, and 20.5 cal/liter, corresponding approximately to 0.01, 0.1, 0.5, 1.0, and 3.0 nauplii/ml. Larvae were stocked at an initial density of 500 per aquarium; methods for maintaining prey concentrations, sampling, and determining growth and survival rates are described in detail by Laurence (1974).

Standard manometer equipment (Warburg res-

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

pirometers) and techniques (Umbreit et al. 1964) were used to measure oxygen consumption for metabolic determinations in relation to temperature and larval size. A description of the specific methods and results has been reported earlier (Laurence 1975).

All combustions for caloric determinations of larval winter flounder tissue were done in triplicate in a Parr 1241 automatic adiobatic calorimeter adapted for a microbomb. Caloric values for copepod prey species and methodology for these determinations are reported by Laurence (1976).

All statistical analyses used in this research are described in Steel and Torrie (1960) and Draper and Smith (1966). Modeling and analyses were done in the FORTRAN IV language on an IBM 370 computer.

EXPERIMENTAL RESULTS

Food Consumed and Relationship to Larval Size

Numerical analysis of stomach contents is not very meaningful in itself. It can, however, be useful in conjunction with the measurement of other parameters. An estimation of the dry weight and caloric value of food consumed per larval dry weight was needed as part of the overall bioenergetic model. Stomach analysis by enumerating copepods in larvae fed high concentrations (2 or 3 nauplii/ml) combined with information on dry weights and caloric values of the copepods provided this. Mean dry weights for the copepod species and life stage were taken from the literature (Conover 1960; Anraku 1964; Hargrave and Geen 1970; Gaudy 1974). Caloric values were determined in our laboratory (Laurence 1976). The average composite values used for the copepods in this study were 1.3 μg dry weight for nauplii, 15.4 μg dry weight for older stages, and 5,251 cal/g dry weight for all copepod tissue. Multiplying the numbers of plankton species and life stage per stomach by the average dry weight values for each plankter type and summing yielded the mean dry weight of the stomach contents. Results of these analyses along with nauplii to older stage ratios of copepods consumed and caloric value per stomach are shown in Table 1. The regression relationship of the logarithms of larval dry body weight and larval stomach contents weight was positively linear (Figure 1) and significantly correlated ($R = 0.87, P = 0.01$).

TABLE 1.—Mean numbers, weights, and caloric values of copepods consumed by larval winter flounder of different sizes. Each sample consists of 25 larvae.

Mean larval dry wt (μg)	Mean no. of copepods per stomach	Nauplius to older stage ratio	Mean dry wt per stomach (μg)	Calorie per stomach
10.4	2.0	1:0	2.6	0.0137
14.3	1.0	1:0	1.3	0.0068
21.5	2.1	1:0	2.7	0.0142
29.4	5.4	1:0	7.0	0.0368
51.1	3.3	29:1	6.0	0.0315
81.2	32.3	12:1	41.9	0.2205
226.8	2.9	12:1	6.9	0.0362
396.6	4.7	3:4	43.8	0.2300
444.2	33.5	22:1	57.7	0.3030
513.9	8.4	1:2	89.9	0.4720
667.6	3.0	1:2	32.1	0.1686

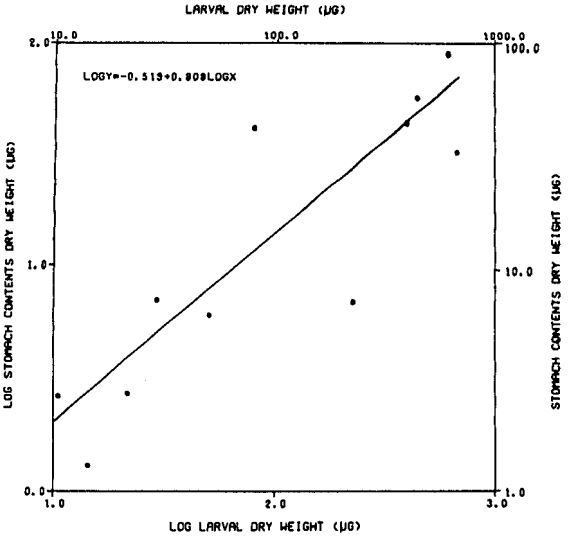

FIGURE 1.—The regression relationship of larval dry body weight to larval stomach contents weight for winter flounder at 8°C.

Prey Density and Intensity of Feeding

The relationship between intensity of feeding and concentration of prey is important in determining food intake. Ivlev (1961b) has analyzed this relationship and expressed it by the following function:

$$\frac{dr}{dp} = \alpha(R - r)$$

where r = size of a unit ration for a unit time
R = maximum size of the ration during the same unit time at the upper limiting level of food concentration beyond which ration size does not increase

α = coefficient of proportionality
p = plankton concentration.

After integration, the function becomes:

$$r = R\ (1 - e^{-\alpha p}).$$

Use of this relationship in analyzing winter flounder feeding as influenced by prey densities of 0.68–47.8 cal/liter, or 0.1–7.0 nauplii/ml, yielded some interesting results (Figure 2). Feeding was reasonably constant in the youngest fish with an asymptote being reached quickly at the lower prey concentrations. Five-week-old larvae displayed a rather classic form of the Ivlev curve with food intake increasing with prey density, reaching a maximum at approximately 6.8 cal/liter or 1.0 nauplius/ml, and then remaining quite stable. The oldest larvae, prior to metamorphosis, showed an increasing food intake through the whole range of plankton densities, right up to 47.8 cal/liter or 7.0 nauplii/ml. In general, there appeared to be an increasing of the upper limiting level of food concentration and a decreasing of the coefficient of proportionality (α) with increasing larval age.

Digestion Rate

Winter flounder larvae were known to be continuous, visual daylight feeders from prior research. Preliminary attempts at establishing digestion rates and unpublished results of night feeding experiments showed that larvae at-

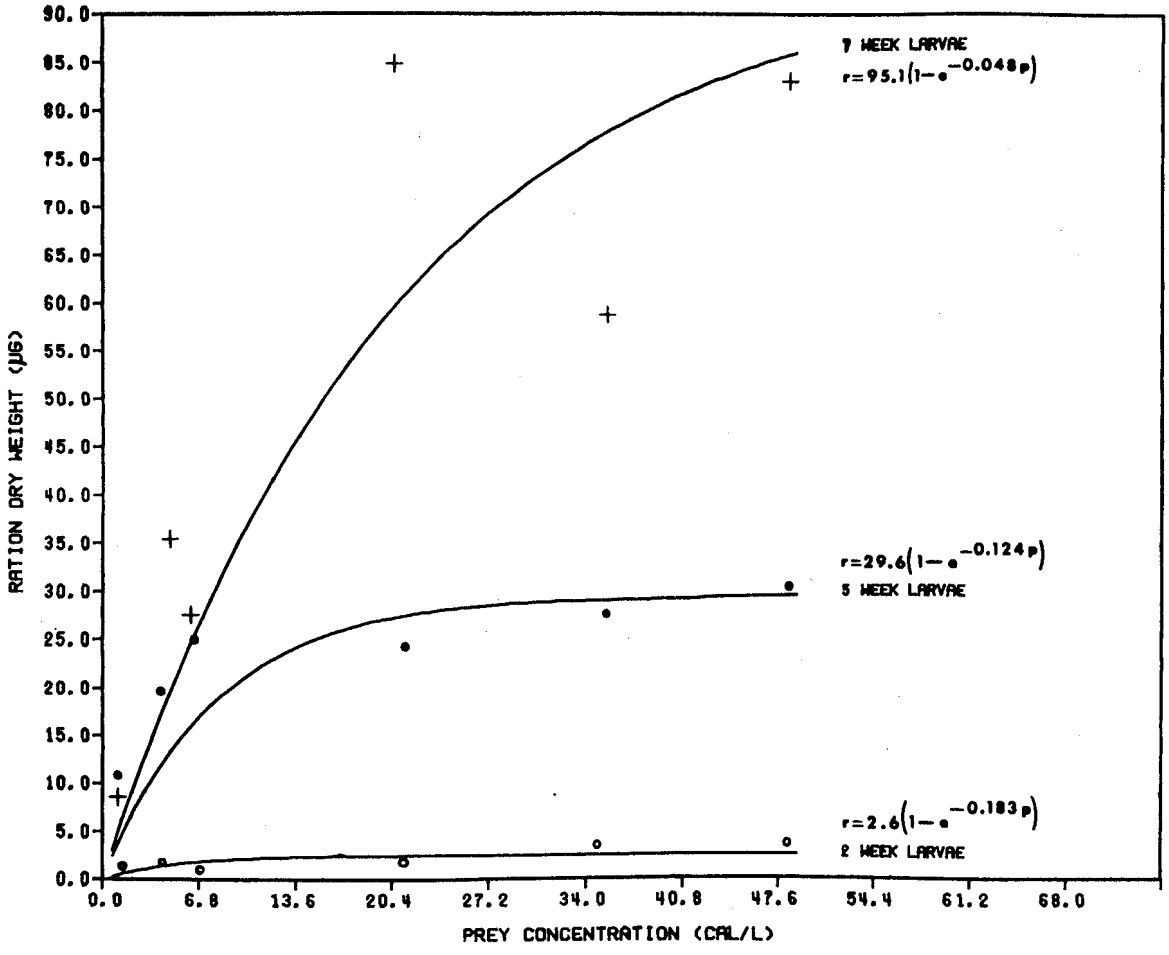

FIGURE 2.—The relationship between planktonic prey concentration and feeding intensity expressed as stomach ration for different aged winter flounder larvae at 8°C.

tempted to feed constantly under daylight conditions and ceased feeding entirely during darkness. Evacuation rates of the gut while larvae were actively feeding were recorded at 8°C for estimates of digestion rates. Results of 10 individual larvae showed a mean, active digestion time of 6.6 h with a range of 5.1–8.4 h.

Effects of Prey Density on Growth and Survival

The effects of five prey densities from 0.068 to 20.5 cal/liter (approximately 0.01–3.0 nauplii/ml) on growth and survival of winter flounder larvae from hatching to metamorphosis at 8°C were examined. Larval survival did not exceed 2 wk at the lower two densities of 0.01 and 0.1 nauplius/ml. Growth expressed as dry weight against time at the three survival densities (3.4, 6.8, and 20.5 cal/liter) was similar (Figure 3), as indicated by the confidence intervals about the slopes of the descriptive regression equations (Table 2). Specific growth rates on a daily basis increased with plankton concentration and were experimentally observed to be 8.62%/day for 3.0 nauplii/ml, 7.68%/day for 1.0 nauplius/ml, and 5.72%/day for 0.5 nauplius/ml.

Plankton density influenced survival more significantly than growth. Specific mortality coefficients calculated by the methods of Laurence (1974), which correct for the number of experimental removals for growth measurements, demonstrated a direct relationship with lower mortality rates at each higher plankton density (Table 3). Plots of predicted specific mortality coefficients through the range of plankton densities from 0.68 to 20.5 cal/liter based on the above results yielded an exponential relationship (Figure 4).

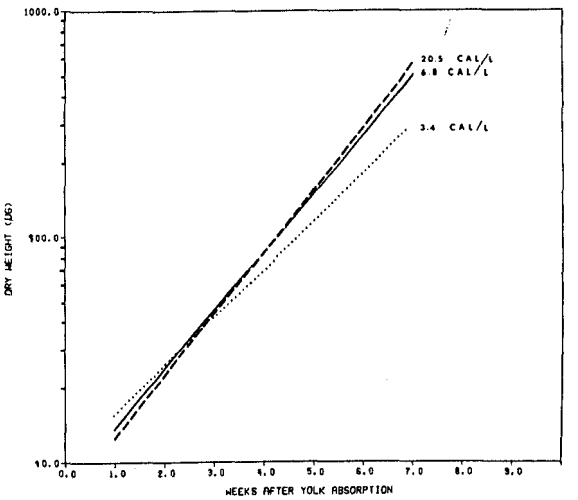

FIGURE 3.—Growth of winter flounder larvae at 8°C and at three different planktonic prey densities.

TABLE 2.—Regression equations and statistical parameters of winter flounder dry weight growth vs. time at 8°C and different planktonic prey densities.

Planktonic concentration (cal/liter)	Growth regression equation	Confidence interval about slope	Correlation coefficient
20.5	$\log Y = 0.849 + 0.269X$	0.212–0.326	0.98
6.80	$\log Y = 0.830 + 0.272X$	0.234–0.311	0.99
3.41	$\log Y = 0.990 + 0.208X$	0.141–0.275	0.97
0.68	No survival to metamorphosis		
0.068	No survival to metamorphosis		

TABLE 3.—Daily mortality coefficients of winter flounder at 8°C as influenced by planktonic prey density.

Planktonic concentration (cal/liter)	Corrected number of survivors out of 500	Days of survival[1]	Specific mortality coefficient
20.50	171	49	0.022
6.80	19	49	0.069
3.40	13	42	0.091
0.68	5	15	0.307

[1]No calculable survival at the lowest plankton density of 0.068 cal/liter.

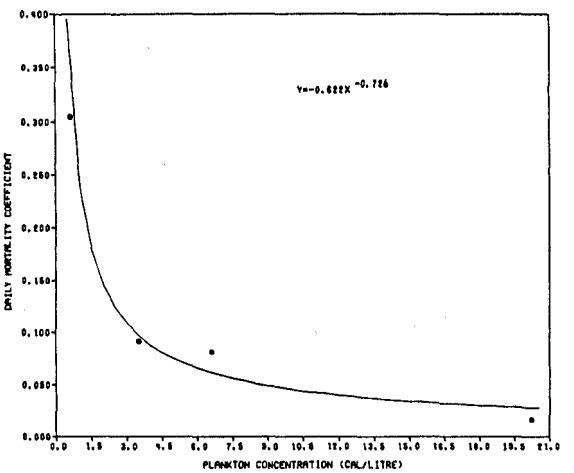

FIGURE 4.—Daily mortality coefficients of winter flounder at 8°C from the period hatching to metamorphosis as influenced by prey density.

Metabolic Rate

Laurence (1975) expressed metabolism of winter flounder from hatching through metamorphosis in terms of oxygen consumption. Regression relationships of mean hourly oxygen

consumption in microliters from hatching through and beyond metamorphosis on dry body weight were nonlinear and fitted best by a third-degree polynomial (Figure 5 from Laurence 1975). A third-degree polynomial was statistically most significant, as indicated by analysis of variance (F = 13.2 for cubic term, 7.4 for quadratic term, and 9.5 for linear term) over the weight range studied (10–4,000 μg). However, in this research the size range for larvae was 10–1,000 μg, and only the predicted data from the first ascending leg of the polynomial at 8°C were used in the computations.

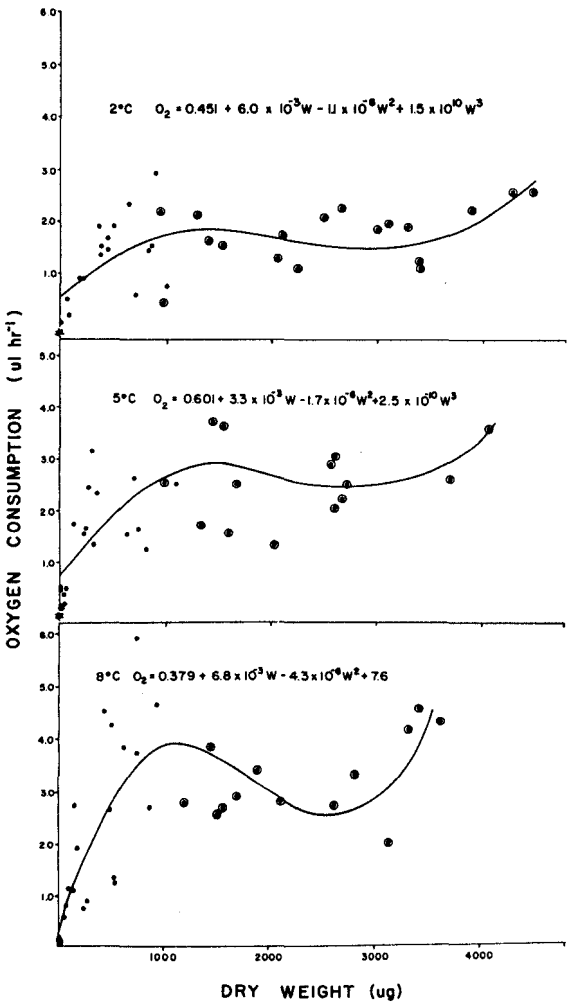

FIGURE 5.—Regression of mean hourly oxygen consumption on dry weight of winter flounder larvae and juveniles at three temperatures. Circled data points indicate metamorphosed juveniles. Results at 8°C used in these studies. (From Laurence 1975.)

BIOENERGETIC MODEL

A general model for the transformation of food to fish flesh and the energy relationships involved has been discussed in detail by Winburg (1956) and Warren and Davis (1967). The basic relationship can be expressed as:

$$Q_+ = Q_* + Q' + Q_- \quad (1)$$

where Q_+ = energy of food consumed
Q_* = energy of waste products in feces and urine
Q' = energy of growth
Q_- = energy of metabolism.

Since a portion of the energy value of food is lost in the feces and urine and not utilized or assimilated, Winburg (1956) proposed the following "balanced equation":

$$Q_+ - Q_* = Q' + Q_- \quad (2)$$

or

$$bQ_+ = Q' + Q_- \quad (3)$$

where b = the coefficient of utilization or, in Brody's (1945) terminology, the physiological useful ration. Equation (3) analyzes the conversion of food energy inside the fish (physiological). However, influences of the environment on food consumption and utilization must also be considered. Many modifications based on my experimental results and additions of methods of other researchers have been incorporated into a model suitable for a broader analysis of the bioenergetics of winter flounder larvae. The following paragraphs present a detailed description of the methods used to derive this model.

Ivlev (1961b) formulated a model founded on the basic bioenergetic equation (Equation (3)) for the utilization of food by plankton-eating fishes. The relationship is:

$$0.7Q_+ = Q' + Q_-. \quad (4)$$

The coefficient of utilization (b) is assumed to be 0.7, based on information provided by Ware (1975) who reviewed the most recent thinking of the efficiency of food conversion. During the course of a day, a larval fish will be active in daylight (while feeding) and relatively passive the remainder of the time (usually at night). It can be assumed that the intensity of metabolism dur-

ing rest is represented by the standard metabolic rate (Q_s) and active metabolism by the active rate (Q). Thus, if it is assumed that a fish actively feeds for a given number (a) of hours, the total daily expenditure of energy for metabolism can be defined as:

$$Q_- = a(Q - Q_s) + 24Q_s. \quad (5)$$

The basic Equation (4) can then be rewritten as:

$$0.7Q_+ = Q' + a(Q - Q_s) + 24Q_s. \quad (6)$$

Also, the energy of food consumed (Q_+) can be equal to the sum of the hourly rations, r (see Prey Density and Intensity of Feeding), or $Q_+ = ar$, and thus:

$$Q_+ = aR(1 - e^{-\alpha P}). \quad (7)$$

Solving Equations (6) and (7) simultaneously by equating the Q:

$$\frac{Q' + a(Q - Q_s) + 24Q_s}{0.7} = aR(1 - e^{-\alpha P}) \quad (8)$$

is obtained. Thus:

$$a = \frac{Q' + 24Q_s}{0.7R(1 - e^{-\alpha P}) - (Q - Q_s)}. \quad (9)$$

Deriving the value of a, a number of different parameters can be computed. They are: 1) critical plankton density below which growth, metabolism and subsequent survival would be adversely affected, 2) food intake, 3) energy expenditure, 4) nonassimilated energy, 5) growth efficiency, 6) percent body weight eaten, and 7) the number of a given plankton species and life stages eaten per day. The following is a step by step explanation of the modifications used to compute these parameters at 8°C for larval dry weight from 10 to 1,000 μg (corresponding to the time period hatching to metamorphosis), for plankton concentrations from 0.5 to 21.7 cal/liter (approximately 0.1–3.0 nauplii/ml), and for growth, metabolic and digestion rates observed in laboratory experiments at 8°C.

1. Stomach contents weight in micrograms of planktonic prey eaten by a given size larva was computed from the regression equation presented in Figure 1.

2. The stomach contents weight per hour, or weight of food consumed per hour, was calculated from a modification of Bajkov's (1936) digestion equation. The modified equation is:

$$F = \frac{ST}{H} \quad (10)$$

where F = weight of food consumed per hour
S = average weight of food in the stomach at the time of sacrifice
T = feeding time in hours
H = number of hours necessary for food to be evacuated from the stomach at a given temperature = 6.6 h at 8°C for actively feeding winter flounder larvae.

Unpublished experiments indicated that winter flounder larvae fed only in daylight hours. Therefore, it was assumed that T was equal to 12.0 h in these experiments, or the approximate number of mean daylight hours in the period mid-February to mid-April, when winter flounder spawn. Also, F was considered to represent the maximum ration of a larva, or R (Prey Density and Intensity of Feeding section, Equations (7)–(9)).

3. R was converted to a caloric value by multiplying by 0.0052519 cal, or the average caloric value/microgram of the copepod species inhabiting Narragansett Bay and serving as potential prey for winter flounder (Laurence 1976).

4. The coefficient of proportionality (α) in Equation (9) was found to change linearly in a negative manner with increasing larval size (see Prey Density and Intensity of Feeding) and was correspondingly adjusted.

5. The growth increment, Q', was computed by multiplying the weight of a larva by the specific growth rate at 8°C for the specified plankton density (see Effects of Prey Density on Growth and Survival). This was converted to calories by multiplying by 0.0050026, or the caloric value for winter flounder tissue as determined in laboratory combustion experiments with a bomb calorimeter.

6. Metabolism for a larva of given weight was calculated from the regression equations for oxygen consumption and weight (Laurence 1975; Figure 5) and converted to calories by multiplying by 0.005 which represents the caloric equivalent of 1 μl of oxygen for the full range of respiratory quotients associated with the utilization of fats,

carbohydrates, and proteins (Swift and French 1954). Active metabolism (Q) was derived by multiplying standard metabolism (Q_s) measured in the oxygen consumption experiments by 2.5. Fry (1947) showed that the active metabolism in small fishes was about twice the standard rate. More recently, however, Ware (1975) demonstrated in a re-analysis of Ivlev's (1961b) data that active metabolism calculated for a variety of growth rates and feeding densities could vary between 2 and 3 times the standard rate. Recognizing that active metabolism is a dynamic factor, it is not unrealistic to assume a multiplier of 2.5 times standard metabolism for an estimate of active metabolism.

7. The number of hours (a) a larva of given weight needed to feed to attain a given growth rate at a given temperature and plankton concentration was computed from Equation (9).

8. Since winter flounder larvae were observed in experiments to be visual feeders, the plankton densities for each weight which predicted 12.0 h feeding time (a) were identified. These were considered critical densities because feeding times longer than this were ecologically impossible due to unsuitable photoperiod.

9. Food intake in calories was computed from Equation (7).

10. Metabolism or energy expenditure was computed from Equation (5).

11. Nonassimilated energy was computed by subtracting the energies of growth (Q') and metabolism (Q_-) from the energy of food intake (Q_+).

12. Gross growth efficiency was calculated from the formula:

$$K_1 = \frac{Q'}{Q_+}$$

where K_1 = gross growth efficiency and Q' and Q_+ are as previously defined.

13. The percent body weight eaten per day was calculated by dividing the caloric value of food intake (Q_+) by the caloric value of the given body weight.

14. The number of naupliar or adult copepods consumed per day at the given parameters was calculated by dividing the caloric value of the food intake (Q_+) by the previously defined average caloric value for nauplii or adults.

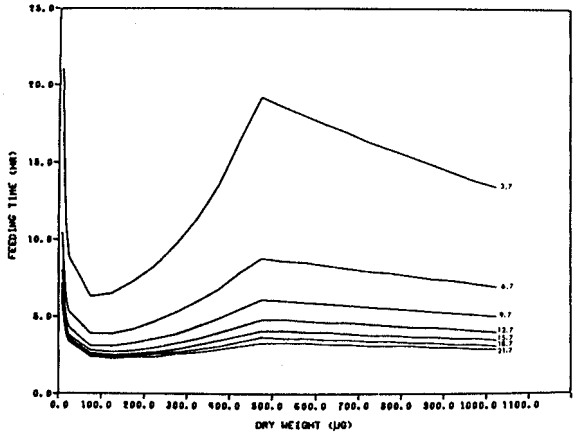

FIGURE 6.—Number of daily feeding hours required by winter flounder larvae to obtain energy for calculated growth and metabolism as influenced by larval dry weight and planktonic prey concentration at 8°C. Numbers for each simulated line indicate prey concentration in calories per liter.

MODEL SIMULATION RESULTS

Daily Feeding Time and Critical Prey Densities

The number of daily feeding hours required to meet growth and metabolism (a, Equation (9)) in relation to larval dry weight and at plankton densities which allowed feeding at some time within the limits of the 12-h day length simulated by the model is plotted in Figure 6. Feeding time at all plankton densities was initially high for the younger, smaller fish which later decreased before increasing again to a peak around 500 µg dry weight, or when metamorphosis starts to take place. A gradual decrease occurred during the metamorphosis period (500–1,000 µg larval dry weight). As was expected, required daily feeding times decreased with increasing prey density.

The critical, minimal prey densities below which longer than 12 h would have been required to obtain energy to meet growth and metabolism over the range of weights showed the highest critical densities during the period corresponding to first feeding with a decrease to a minimum shortly after (10–75 µg larval dry weight, Figure 7). An increase was then noted until the beginning of metamorphosis (500 µg) after which the critical prey density gradually decreased to complete metamorphosis (1,000 µg). The range of critical, minimum densities for the whole period was from 2.1 to 5.7 cal/liter, or approximately 0.3 to 0.8 nauplius/ml.

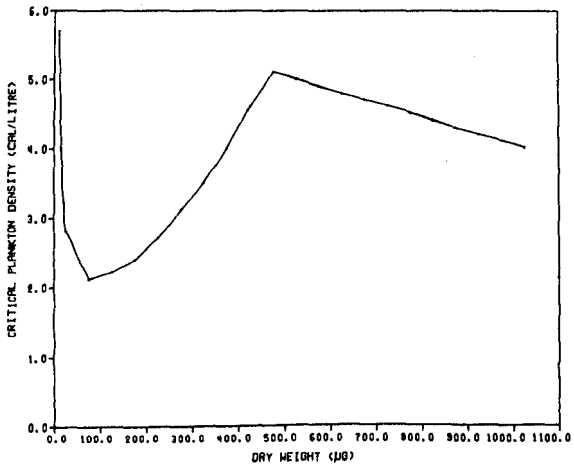

FIGURE 7.—Critical, minimum prey densities, below which feeding longer than the available photoperiod would permit to obtain energy for calculated growth and metabolic processes, over the weights range from hatching to metamorphosis for winter flounder at 8°C.

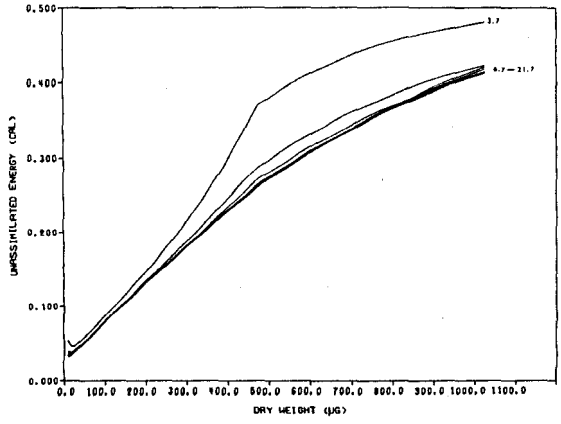

FIGURE 9.—Nonassimilated energy of winter flounder larvae at 8°C over the range of dry body weight from hatching to metamorphosis and at different planktonic prey concentrations. Numbers for each simulation indicate prey concentration in calories per liter; 6.7–21.7 cal/liter simulations are in ascending order from top to bottom.

Physiological Energy Utilization

Predicted daily metabolic energy utilized by winter flounder larvae from hatching to metamorphosis (Q_-, Equation (5)) showed a decrease shortly following hatching which later increased until initiation of metamorphosis when there was a leveling off (Figure 8). Energy expended was substantially higher at the lower prey concentrations with the differences minimized with increasing concentration. Predicted daily unassimilated energy, or energy not utilized in physiological processes and lost to the larval system, followed a similar trend to metabolic energy (Figure 9). In general, the ratio of nonassimilated to metabolic energy overall factor combinations was approximately 1:2.

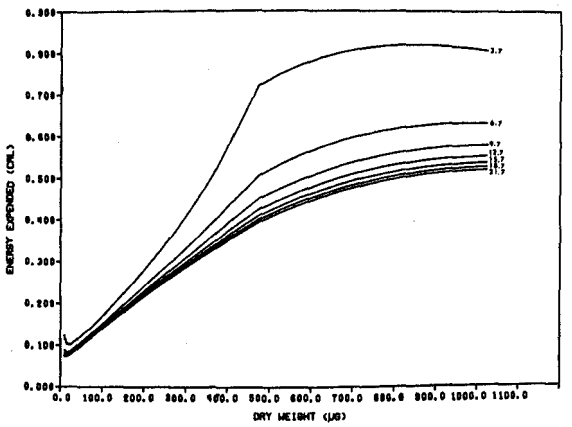

FIGURE 8.—Metabolic energy utilized by winter flounder larvae at 8°C over the range of dry body weight from hatching to metamorphosis and at different plankton concentrations. Numbers for each simulated line indicate prey concentration in calories per liter.

Required Food Ration and Growth Efficiency

Predicted daily caloric food requirements (Figure 10, Equation (7)) after an initial decrease following first feeding (10–30 µg dry weight) increased until the beginning of metamorphosis (500 µg), after which the rate of increase slowed until complete metamorphosis (1,000 µg). Food requirements were greater at lower prey concentrations with decreasing differences at higher concentrations. Conversion of caloric values of daily food requirements by division by mean caloric values of the copepod life stages per unit weight showed the numbers of nauplii or older stages necessary for consumption (Figure 11). Actual feeding experiments demonstrated that larvae do not prey entirely on one particular copepod life stage. The stages they consume are more a function of larval and copepod size. Smaller larvae initiate feeding on nauplii and gradually eat increasingly greater percentages of

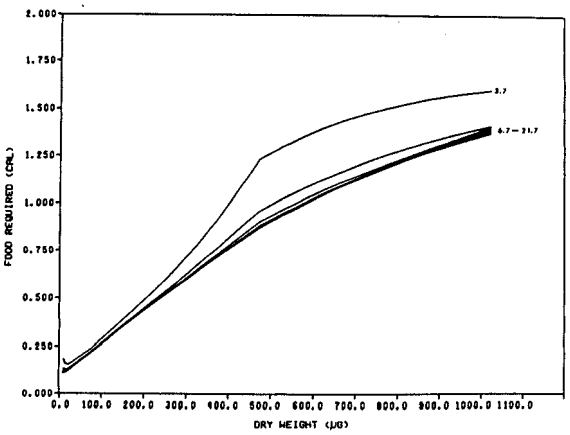

FIGURE 10.—Daily food requirements of winter flounder larvae at 8°C over the range of dry weight from hatching to metamorphosis and at different planktonic prey concentrations. Numbers for each simulation indicate prey concentration in calories per liter; 6.7–21.7 simulations are in ascending order from top to bottom.

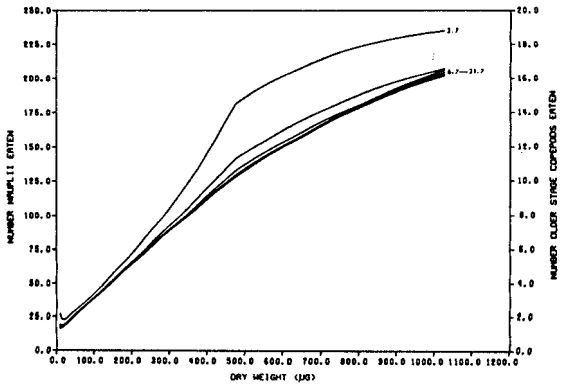

FIGURE 11.—Predicted number of nauplii or older stage copepods required for daily consumption by winter flounder larvae at 8°C over the range of dry body weights from hatching to metamorphosis and at different planktonic prey concentrations. Numbers for each simulation indicate prey concentration in calories per liter; 6.7–21.7 simulations are in ascending order from top to bottom.

older stage copepods as larval size increases (Figure 12).

The percentage of body weight consumed per day index (Figure 13) demonstrated sharply decreasing values during the first weeks of life (10–75 µg), after which values remained fairly stable until metamorphosis. More food was consumed per body weight at lower plankton densities. The differences became minimal with increasing plankton density.

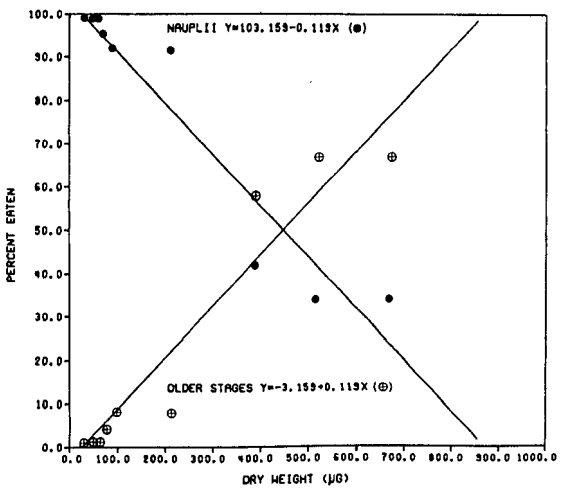

FIGURE 12.—Regression relationships of percentages of nauplii and older stage copepods eaten by winter flounder larvae of different sizes at 8°C.

Predicted gross growth efficiencies increased sharply from first feeding until a dry body weight of 100 µg, after which they continued to increase but at a decelerated rate (Figure 14). Efficiencies were lower at lower plankton concentrations, and the differences became smaller as plankton concentration increased.

DISCUSSION

A majority of the prior research has dealt with instantaneous estimates of larval food needs (Chiba 1961; Braum 1967) rather than a descriptive relationship over the range of larval sizes from hatching to metamorphosis. Larval winter flounder exhibited a linear increase in food consumption, as indicated by stomach contents with increasing size (Figure 1). A linear relationship was also reported for larval largemouth bass, *Micropterus salmoides* (Laurence 1971b). Stepien (1974) observed an exponential increase for the larvae of sea bream, *Archosargus rhombodalis*, at much higher temperatures (23°–29°C) than the 8°C studied for winter flounder in this research.

The amount of food a larval fish consumes during a day depends on the size of the fish and density of the prey organisms available (Ivlev 1961a, b). This is especially evident for winter flounder larvae for which the traditional Ivlev relationship changes with age or size (see Prey Density and Intensity of Feeding, Figure 2). Smaller, younger larvae reached maximum ration (R, Equation (7))

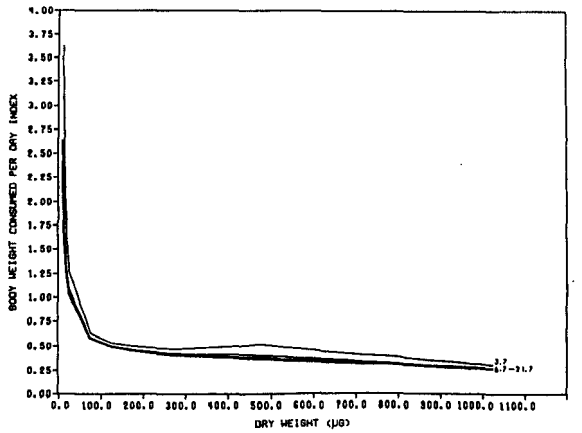

FIGURE 13.—Index of body weight consumed per day by winter flounder larvae at 8°C over the range of dry weights from hatching to metamorphosis and at different planktonic prey concentrations. Numbers for each simulation indicate prey concentration in calories per liter; 6.7–21.7 simulations are in ascending order from top to bottom.

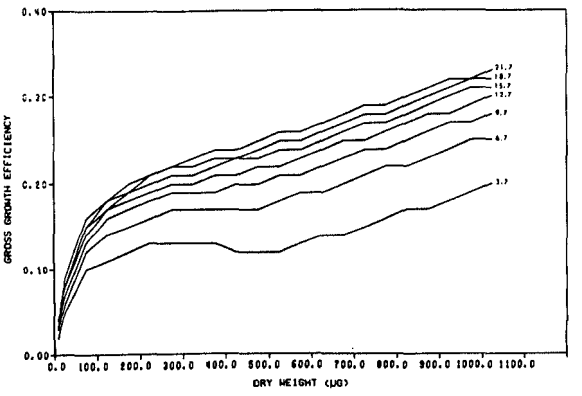

FIGURE 14.—Gross growth efficiencies of winter flounder larvae at 8°C over the dry body weights from hatching to metamorphosis and at different plankton concentrations. Numbers for each simulation indicate prey concentration in calories per liter.

at lower prey densities, while larger, older larvae approached maximum feeding ration at increasingly higher densities. The higher coefficient of proportionality (α, Equation (7)) values for the smaller larvae suggests that they have an easier time capturing their maximum ration. In fact, they reach their maximum ration at lower prey densities because their stomach capacity is very small and limited, while large larvae with greater stomach volumes can take advantage of higher plankton densities. From the standpoint of successful captures to obtain the maximum ration, smaller, younger larvae are actually much less efficient than larger.

This size effect on feeding ration over a range of prey densities has not been specifically examined for fish larvae before. Powers (1974) theoretically evaluated tha Ivlev relationship with laboratory feeding data for an amphipod, *Anisogammarus confervicolus*. He examined changing coefficients of proportionality (α) at constant maximum ration. The results showed that the asymptote is approached more quickly at higher α's, similar to the results noted in this research. Powers did not analyze maximum feeding ration as a function of animal size at changing α's. He did, however, state that animal size would probably have an effect since larger animals are better predators than smaller ones.

The initial sharp reduction in feeding times predicted by the model following hatching until a dry weight of 75 µg (Figure 6) was undoubtedly due to the increased ability of growing winter flounder larvae to capture prey. This is supported by Schumann (1965), who reported that larvae of Pacific sardine, *Sardinops sagax*, which were initially successful at feeding increased their searching ability and the probability of capturing a subsequent prey. The increase in predicted feeding times from 75- to 500-µg size was due to the exponential increase in metabolic rate for premetamorphosed larvae (Laurence 1975). The reduction in predicted feeding time from the initiation of metamorphosis until its completion (500–1,000 µg) was related to the decrease in absolute metabolism due to behavioral changes of metamorphosing winter flounder (Laurence 1975) and their greatly increased efficiency at capturing prey, which required less energy expenditure. The decrease in predicted feeding time with increase in prey concentration was due to the increased chance of prey encounter and capture. Zaika and Ostrovskaya (1972) also confirmed this for Baltic smelt and Pacific herring, *Clupea harengus pallasi*, larvae when they theoretically showed that the time spent searching for food decreased exponentially with an increase in food concentration.

Most larval fish have been reported as visual feeders (Houde 1973) and require daytime light intensities for optimum feeding (Blaxter 1969). In view of this, it is surprising that little research has been done on the relationship of feeding parameters and available time for feeding. Ivlev (1961b) combining field and laboratory data for

Atlantic herring, *C. harengus,* from the Gulf of Finland reported that, at observed plankton concentrations in the field, the calculated time of feeding was 15 h. This coincided exactly with the length of day. Laurence (1971a), working with the stipulation of a 14-h feeding period for largemouth bass larvae, found that prey concentrations of 7.0 cal/liter (400 organisms/liter) were limiting. The results of this research show that simulated critical prey densities, below which winter flounder larvae do not have enough daylight hours for feeding to meet growth and metabolic energy requirements, actually vary with age and stage of development (Figure 7). The critical densities range from a high of 5.7 (0.8 nauplius/ml) to a low of 2.1 cal/liter (0.3 nauplius/ml) when feeding behavior has been established but before growth and metabolic demands are high. Critical density then increases until initiation of metamorphosis when it remains fairly constant around 4.5 cal/liter (0.6 nauplius/ml). Results such as these have not been quantitatively reported in the literature before. Most previous laboratory studies for a variety of species delineate constant critical prey densities for the larval period usually in the range 0.1–1.0 organism/ml (Kramer and Zweifel 1970; O'Connell and Raymond 1970; Saksena and Houde 1972; Laurence 1974; Houde 1975), although Rosenthal and Hempel (1970) reported that prey densities for optimum feeding (not critical densities) for larval Atlantic herring were higher for younger than older larvae.

The critical prey densities for larval survival of approximately 0.5 organism/ml noted in this and the other cited laboratory research are somewhat disparate with densities described from field data. Lisivnenko (1961) noted that larval Baltic herring were much less abundant in years when prey abundance was <0.01 organism/ml. Sysoeva and Degtereva (1965) reported that the minimum abundance of *Calanus finmarchicus,* when the intensity of feeding of cod, *Gadus morhua,* larvae decreased, was from 0.01 to 0.005/ml and that a concentration of 0.02/ml provided sufficient food for survival. It is my opinion that the results reported for laboratory studies may be more accurate than the field study data presented thus far. The laboratory studies represent highly controlled experiments with accurate counts of prey organisms. On the other hand, the field studies give estimates of prey abundance which represent average densities over linear or oblique sampling distances. Planktonic prey organisms have contagious distributions and larvae may well be associated with "patches" of prey that are more densely concentrated than indicated by plankton net tows (Wyatt 1973). Many larval fish researchers feel that density dependent mechanisms control larval survival (Cushing and Harris 1973), and the concept of contagious distributions in which larvae and prey are associated in "clumps" that may or may not be associated and occupying the same area is one of the most logical ways to explain the fluctuations noted for natural larval mortality. Also, field zooplankton sampling designs rarely use nets with mesh smaller than 200 μm. Most of the significant food organisms utilized by larval fishes especially in the early stages are <200 μm in smallest dimension (Houde 1973) and would be lost in field sample estimates. Use of the plankton pump may prove to be more accurate in locating patches of zooplankton and sampling the size organisms that larval fish consume. Recently, Heinle and Flemmer (1975), using a moving plankton pump, reported concentrations of nauplii of *Eurytemora affinis* in the Chesapeake Bay area as high as 2.8/ml with concentrations of 1.0–1.8/ml not at all uncommon. These concentrations are more than adequate for good growth and survival of winter flounder larvae and many other larval species.

The initial, predicted decrease in metabolic energy expended (Figure 8) during the period of feeding initiation and shortly after (10–30 μg dry weight) is undoubtedly explained by the increased feeding success with experience by first feeding larvae. First feeding individuals have a lower success ratio of captures and have to expend more energy in searching for prey than older and more accomplished feeders. This success or fail period is critical to eventual survival and is relatively short in duration for winter flounder, occurring during the first 8 days after feeding begins at 8°C. The increase in metabolic energy expended from 30- to 500-μg dry weight after successful feeding establishment is due to normal increases in energy demand for all processes with rapid increases in size usually seen in larval fishes. The leveling off of metabolic energy demand during the metamorphosis period (500–1,000 μg dry weight) may be unique to flatfishes due to marked morphological and behavioral changes (Laurence 1975) and increased predatory efficiency requiring less energy expenditure.

The decrease in metabolic energy expenditure with increasing prey concentration is logically

explained by the increased chance of successful feeding at higher plankton concentrations and concurrent decrease in energy expended to obtain prey. Warren and Davis (1967) concurred with this type relationship, stating that the density of food determines an animal's energy cost in obtaining the food. Decreasing metabolism with increasing food concentration is contrary to reported laboratory studies using fish older than the larval stages. Paloheimo and Dickie (1966a) and Beamish and Dickie (1967), examining data from other researchers, concluded that higher average metabolic rates result at higher feeding rates. However, it may be presumptuous to assume this type relationship for fish larvae. Most older, nonplanktivorous feeding fishes, such as those referred to in the above citations, are satiation or periodic feeders. In fact, most of the experimental data cited above were for restricted daily diets at different levels. Larval fish, like the winter flounder, are active continuous feeders and the assumption in this model was continuous feeding at maintained prey densities. Older fish have more body reserves and can exist on maintenance rations to which they can adjust metabolically in contrast to larval fish which must feed continuously and are committed to growth or else die. In fact, the concept of maintenance probably is not relevant to larval fish feeding and energetics. So, it seems logical that fish larvae feeding continuously and committed to relatively high growth rates would optimize growth by reduced metabolic expenditure which would result from the increased contact and efficiency of capture at higher prey densities and resultant feeding levels. The research of Wyatt (1972) with plaice larvae tends to further support this concept. He noted that activity, which he attributed to food searching, decreased with increasing prey concentration.

The trends of nonassimilated energy over the range of weights and plankton concentrations in this research are similar to those for metabolic energy expenditure and food consumption (Figure 9). This is not surprising due to the interrelationships of these factors. The decrease in nonassimilated energy with increasing weight (10–30 μg) for first feeding larvae is apparently due to their initial inefficient digestion which improves with morphological development. Visual examination of food in the anterior portions of the digestive tracts of young larvae during the digestion rate studies indicated relatively intact nauplii. This has been observed for other larval fish species. Rosenthal and Hempel (1970) noted that the efficiency of digestion in Atlantic herring fed *Artemia* nauplii was very low compared with older larvae. Morphological development of the alimentary tract during the larval stage was studied by Nishikawa (1975) who noted an increase in stomach size and extension of the digestive tract as a whole in relation to increasing standard length. He postulated that these morphological developments cause a rapid increase in the function of the organs during the larval period. The subsequent increase in nonassimilated energy with size of winter flounder larvae is merely proportional to the increased ration.

Daily food requirements of winter flounder larvae were initially higher for the period associated with first feeding (10–30 μg, first 2–3 wk after hatching, Figure 10). These short-term higher requirements were due to the inefficient manner in which newly feeding larvae captured prey and the associated, higher energy expenditure. Researchers have reported that young fish larvae are much less adept and successful at capturing prey than older larvae. Braum (1967) showed that freshwater whitefish larvae, *Coregonus wartmanni,* increased their successful captures from 3 to 21% during the first 16 days of feeding. Schumann (1965) noted an obvious increase in proficiency at capturing food with increased age of Pacific sardine larvae. The reasons for increased success with age are increased visual perception of food organisms and increased locomotor abilities with advancing development (Blaxter 1965; Rosenthal and Hempel 1970). The subsequent increase in required ration with larval size was the result of normal increased energy demand of growth and metabolism associated with larger sized larvae. An interesting fact is the decrease in rate of food requirement noted in metamorphosing larvae (500–1,000 μg). This may be associated with the previously mentioned decrease in routine metabolic rate peculiar to flatfish larvae and increased efficiency of prey capture during the metamorphosis period. Riley's (1966) results for another flatfish, the plaice, *Pleuronectes platessa,* substantiate this observation. He noted declining ingestion rates and rations during metamorphosis.

Conversion of the caloric values of daily food required into numbers of nauplii or older stages consumed (Figure 11) showed, of course, the same trends for food required. This conversion does,

however, give a different perspective in that it shows the actual numbers of organisms that winter flounder larvae require on a daily basis. The differences in numbers between nauplii and older stages reflect the differences in sizes providing equivalent caloric intake. Also, winter flounder larvae did not feed entirely on nauplii, but changed in part to larger stage copepods as they grew older. Size selection of prey by larval fishes has been shown to be a factor of mouth size which increases with increased larval size (Shelbourne 1965; Blaxter 1969; Detwyler and Houde 1970; Shirota 1970). The numbers of nauplii consumed per day ranged from 19 to 235 over the range of sizes and plankton densities. These values are similar to requirements for other larval species (Chiba 1961; Braum 1967; Rosenthal and Hempel 1970), although temperature, larval species and size, and food organisms can account for variable results.

Decrease in percent food eaten per day with body weight (Figure 13) is in accordance with results of other researchers and was due to the relative decrease in the rate of food intake compared with the growth rate with larval development. Pandian (1967) observed decreases in percent eaten per day with increases in body size of *Megalops cyprinoides* and *Ophiocephalus striatus,* as did Laurence (1971b) for larval largemouth bass and Stepien (1974) for larval sea bream.

The percentages of body weight consumed per day predicted in this research were high from over 300% at the smallest larval sizes and lowest prey concentration to 27–31% at the higher prey concentrations and largest larval sizes. Percent body weight eaten per day is typically much greater for larval and juvenile fishes as compared with adults since there is a much higher energy demand for growth purposes (Winburg 1956). Stepien (1974), in the only other known comparable research on marine larvae, also reported high percentages. His results for sea bream at 29°C were from 222.4% for 2-day hatched larvae to 79% for 7-day-old larvae. Sorokin and Panov (1965) reported 40–60% body weight eaten per day by larval freshwater bream.

The gross growth efficiencies recorded in this research increased rapidly with size for the smallest larvae (10–75 μg) and then increased at a decelerated rate for the remainder of the larval period to metamorphosis (Figure 14). Increased gross growth efficiency at greater body weights observed in my experiments is contrary to the results of research with older fishes. Parker and Larkin (1959) stated that within any growth stanza the gross efficiency must decline with increasing size, as a greater portion of the food must be used in maintenance. This may not be true for larval fishes, as their development is so rapid that a large portion of the energy derived from food intake is used in growth. It is my opinion that larval fishes could not exist on a maintenance ration. Rapid growth is a definite prerequisite for successful survival in the environment of larval fishes, and they must either consume food at high levels with resultant rapid growth or die. The ability of larvae to increase their feeding efficiency with increased size could also contribute to greater growth efficiency.

Divergent opinions have been expressed by researchers concerning the relationship between growth efficiency and feeding level or prey concentration. Paloheimo and Dickie (1966b) stated that growth efficiency declined with increasing ration. Warren and Davis (1967) showed that growth efficiency increased to two-thirds the maximum feeding level and then decreased. Finally, Davies (1964) demonstrated that efficiency of digestion and absorption of food by goldfish, *Carassius auratus,* was improved by increasing food input over a given weight range. He postulated that secretion of digestive fluids was stimulated by the effects of increased food. In all cases the studies and analyses were done with adult fishes. Winter flounder larvae increased their gross growth efficiencies with increased plankton density similar to Davies' results. However, the causative mechanism was most likely the increased efficiency of prey capture with increased prey encounter at higher densities with resultant metabolic savings for growth rather than increased secretion of digestive fluids. Growth efficiency is most likely a dynamic factor not subject to generalizations and dependent on life stage, type of feeding strategy, or prey type.

The range of values of growth efficiency for larval winter flounder on this research were from 5 to 33%, depending on larval size and plankton concentration. These values are similar to those for other young fishes (Ivlev 1939a; Sorokin and Panov 1965; Edwards et al. 1969; Laurence 1971a; Frame 1973; Stepien 1974).

The above discussions have revealed that there are interrelationships between the bioenergetic parameters simulated by the model and that the whole system works in a circular pathway to

maintain an energy balance in the larva's body. Energy expended at a given temperature promotes growth and results in a metabolism that produces activity, which in turn acts on the planktonic prey to provide an assimilated food intake that supplies energy for metabolism and growth. The whole process at a given temperature is in turn influenced by the size or age of larvae and the planktonic prey concentration. A good example which depicts the effect of larval age or size on these interrelationships and one which points to a definite "critical period" shortly after hatching around the period of feeding initiation is shown in Figure 15. In this figure the caloric expenditures for the important bioenergetic parameters over the range of weights from 10 to 50 μg are summed for all plankton concentrations. A definite divergence of energy away from growth to metabolism and nonassimilation with a resultant increased food requirement is shown during early life (10–30 μg). This period coincides with first feeding and is the time when larvae need to grow at a fast rate because of their small size, fragility, and vulnerability to predators. This identified "critical period" is caused by a number of factors and interrelationships including: 1) developmental factors of which reduced visual perception and locomotor (swimming) abilities in young larvae prevent efficient prey capture compared with older and better developed larvae; 2) less efficient conversion of food to flesh because of higher metabolic expenditure associated with more searching due to less efficient prey capture; 3) less efficient digestion in young larvae causing a smaller fraction of the food to be assimilated and be available for potential growth. As the larvae grow larger and older, especially during the metamorphosis period (50–1,000 μg), they become more efficient at converting food to growth. The slopes of the lines connecting the simulated values of the important bioenergetic components summed for all prey concentrations over the weight range of hatching to metamorphosis in Figure 16 show that the rate of growth accelerates more rapidly towards food consumption rate than metabolic and nonassimilation rates with increasing larval size after the critical period.

In addition to the critical period, plankton density is an important determinant of larval survival and, of course, interacts crucially during the critical period. The overall influence of prey density is shown in Figure 17 where the caloric expenditures of the important bioenergetic parameters simulated by the model are summed over all weights at each plankton concentration. It can easily be seen that low prey densities strongly affect the dispensation of energy available from food consumption in comparison with high densities. A greater portion of the energy intake is utilized for metabolism and is not assimilated

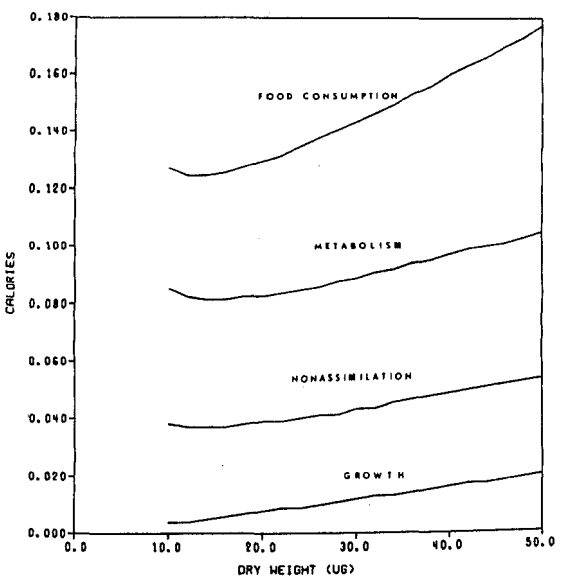

FIGURE 15.—Caloric energy expenditure for the major bioenergetic parameters of winter flounder larvae summed for all prey concentrations over the range of dry weights from 10 to 50 μg at 8°C.

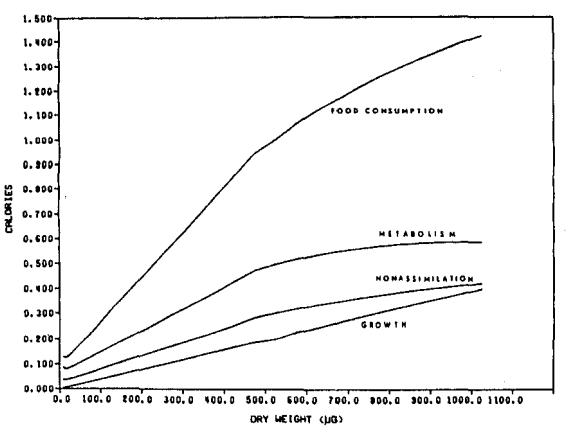

FIGURE 16.—Caloric energy expenditure for the major bioenergetic parameters of winter flounder larvae summed for all prey concentrations over the range of dry weights from hatching to metamorphosis at 8°C.

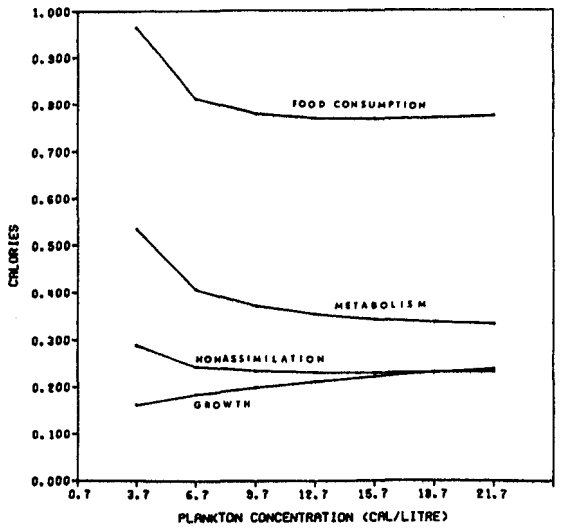

FIGURE 17.—Caloric energy expenditure for the major bioenergetic parameters at 8°C of winter flounder larvae summed for all dry weights from hatching to metamorphosis at different planktonic prey concentrations.

than is used for growth at lower prey densities. Also, the food requirements are higher at the lower densities which causes problems because food is harder to obtain at lower densities.

In conclusion, these experimental studies and model simulations demonstrate that there is strong evidence for a "critical period" of mortality in the larval stage of winter flounder and that planktonic prey density is one of the most important factors affecting survival during the larval stage. Additionally, the bioenergetic model developed presents a means to assess other trophic interactions in the marine, planktonic community. Larval fish are planktonic carnivores and the food requirements predicted by the model in combination with biomass estimates of larvae and prey and survival estimates of larvae can be used to predict the impact of larval grazing on their prey. This type of research is currently being pursued in continuing studies.

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