A Laboratory Study of the Bioenergetics of Larval Walleye Pollock, *Theragra chalcogramma*

Yoh Yamashita and Kevin M. Bailey

ABSTRACT: Rates of growth, oxygen consumption, and ingestion were measured for larval walleye pollock, *Theragra chalcogramma*, in the laboratory. These measurements were used to relate assimilation and growth efficiencies to larval age (and size) and prey ration level. Larval growth was 0.06 mm/d during the transition from endogenous to exogenous food (days 4–16), and increased to 0.16 mm/d (days 19–21). Ingestion ranged from 24 to 58% body dry weight/d. Oxygen consumption rates were measured and used to partition total daily metabolic expenditures into four components: resting metabolism; SDA; lights-on generated nonfeeding activity; and active (feeding) metabolism, which accounted for 45.7, 13.3, 11.1, and 29.9% of the total daily metabolic rate, respectively. Net assimilation efficiency ranged from 24 to 64% and gross growth efficiency ranged from 9 to 35%, depending on larval age and size. Little difference was observed in efficiencies at low and high ration levels. The daily caloric requirement to support metabolism and growth of first-feeding larvae was calculated at 0.16 calories, which is equivalent to 76 copepod nauplii. This value is higher than ingestion estimates from field studies.

Capture and transformation of energy into body mass is especially critical during the larval stage of marine fishes. Specific growth rate is highest during this stage and weight may increase by three orders of magnitude (Smith 1985; Houde 1987). Furthermore, duration of the larval stage, as regulated by growth rate, is recognized as a crucial factor in determining year class strength (Houde 1987; Miller et al. 1988). Growth efficiency, the proportion of ingested energy used in growth, depends on a number of factors including environmental conditions, prey quality, prey abundance, and larval size and age.

Walleye pollock, *Theragra chalcogramma*, is the most abundant commercial species in the northeastern Pacific Ocean, comprising 80% of the total groundfish catch (Bakkala et al. 1986). Several studies have evaluated the bioenergetics of late larvae, juveniles, and adults (Fukuchi 1976; Nishiyama 1981; Harris 1985; Smith and Paul 1986; Dwyer et al. 1987; Smith et al. 1988) but there are relatively few studies of bioenergetics of early larvae, and their growth efficiency is unknown. Incze et al. (1984) reviewed the early life history of this species and calculated daily ration based on literature-derived values of growth and respiration. Clarke (1984) made a similar estimate. Early studies of larval walleye pollock respiration were limited because larvae were not successfully grown in the laboratory. Likewise, estimation of larval growth, determined from otolith ageing, was limited by the lack of daily increment validation. Recently, walleye pollock larvae have been successfully reared in the laboratory (Bailey and Stehr 1986), and daily growth increments on otoliths have been validated (Nishimura and Yamada 1984; Bailey and Stehr 1988).

In the present study we estimate components of the energy budget of larval walleye pollock reared in the laboratory. These components include rates of ingestion, growth, and metabolism. Oxygen consumption was measured at different levels of activity in order to model daily metabolic costs. We also calculated efficiencies of assimilation and growth for larvae as influenced by ration and age.

MATERIALS AND METHODS

Rearing of Larvae

Experiments were carried out from March to May 1988. Eggs from ripe females, collected in Puget Sound, were fertilized and reared according to methods described by Bailey and Stehr (1986). Yolk-sac larvae were transferred to 120 L black fiberglass tanks set in a water bath. Initial stocking density was 1,200 larvae per tank. Overhead fluorescent lights, on a 14 h

Yoh Yamashita, Ocean Research Institute, The University of Tokyo, Tokyo 164, Japan; present address: Tohoku Regional Fisheries Research Laboratory, Shinhama-cho 3-27-5, Shiogama 985, Japan.
Kevin M. Bailey, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way, N.E., Building 4, BIN C15700, Seattle, WA 98115.

Manuscript Accepted April 1989.
Fishery Bulletin, U.S. 87: 525–536.

light:10 h dark cycle, illuminated the tanks at an intensity of 5–8 $\mu E/s/m^2$ just below the water surface. Water was replaced with filtered seawater at 10–15% per day. Larvae were fed rotifers, *Brachionus plicatilis*, that had been cultured on a mixture of *Isochrysis* spp., *Chaetoceros* spp., and yeast.

Three rearing experiments were done using larvae hatched from eggs collected on different days. In the first experiment, growth, rate of gastric evacuation, and daily ration were measured in larvae reared at high (11.2 ± 1.4 SD rotifers/mL) and low (2.0 ± 1.4 SD rotifers/mL) rations. Mean temperature in both tanks was 6.4°C (±0.2 SD). In the second and third experiments, oxygen consumption rates for larvae were determined. Rotifer densities were maintained at about 10 individuals/mL. Average temperature was 6.3° ± 0.1°C (SD). Temperatures of 6.0°–6.5°C are common in Shelikof Strait (Gulf of Alaska) in May when early-stage larval walleye pollock are most abundant (Kendall et al. 1987).

Growth Rates

The standard lengths (SL) of live larvae were measured to the nearest 0.03 mm using a dissecting microscope, the gut contents were removed, and the larvae were dipped in distilled water and then dried for 24 hours at 60°C. Dry weights were measured to the nearest 0.1 μg on a Cahn 25 electrobalance. Yolk-sac dry weight was estimated as the difference between the mean dry weight of larvae with yolk sacs and the mean dry weight of larvae whose yolk sacs had been excised. Instantaneous rate of growth (G) and relative rate of growth (K) were estimated from the following equations (Ricker 1975):

$$W_t = W_0\, e^{G \cdot t}, \text{ where}$$

$$G = (\ln W_t - \ln W_0)/t, \text{ and}$$

$$W_t = W_0(1 + K)^t, \text{ where}$$

$$K = e^G - 1.$$

W_0 is the initial dry weight (in μg) and W_t is the dry weight at time t (in days). Daily specific growth rate is defined as G (× 100%) (Laurence 1975).

In order to compare subarctic walleye pollock with the subtropical larvae used in other studies, we used methods and analyses to parallel those of Houde and Schekter (1981, 1983) and Theilacker (1987). One major difference was that we did not use nonfeeding larvae, but sampled randomly from feeding larvae. Theilacker (1987) used all randomly sampled larvae including nonfeeding larvae to estimate ingestion and growth; Houde and Schekter (1981, 1983) sampled only feeding larvae to measure ingestion, and feeding and nonfeeding larvae to measure growth. In some species, relatively few larvae may feed on cultured prey at low densities in laboratory conditions. This may not have been a problem in the Theilacker (1987) and Houde and Schekter (1981, 1983) studies. In our studies we considered feeding incidence as a behavioral problem not to be included as a factor in a study of energetic efficiency. Since our objective was to compare efficiencies of larvae feeding at high and low rations, we opted to exclude nonfeeding larvae from our samples.

Evacuation Rates

Instantaneous rates of gastric evacuation were measured for actively feeding larvae. Larvae were fed rotifers, dyed with Alcian Blue, at prey densities of 2.2–4.0/mL. After 1.2–1.5 hours larvae were transferred to a tank containing undyed rotifers either at 11.1–15.6 rotifers/mL for the high ration treatment or at 0.8–1.8 rotifers/mL for the low ration treatment. Larvae were sampled at intervals from 20 to 60 minutes, and widths of rotifers and their degree of digestion determined. Mean gut-clearance times were estimated for the duration between ingestion and defecation of dyed rotifers.

Theilacker and Kimball's (1984) method was used to determine that 54% of rotifer dry weight was lost after 4 hours of digestion. Based on that loss, three correction factors for the degree of rotifer digestion were used to calculate ingestion: 0.9 for recently ingested rotifers; 0.7 for moderately digested rotifers, which still had abundant chlorophyll from ingested phytoplankton; and 0.5 for well-digested rotifers with almost no chlorophyll. The total dry weight of dyed rotifers in the gut was determined by summing the product of the width-specific dry weight for each rotifer (Theilacker and Kimball 1984) and the appropriate digestion factor. Data were fitted to the model:

$$A_t = A_0\, e^{-R \cdot t}$$

where A_0 and A_t are the ratios of the dry weight

of dyed rotifers in the gut to larval dry weight at times 0 and t (in hours). R is the calculated instantaneous rate of gastric evacuation.

Ingestion Rate

About 10 larvae from both high and low prey-ration tanks were sampled 5 times each day at 1.5–3 h intervals during the light period. Prey were removed from larval guts, counted, their widths measured, and the degree of larval digestion determined. Total gut content in dry weight per larva was determined by summing the product of the width-specific dry weights of rotifers and digestion factors.

Asymptotic curves of the form

$$S = S_{\max} \times (1 - e^{-F \cdot t}),$$

were used to describe ingestion rates, where S is the ratio of gut content to larval dry weight (× 100%) at time t (in hours) after initiation of light period, $S_{\max}$ is the asymptotic gut content (%) and F is the instantaneous rate of gut filling.

Weight-specific daily ration (I) as a percent of body weight was estimated for larvae using the Elliot and Persson (1978) model:

$$I = \sum_{i=1}^{m} (S_i - S_{i-1}\, e^{-R \cdot t_i})\, Rt_i/(1 - e^{-R \cdot t_i})$$

In this model, t_i is the duration of each time interval (i) in hours; S_i is the mean gut content at the end of interval (i) as a percent of larval dry body weight; and m is the total number of intervals during a light cycle. S_0 was assumed to be 0; and S_m, the gut contents at the end of the light period, was approximated as $(S_{m-1} + S_{m-2})/2$.

Metabolic Rates

Oxygen consumption rates were measured using the micro-Winkler technique (Carrit and Carpenter 1966; Strickland and Parsons 1972). We assumed that there are four metabolic activity levels: 1) resting or basal (M_{re}); 2) routine (M_{ro}), which includes M_{re} plus a cost for an lights-on generated activity; 3) feeding (M_{fn}), which includes M_{re} and an additional cost for specific dynamic action (SDA); and 4) active (M_a), which includes M_{re} plus increments due to lights-on activity and SDA, and an additional cost of pursuing and capturing prey.

Oxygen consumption rates for the different levels were measured as follows:

1. M_{re}: larvae were allowed to void their guts for 24 hours and were then incubated in dissolved oxygen (DO) bottles for 24 hours in complete darkness.
2. M_{ro}: larvae were allowed to void their guts for 24 hours and were incubated for 12 hours in the light during daytime.
3. M_{fn}: larvae with full guts after a 12 h feeding period were incubated for 12 hours in the dark during nighttime.
4. M_a: larvae with a few rotifers in their guts were incubated for 12 hours in the light during daytime with rotifers at a density of 5 individuals/mL.

Sixty milliliter DO bottles were used for conditions 1–3 and 300 mL DO bottles for condition 4. The bottles were set in a black container filled with seawater. Each bottle contained 5–30 larvae depending on larval and bottle size. Three to five replicates with control blanks (containing rotifers in condition 4) were carried out for each age and condition at 6.2 ± 0.1(SD)°C. Light intensity at the top of bottles was 6–9 μE/s/m^2 during the light period.

The value for M_{re} used here may be larger than that of other studies that use anesthetized larvae (Holliday et al. 1964; de Silva and Tytler 1973; Davenport and Lönning 1980; de Silva et al. 1986), as larvae normally move at night, even though at a much reduced level (Batty 1987). However, our method eliminates possible biases involved with the use of anesthetics. The active metabolism (M_a) was probably underestimated owing to restricted activity and feeding in 300 mL bottles, and to effects of handling. Restricted feeding in DO bottles was evidenced by the lower number of ingested rotifers in guts at the end of experiments compared with the number of ingested rotifers in the guts of larvae in the 120 L tank.

Energy Budget

Energy budgets (in calories per day) were determined for feeding larvae from 7 to 21 days from posthatching using the equation:

$$I = G + M + E$$

where I = ingestion, G = growth, M = metabolism, E = nitrogenous and fecal excretions. Excretion was not measured, but the total loss of

wastes can be estimated by difference. Also, the efficiencies we used—G/I, M/I, $(G + M)/I$, and $G/(G + M)$—are not dependent on excretion measurements.

Average daily ingestion in dry weight was calculated as (mean larval weight) × (weight-specific daily ingestion). Dry weight of rotifers was converted to caloric equivalents using a factor of 4.4 cal/mg (Theilacker and Kimball 1984).

Daily growth of larvae at (t_i) was calculated from the daily growth rate (K) for the interval $t_i - t_{i+1}$. Dry weight was converted to calories using a factor of 5.077 cal/mg estimated for larval walleye pollock (Fukuchi 1976; Harris et al. 1986). Fukuchi (1976) also provided constants for converting dry weight to net weight, nitrogen, and carbon (8.59, 0.092, and 0.131, respectively).

Daily O_2 consumption rate (M_{24}) μL/d/individual (14 h light and 10 h dark photoperiod) was calculated as

$$M_{24} = 2 \times (M_{ro}) \times 14 + (M_{fn}) \times 10.$$

Oxygen consumption was converted to calories using an oxycaloric equivalent of 4.63 cal/mL O_2 (Brett and Groves 1979). We attempted to measure active metabolic rates as described above, but larvae did not actively feed. Therefore, active metabolic rate was approximated as twice the routine metabolic rate (Houde and Schekter 1983; see also Lasker 1970).

RESULTS

Growth rates

Hatching began 7–8 days after fertilization, and by 3–5 days later more than 80% of the eggs had hatched. The day of 50% hatching was designated as the day of hatching for all larvae.

By day 6 after hatching, yolk-sac dry weight was less than 5% of the initial weight; the yolk was absorbed completely by days 11–15. A small percentage of larvae started feeding on day 5 and most larvae started on day 6. Therefore, day 6 was designated as the onset of feeding. Newly hatched yolk-sac larvae averaged 3.80 mm (SL) and 55.5 μg (dry weight), and by day 4 (existing only on yolk) averaged 4.59 mm and 47.5 μg. By day 21, high ration larvae grew to 6.02 mm (mean SL) and 120.9 μg (mean dry weight) and low ration larvae grew to 5.94 mm and 116.2 μg. The linear growth rate in SL during yolk-sac period (from days 0 to 4) was 0.20 mm/d; it decreased to 0.07 (high ration) and 0.06 (low ration) mm/d during the transition from endogenous to exogenous energy (from days 4 to 16), and then increased to 0.13 (high ration) and 0.12 (low ration) mm/d (from days 16 to 21). Specific growth rate in weight from days 7 to 21 was estimated as 6.71%/d for high ration and 6.04%/d for low ration larvae. Standard length (SL) and dry weight (W) were related by a power function:

$$\text{high ration: } W = 0.1261 \times \text{SL}^{3.812} \quad (r = 0.980 \quad N = 45)$$

$$\text{low ration: } W = 0.1754 \times \text{SL}^{3.615} \quad (r = 0.979 \quad N = 45).$$

Although the length-specific weight gain of high ration larvae tended to be greater than that of low ration larvae, the difference between the two food levels was not statistically significant (F-test for difference between two linear regression slopes, $P > 0.1$).

Evacuation Rates

The weight of dyed rotifers in larval guts decreased exponentially for the first 5–7 hours, then the rate of larval digestion slowed. Instantaneous rates of gastric evacuation (R) were estimated from the exponential phase for 8–9 d old larvae and 17–21 d old larvae. Rates for younger larvae were higher than those for older larvae, and high ration larvae had higher evacuation rates than low ration larvae (Table 1). The same tendencies were found in gut clearance times. Coiling of the midgut is initiated at about 5.2 mm SL (day 14) and is completed at about 5.8 mm (day 20), effecting the differentiation of foregut and intestine. The relationship between R and the percentage of larvae having coiled midgut (>5.5 mm SL) showed higher evacuation rates for larvae without the coiled gut.

Ingestion Rate

By our observation, larval walleye pollock are continuous feeders. There was no significant difference (Chi-square test: $P > 0.1$) between widths of rotifers in larval guts and widths of rotifers in cultures provided to larvae as food.

The ratio of gut contents to larval dry weight generally increased asymptotically with time (Fig. 1). Maximum mean percent of gut contents measured after 14 h feeding were 6.9% and 5.1% for 7 d old high ration and low ration larvae, respectively. These values increased to about 10% by day 13 and thereafter remained fairly

TABLE 1.—Instantaneous rates of gastric evacuation and gut clearance time related to age and feeding condition of larval walleye pollock at 6.4°C. Data were fitted to the equation: $A_t = A_0\ e^{-Rt}$ (see text). Also shown is the percent of larvae in the experiments greater than 5.5 mm SL, as an indicator of those with midgut coiling.

Age (d)	Feeding condition	Instantaneous evacuation rate (R)	A_0	Gut clearance time (h)	% Larvae >5.5 mm SL	N
8	high ration	0.473	3.399	5.3	0	93
9	low ration	0.415	2.571	6.1	0	97
17	low ration	0.263	2.601	10.1	64	61
18	high ration	0.256	3.082	9.6	79	61
21	high ration	0.327	4.743	9.4	73	40

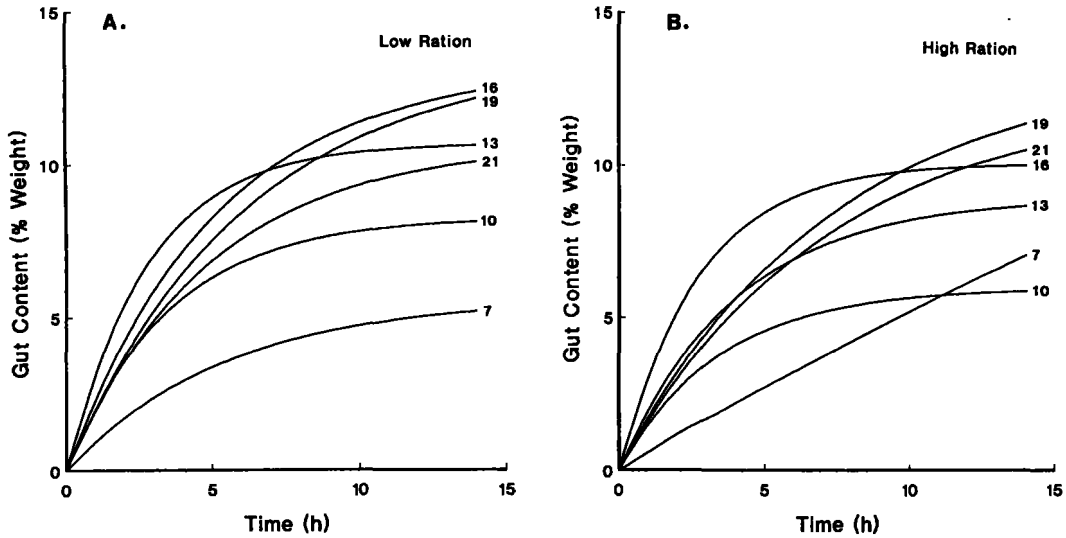

FIGURE 1.—Curves to describe food intake of low ration (A.) and high ration (B.) pollock larvae. Data were fitted to the equation: $S = S_{max} \times (1 - e^{-F \cdot t})$, where S is percent dry weight of gut contents to larval dry weight at time t (h) after initiation of light period; S_{max} is the asymptotic gut content (%); and F is the instantaneous rate of gut filling. Numbers after each line indicate age in days.

constant (Table 2). About 10–12% seems to be the maximum capacity of larval pollock guts within the range of stages examined. These measured maximum values are close to S_{max} values predicted from the asymptotic gut content curve (Table 2). The value for 7 d old high ration larvae was an exception; the ingestion curve appeared to be nearly linear and the resulting S_{max} high (Fig. 1; Table 2)

To estimate daily ration, instantaneous rates of gastric evacuation under specific age and feeding conditions were taken from Table 1. At day 7, one day after feeding commenced, weight-specific daily ration was low, about 24–29% (Table 2). Daily ration increased to a level of about 55% at days 13–16. In spite of the observed constant values of maximum percent gut contents with age, daily ration decreased to about 35% by day 21. The difference in daily ration between the high and low ration conditions was not significant (ANOVA, $P > 0.1$).

Metabolic Rates

Results of oxygen consumption rate measurements are summarized in Table 3. From day 0 to day 4 after hatching there was no remarkable difference in respiration between daytime (M_{ro}) and night (M_{re}). After day 6, when most larvae commenced feeding, O_2 consumption rate increased as age and weight of larvae increased, and M_{ro} was from 25 to 68% higher than M_{re}. O_2 consumption rates in the four conditions were significantly different (ANOVA, $P < 0.01$).

TABLE 2.—Summary of ingestion experiments for larval walleye pollock. S_{max} is estimated asymptotic gut content and F is instantaneous rate of gut filling. Parameters were estimated from the equation: $S = S_{max} \times (1 - e^{-Ft})$ (see text).

Diet	Age (d)	N	Asymptotic curve model: Instantaneous rate of gut filling (F)	Asymptotic curve model: Asymptotic[1] gut content (S_{max})	Asymptotic curve model: Estimated[1] gut content after 14 h feeding	Max mean gut content of reared larvae (%)	Daily ration (%)
High ration	7	30	0.017	33.5	7.1	6.9	29.4
	10	37	0.292	6.0	5.9	6.4	37.3
	13	41	0.250	9.0	8.7	9.8	50.9
	16	35	0.371	10.1	10.0	10.8	53.2
	19	40	0.138	13.3	11.4	11.2	42.1
	21	41	0.141	12.2	10.5	10.9	37.0
Low ration	7	32	0.185	5.6	5.2	5.1	24.2
	10	37	0.288	8.3	8.1	8.5	42.3
	13	41	0.362	10.7	10.6	11.0	58.5
	16	35	0.196	13.3	12.4	11.5	49.6
	19	40	0.162	13.6	12.2	11.3	38.1
	21	41	0.205	10.7	10.1	9.8	33.7

[1]Percent of gut content to larval dry weight.

TABLE 3.—Oxygen consumption rates at 6.2°C for larval walleye pollock at different experimental activity levels. The number of replicates per treatment was 3-5. Values in parentheses are for yolk-free weights.

Age (d)	Mean dry weight (µg)	Oxygen consumption activity level: Resting (M_{re}) µL/h/ind	SD	µL/h/mg	Routine (M_{ro}) µL/h/ind	SD	µL/h/mg
0	54.2	0.068	0.011	1.25(2.06)	0.068	0.003	1.26(2.08)
3	53.1	0.082	0.008	1.55(1.89)	0.086	0.019	1.61(1.96)
4	48.3	0.076	0.004	1.58(1.72)	0.077	0.012	1.59(1.76)
6	47.6	0.083	0.008	1.74(1.76)	0.112	0.019	2.35(2.38)
11	55.1	0.098	0.009	1.78	0.123	0.037	2.24
14	68.1	0.104	0.026	1.53	0.140	0.023	2.06
19	87.9	0.129	0.021	1.47	0.217	0.064	2.47
20	89.8	0.137	0.030	1.53	0.226	0.022	2.52
23	131.3	0.212	0.026	1.61	0.269	0.051	2.05

Age (d)	Mean dry weight (µg)	Oxygen consumption activity level: Feeding (M_{fn}) µL/h/ind	SD	µL/h/mg	Active (M_a) µL/h/ind	SD	µL/h/mg
6	47.6	0.100	0.014	2.09(2.12)	0.136	0.016	2.87(2.91)
11	55.1	0.134	0.024	2.43	0.153	0.042	2.78
14	68.1	0.134	0.017	1.97	0.193	0.036	2.83
19	87.9	0.153	0.026	1.74	0.251	0.036	2.86
20	89.8	0.185	0.020	2.06	0.304	0.008	3.39
23	131.3	0.287	0.067	2.19	0.406	0.074	3.07

The relationships of O_2 consumption rate (µL/h/individual) and mean larval dry weight (W, in µg) of feeding larvae for the different metabolic levels were

$$M_{re} = 0.00276\ W^{0.8707} \quad (r = 0.844,\ n = 26)$$
$$M_{ro} = 0.00253\ W^{0.9699} \quad (r = 0.807,\ n = 27)$$
$$M_{fn} = 0.00308\ W^{0.9059} \quad (r = 0.845,\ n = 25)$$
$$M_{a} = 0.00176\ W^{1.1154} \quad (r = 0.906,\ n = 25)$$

The metabolic mass exponents, particularly for routine metabolism, were close to unity.

For prefeeding larvae, weight-specific O_2 consumption rate (μL/h/mg) increased with age (Table 3). This is probably associated with increasing somatic tissue, because yolk is thought to be nonrespiring (Rombough 1988). Weight-specific rates, using yolk-free dry weight, decreased with age. As the eye became functional, at days 5 and 6, a rapid rise in routine metabolism followed the increase in light-stimulated activity. From days 6 to 23 there were no significant trends in the dry weight specific O_2 consumption rate with age for any treatments (ANOVA with regression, $P > 0.1$).

By difference ($M_{ro} - M_{re}$), lights-on generated activity of feeding larvae accounted for an average O_2 consumption of 0.67 μL/h/mg. Nighttime SDA ($M_{fn} - M_{re}$) accounted for 0.47 μL/h/mg, and feeding activity associated with hunting and capture of prey ($M_a - M_{ro} - 0.47 - 0.67$) accounted for 0.22 μL/h/mg. Given that the active-feeding metabolic rate was probably underestimated by our technique as noted previously, and that the active metabolic rate can be estimated as $2 \times M_{ro} = 4.56$ μL/h/mg, the above increment for active metabolism would be 1.81 μL/h/mg.

Energy Budget

Energy budget components and efficiencies are given in Table 4. Gross growth efficiency ($G/I \times 100$) ranged from 13.2 to 34.5% for high ration and from 9.1 to 32.6% for low ration larvae. The relationship of G/I and age was a U-shaped function with low efficiency in middle stages (Fig. 2). The ratio of metabolizable energy to ingestion ($((G + M)/I \times 100)$ is termed net assimilation efficiency. Net assimilation efficiency also showed a U-shaped relationship with age, ranging from 30.5 to 58.4% and from 24.4 to 63.5% for high ration and low ration larvae, respectively. The ratio of the growth component to metabolizable energy ($G/(G + M) \times 100$) gradually increased from 40-42% at day 7 to 55-59% at day 21.

DISCUSSION

The growth rates of walleye pollock larvae in our experiments compared favorably to those of

TABLE 4.—Daily energy budget components and efficiencies of larval walleye pollock. H and L indicate high ration and low ration levels, respectively.

Age:	7	7	10	10	13	13	16	16	19	19	21	21
Feeding condition	H	L	H	L	H	L	H	L	H	L	H	L
Mean SL (mm)	4.77	4.81	4.94	4.96	5.13	5.15	5.38	5.35	5.71	5.69	6.02	5.94
Mean dry weight												
(W_D)(μg)	46.5	48.6	54.0	57.3	67.6	68.4	80.2	78.1	98.0	96.6	120.9	116.2
(cal)[1]	0.236	0.247	0.274	0.291	0.343	0.347	0.407	0.397	0.498	0.492	0.614	0.590
Ingestion (I)												
(μg/d)	13.66	11.75	20.14	24.26	34.43	40.00	42.67	38.73	41.28	36.95	44.67	39.16
(cal/d)[2]	0.060	0.052	0.089	0.107	0.151	0.176	0.188	0.170	0.182	0.163	0.197	0.172
Growth (G)												
(μg/d)[3]	2.37	2.72	4.21	3.50	3.99	3.08	5.53	5.86	10.88	9.21	13.42	11.04
(cal/d)[2]	0.012	0.014	0.021	0.018	0.020	0.016	0.028	0.030	0.055	0.047	0.068	0.056
Metabolism (M)												
(μL O_2/d)	3.94	4.11	4.57	4.85	5.72	5.79	6.79	6.61	8.29	8.29	10.23	9.84
(cal/d)[4]	0.018	0.019	0.021	0.022	0.026	0.027	0.031	0.031	0.038	0.038	0.047	0.046
G/I[5] (%)	20.0	26.9	23.6	16.8	13.2	9.1	14.9	17.6	30.2	28.8	34.5	32.6
M/I[5] (%)	30.0	36.5	23.6	20.6	17.2	15.3	16.5	18.2	20.9	23.3	23.9	26.7
$(G + M)/I$[5] (%)	50.0	63.5	47.2	37.4	30.5	24.4	31.4	35.9	51.1	52.1	58.4	59.3
$G/(G + M)$[5] (%)	40.0	42.4	50.0	45.0	43.5	37.2	47.5	49.2	59.1	55.3	59.1	54.9
I/W_D[5] (%)	25.4	21.1	32.5	36.8	44.0	50.7	46.2	42.8	36.5	33.1	32.1	29.2

[1]Larval dry weight was converted to calories by a factor of 5.077 cal mg^{-1}.
[2]Rotifer dry weight was converted to calories by a factor of 4.4 cal mg^{-1}.
[3]Daily growth was calculated using the relative rate of growth (K) at each day interval.
[4]Oxygen volume was converted to calories by a factor of 4.63 cal mL^{-1} O_2.
[5]Efficiencies were expressed on caloric basis.

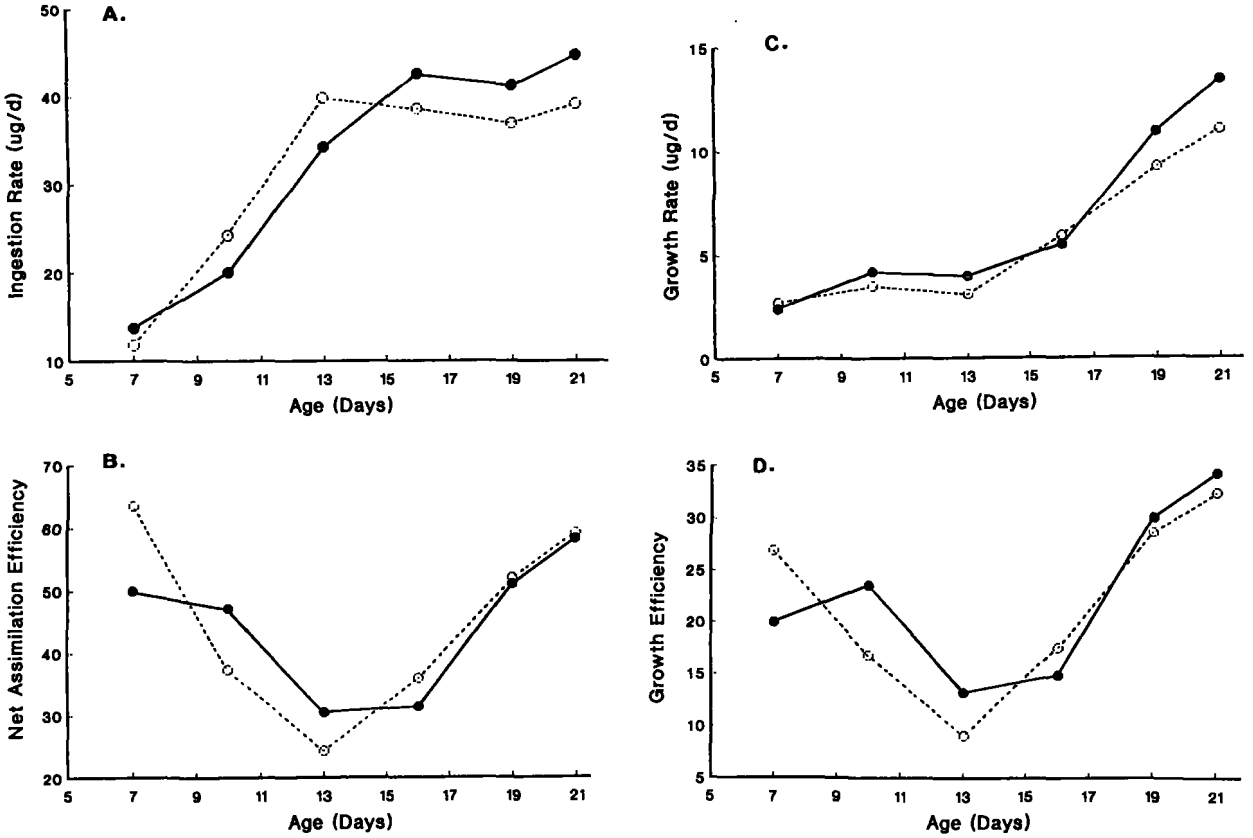

FIGURE 2.—Ingestion rates (A.); net assimilation efficiencies (B.); growth rates (C.); and growth efficiencies (D.) of reared walleye pollock larvae. Closed circles and open circles indicate well fed and poorly fed larvae, respectively.

larvae caught at sea. In the laboratory, yolk-sac larvae from days 0 to 4 (posthatch) were growing 0.20 mm/d at 6.4°C. Growth rates decreased to 0.06 mm/d just after onset of feeding (4.8 mm SL) and increased to 0.16 mm/d from days 19 to 21 (5.8 mm SL). Growth rates of field-collected walleye pollock larvae, determined from otolith increments, ranged from 0.12 to 0.25 mm/d, linearized over ages 7–45 days (6.0–14.6 mm SL) for larvae caught in the Gulf of Alaska in 1983 (at 5.5°–7.0°C (Kendall et al. 1987)). In 1987 the growth rate of Gulf of Alaska walleye pollock larvae at 5.8 mm SL was 0.18 mm/d as determined from the growth equation given in Yoklavich and Bailey (1989). Growth of field-caught larvae, like laboratory-reared larvae, was slow at ages corresponding to the transition from endogenous to exogenous feeding. Specific growth in dry weight was 7%/d. This is somewhat slower than the wet weight-specific growth rates estimated from field-caught larvae at 10%/d (Fukuchi 1976; Nishiyama 1981). These weight-specific growth rates are much lower than those of subtropical species (from 15 to 50%/d) (Houde and Schekter 1983; Theilacker 1987), but they are similar to those of other subarctic species (Laurence 1975; 1978)

Decreased evacuation rates with increased larval size (and age) were closely related to the development of the digestive system, especially midgut coiling, which begins at about 5.2 mm SL (13–16 days) and is completed at about 5.8 mm (19–21 days). Our gut clearance times (5.3–6.1 hours) for first-feeding larvae fed rotifers are similar to the 5 hours found by Paul (1983) for pollock larvae fed copepod nauplii at 5.5°C. Generally these gut clearance times are considerably slower than those of warm-water species, e.g., northern anchovy at 1.15–1.5 hours (Theilacker 1987). Walleye pollock larvae with high ingestion rates in high prey densities had faster rates of gut clearance compared with those held in low prey densities. Furthermore, larvae with full guts placed in prey-free water had very slow clearance rates, indicating that continuous feeding facilitates movement of ingested prey through the guts.

Specific daily ration increased from 21 to 25% at day 7 to a peak value of 46-51% at days 13–16 as a function of increasing ingestion rates. It

declined to 29–32% at day 21 as a result of the longer gut clearance times discussed previously. The inverted U-shaped function observed here was also noted by Houde and Schekter (1981) while studying three species of subtropical larvae. Daily rations for warm-water species are considerably higher than those found in this study, ranging from 202 to 379%, 165 to 297%, and 121 to 234% per day on a caloric basis for bay anchovy, *Anchoa mitchilli*, lined sole, *Achirus lineatus*, and sea bream, *Archosargus rhomboidalis*, respectively (Houde and Schekter 1983); values of 26–70% were found for northern anchovy converted to a caloric basis from data in Theilacker (1987); and values of 42–160% on a dry weight basis for summer flounder, *Paralichthys dentatus*, (Buckley and Dillmann 1982).

Our values of routine metabolism at 6.2°C in Table 4 correspond quite closely to values for walleye pollock and cod found by other investigators. For example, our values of 2.24 and 2.06 μL/h/mg for 11 and 14 d old larvae are similar to values of 1.86 and 2.14 for 11 and 14 d old pollock larvae at 4°C found by Clarke (1984). Adopting a Q_{10} value of 2.3 (Brett and Groves 1979), Clarke's values are equivalent to 2.23 and 2.57 μL/h/mg at 6.2°C. Routine metabolic rates for young cod larvae at 5°C have been measured at 1.6 (Davenport and Lönning 1980) and at 1.8–2.0 μL/h/mg (Solberg and Tilseth 1984).

We attempted to partition metabolism into its component parts for estimating daily metabolic cost. From the equation for total daily metabolism, the four components—SDA, lights-on generated nonfeeding activity, resting metabolism, and feeding activity—accounted for 13.3, 11.1, 45.7, and 29.9% of the total daily metabolic expenditure. Because of the experimental nature of these measurements, they should be considered a first approximation, subject to refinement. For example, degradation of rotifers that were defecated in the DO bottles could have consumed some of the available oxygen and should be controlled for in future studies. Our values for resting metabolism may include some cost for biosynthesis because a 24 h period of nonfeeding acclimation time is probably not enough to eliminate the effect of SDA (Brett and Groves 1979). The value for active feeding metabolism seems high compared with the relatively inactive behavior of walleye pollock larvae. The assumption that active metabolic rate is twice the routine metabolic rate may have resulted in an overestimate of this component.

Net assimilation efficiency [$(G + M)/I$], ranged from 24 to 64% in our study, as a U-shaped function related to age. These efficiencies are low compared with generalized rates of 65–75% for young fish given by Ware (1975) and 73% for young carnivorous fish given by Brett and Groves (1979). However, the assimilation rate during larval life seems to change greatly during development, and rates are usually quite low for young larvae. For example, net assimilation efficiency for northern anchovy changed with increasing larval size from 44.4 to 65.7% for well-fed larvae (Theilacker 1987). Net assimilation efficiency for bay anchovy, lined sole, and sea bream ranged from 17.2 to 33.7%, 26.6 to 46.1%, and 37.2 to 67.6%, respectively, for different developmental stages of these fishes (Houde and Schekter 1983).

High assimilation efficiency during the first few days of feeding may be due partly to residual yolk contributing to "ingestion". Yolk is converted into body tissue very efficiently (Lasker 1962). Assimilation efficiency decreased to a low point at day 13 of our experiments. We suggest that development of the digestive system lagged behind that of behavioral feeding prowess, and that low assimilation efficiencies were linked to the growth lag observed during the transition from endogenous to exogenous food. Assimilation efficiency and growth rate increased when ingestion reached a maximum and the alimentary canal developed midgut coiling, resulting in longer gut clearance time.

Gross growth efficiency (G/I) ranged from 11 to 34% as a U-shaped function of age (and size). Houde and Schekter (1983) reported similar U-shaped functions with size ranging from 10.9 to 20.8% for bay anchovy, from 12.8 to 23.3% for lined sole, and from 21.4 to 41.3% for sea bream. Most values for larvae are suggested to be in the 5–40% range (Houde and Schekter 1983) or 14–41% range (Theilacker and Dorsey 1980). The efficiencies of pollock larvae are consistent with these ranges. Our gross growth efficiencies are lower than those of 30–47% found by Theilacker (1987) for well-fed northern anchovy larvae.

Growth rates, ingestion rates, assimilation efficiencies, and growth efficiencies determined from this study differed surprizingly little between high and low rations. These results indicate that larvae robust enough to successfully initiate feeding at low prey densities were able to maintain high rations, and furthermore that growth responded very little to increased prey density. Lower levels of ration used here may be

necessary to assess the influence of marginal feeding conditions on growth or assimilation efficiency. Although we did not monitor feeding incidence and survival closely, both were higher in the high ration treatments. Consequently, including nonfeeding larvae in our study probably would have made differences appear in growth and ingestion rates between ration levels. Paul (1983) found fairly high incidences of pollock larvae feeding at low densities on copepod nauplii; however, the extreme smallness (250–1,000 mL) of containers used in that study probably invalidates the results.

According to Nishiyama and Hirano's (1985) formula for estimating mean gut content as a percent of wet body weight, guts of field-caught larvae 6 mm in total length (TL) should contain about 2% body weight. By contrast, larvae in our experiments contained 10–12% dry body weight. These results would indicate that either larvae in the field are not consuming prey at maximum rates, or there is a problem with collecting larvae from the field. Pollock larvae could be defecating when captured with nets; however, we observed that walleye pollock larvae did not defecate when probed with a dissecting needle, in contrast to anchovy larvae (Yamashita in press).

We can approximate mean caloric consumption of pollock larvae caught in the Bering Sea from the data of Dagg et al. (1984), who estimated that at an average temperature of 4.5°C, larvae 5.2 mm in length ingest 18.3 copepod nauplii/d. The mean length of copepod nauplii eaten by pollock larvae (5.2 mm TL) is 0.22 mm, as estimated from equations given by Nishiyama et al. (1986), and an equivalent wet weight is 1.38 μg (Nishiyama and Hirano 1985). Assuming 70% water content (Ikeda 1970) and the caloric content of adult *Pseudocalanus* (Laurence 1976), the mean caloric content of the average naupliar prey would be 0.0021 calories. Daily ingestion of larvae in the study of Dagg et al. (1984) would be 0.038 calories. Assuming 50% assimilation efficiency, 0.019 calories are available for metabolism and growth. This value, however, does not meet even the daily caloric requirement of 0.023 calories for metabolism alone, at 4.5°C (converted from 0.027 calories for metabolism of 13 d old larvae, 5.1–5.2 mm SL, at 6.2°C with an assumption of Q_{10} = 2.3 from Brett and Groves 1979). A daily caloric ingestion of about 0.16 calories is required for growth and metabolism for this size of larva from the results of our study. This value would be equivalent to 76 nauplii. Of course, prey size and metabolizable energy content may vary significantly.

The mean number of copepod nauplii at the depth of their maximum abundance in the Bering Sea during normal first-feeding of pollock larvae is 10–20/L (Clarke 1984; Dagg et al. 1984). These values are low compared with previously reported ranges of naupliar densities in the sea (e.g., Houde 1978; Hunter 1981). We believe that the low prey density, low percentage of gut contents to body weight of field-caught larvae, and the energetic requirements of larvae compared with estimated ingestion rates from field studies indicate that pollock larvae, like anchovy (Lasker 1975), are probably subject to food shortages in the sea. Since the growth response of walleye pollock larvae (at the low temperatures used in this study and in the sea) is low, one would not expect to see periodic episodes of low ration expressed markedly in mean larval growth rates (Yoklavich and Bailey 1989), but episodes of low ration would be better assessed on an individual basis, using chemical or histological methods.

ACKNOWLEDGMENTS

We thank T. Sibley, A. Kendall, G. Stauffer, and R. Francis for facilitating the visit of Y. Yamashita to Seattle. We thank M. Yoklavich, A. Kendall, G. Theilacker, and H. Mulligan for reviewing the manuscript and N. Merati, M. Yoklavich, and N. Navaluna for help in larval rearing activities. Much more than an acknowledgment is owed to Dr. Reuben Lasker for his influence on the authors. His early work on energetics introduced us to this field; his later work showed the importance of energetics to understanding recruitment processes. Beyond energetics, his enthusiasm for progress was inspirational.

LITERATURE CITED

Bailey, K. M., and C. L. Stehr.
1986. Laboratory study on the early life history of the walleye pollock, *Theragra chalcogramma* (Pallas). J. exp. mar. Biol. Ecol. 99:233–246.
1988. The effects of feeding periodicity and ration on the rate of increment formation in otoliths of larval walleye pollock *Theragra chalcogramma*. J. exp. mar. Biol. Ecol. 122:147–161.

Bakkala, R. G., T. Maeda, and G. McFarlane.
1986. Distribution and stock structure of pollock (*Theragra chalcogramma*) in the North Pacific Ocean. Int. North Pac. Fish. Comm. Bull. 45:3–20.

Batty, R. S.
1987. Effect of light intensity on activity and food-searching of larval herring, *Clupea harengus*: a laboratory study. Mar. Biol. (Berl.) 94:323–327.

Brett, J. R., and T. D. D. Groves.
1979. Physiological energetics. *In* W. S. Hoar, D. J. Randall, and J. R. Brett (editors), Fish physiology, vol. 8, p. 279–352. Acad. Press, N.Y. and Lond.

Buckley, L. J., and D. W. Dillmann.
1982. Nitrogen utilization by larval summer flounder, *Paralichthys dentatus* (Linnaeus). J. exp. mar. Biol. Ecol. 59:243–256.

Carritt, D. E., and J. H. Carpenter.
1966. Comparison and evaluation of currently employed modification of the Winkler method for determining dissolved oxygen in seawater; a NASCO report. J. Mar. Res. 24:286–318.

Clarke, M. E.
1984. Feeding behavior of larval walleye pollock, *Theragra chalcogramma* (Pallas) and food availability to larval pollock in the southeastern Bering Sea. Ph.D. Thesis, Univ. California, San Diego, 208 p.

Dagg, M. J., M. E. Clarke, T. Nishiyama, and S. L. Smith.
1984. Production and standing stock of copepod nauplii, food items for larvae of the walleye pollock *Theragra chalcogramma* in the southeastern Bering Sea. Mar. Ecol. Prog. Ser. 19:7–16.

Davenport, J., and S. Lönning.
1980. Oxygen uptake in developing eggs and larvae of the cod, *Gadus morhua* L. J. Fish Biol. 16:249–256.

de Silva, C. D., and P. Tytler.
1973. The influence of reduced environmental oxygen on the metabolism and survival of herring and plaice larvae. Neth. J. Sea Res. 7:345–362.

de Silva, C. D., S. Premawansa, and C. N. Keembiyahetty.
1986. Oxygen consumption in *Oreochromis niloticus* (L.) in relation to development, salinity, temperature and time of day. J. Fish Biol. 29:267–277.

Dwyer, D. A., K. M. Bailey, and P. A. Livingston.
1987. Feeding habits and daily ration of walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea, with special reference to cannibalism. Can. J. Fish. Aquat. Sci. 44:1972–1984.

Elliott, J. M., and L. Persson.
1978. The estimation of daily rates of food consumption for fish. J. Anim. Ecol. 47:977–991.

Fukuchi, M.
1976. Some aspects of bioenergetics of walleye pollock (Theragra chalcogramma Pallas) at early life stages. Ph.D. Thesis, Univ. Hokkaido, Hakodate, 114 p.

Harris, R. K.
1985. Body composition (carbon, nitrogen and calories) and energetics of immature walleye pollock, *Theragra chalcogramma* (Pallas), in the southeast Bering Sea. Ph.D. Thesis, Univ. Alaska, Fairbanks, 116 p.

Harris, R. K., T. Nishiyama, and A. J. Paul.
1986. Carbon, nitrogen and caloric content of eggs, larvae, and juveniles of the walleye pollock, *Theragra chalcogramma*. J. Fish Biol. 29:87–98.

Holliday, F. G. T., J. H. S. Blaxter, and R. Lasker.
1964. Oxygen uptake of developing eggs and larvae of the herring (*Clupea harengus*). J. Mar. Biol. Assoc. U.K. 44:711–723.

Houde, E. D.
1978. Critical food concentrations for larvae of three species of subtropical marine fishes. Bull. Mar. Sci. 28:395–411.
1987. Fish early life dynamics and recruitment variability. Am. Fish. Soc. Symp. 2:17–29.

Houde, E. D., and R. C. Schekter.
1981. Growth rates, rations and cohort consumption of marine fish larvae in relation to prey concentrations. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178:441–453.
1983. Oxygen uptake and comparative energetics among eggs and larvae of three subtropical marine fishes. Mar. Biol. (Berl.) 72:283–293.

Hunter, J. R.
1981. Feeding ecology and predation of marine fish larvae. *In* R. Lasker (editor), Marine fish larvae, p. 34–77. Univ. Wash. Press, Seattle and Lond.

Ikeda, T.
1970. Relationship between respiration rate and body size in marine plankton animals as a function of the temperature of habitat. Bull. Fac. Fish. Hokkaido Univ. 21:91–112.

Incze, L. S., M. E. Clarke, J. J. Goering, T. Nishiyama, and A. J. Paul.
1984. Eggs and larvae of walleye pollock and relationships to the planktonic environment. *In* D. H. Ito (editor), Proceedings of the workshop on walleye pollock and its ecosystem in the eastern Bering Sea, p. 109–159. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC–62.

Kendall, A. W., Jr., M. E. Clarke, M. M. Yoklavich, and G. W. Boehlert.
1987. Distribution, feeding, and growth of larval walleye pollock, *Theragra chalcogramma*, from Shelikof Strait, Gulf of Alaska. Fish. Bull., U.S. 85:499–521.

Lasker, R.
1962. Efficiency and rate of yolk utilization by developing embryos and larvae of the Pacific sardine *Sardinops caerulea* (Girard). J. Fish. Res. Board Can. 19:867–875.
1970. Utilization of zooplankton energy by a Pacific sardine population in the California current. *In* J. H. Steele (editor), Marine food chains, p. 265–284. Oliver & Boyd, Edinb.
1975. Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull., U.S. 73:453–462.

Laurence, G. C.
1975. Laboratory growth and metabolism of the winter flounder *Pseudopleuronectes americanus* from hatching through metamorphosis at three temperatures. Mar. Biol. (Berl.) 32:223–229.
1976. Caloric values of some north Atlantic calanoid copepods. Fish. Bull., U.S. 74:218–220.
1978. Comparative growth, respiration and delayed feeding abilities of larval cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) as influenced by temperature during laboratory studies. Mar. Biol. (Berl.) 50:1–7.

Miller, T. J., L. B. Crowder, J. A. Rice, and E. A. Marschall.
1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. Can. J. Fish. Aquat. Sci. 45:1657–1670.

Nishimura, A., and J. Yamada.
1984. Age and growth of larval and juvenile walleye pollock, *Theragra chalcogramma* (Pallas), as determined by otolith daily growth increments. J. exp. mar. Biol. Ecol. 82:191–205.

Nishiyama, T.
1981. Food energy requirement of walleye pollock in the southeast Bering Sea. *In* PROBES: Processes and Resources of the Bering Sea Shelf, p. 269–308. Prog. Rep. 1981.

Nishiyama, T., and K. Hirano.
1985. Prey size and weight relations in larval walleye pollock (*Theragra chalcogramma*). Bull. Plankton Soc. Jpn. 32:49–59.

Nishiyama, T., K. Hirano, and T. Haryu.
1986. The early life history and feeding habits of larval walleye pollock *Theragra chalcogramma* (Pallas) in the southeast Bearing Sea. INPFC Bull. 45:177–227.

Paul, A. J.
1983. Light, temperature, nauplii concentrations, and prey capture by first feeding pollock larvae *Theragra chalcogramma*. Mar. Ecol. Prog. Ser. 13:175–179.

Ricker, W. E.
1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191:1–382.

Rombough, P. J.
1988. Respiratory gas exchange, aerobic metabolism, and effects of hypoxia during early life. *In* W. S. Hoar and D. J. Randall (editors), Fish physiology, vol. 11, p. 59–161. Acad. Press, N.Y. and Lond.

Smith, P. E.
1985. Year-class strength and survival of 0-group clupeoids. Can. J. Fish. Aquat. Sci. 42:69–82.

Smith, R. L., and A. J. Paul.
1986. A theoretical energy budget for juvenile walleye pollock in Alaskan waters. INPFC Bull. 47:79–85.

Smith, R. L., A. J. Paul, and J. M. Paul.
1988. Aspects of energetics of adult walleye pollock, *Theragra chalcogramma* (Pallas), from Alaska. J. Fish. Biol. 33:445–454.

Solberg, T., and S. Tilseth.
1984. Growth, energy consumption and prey density requirements in first feeding larvae of cod (*Gadus morhua* L.). *In* E. Dahl, D. P. Danielssen, E. Moksness, and P. Solemdal (editors), The propagation of cod *Gadus morhua* L., Part 1, p. 145–166. Inst. Mar. Res., Flødevigen Biol. Stn., Arendal, Norway.

Strickland, J. D. H., and T. R. Parsons.
1972. A practical handbook of seawater analysis. 2nd ed. Bull. Fish. Res. Board Can. 167:1–310.

Theilacker, G. H.
1987. Feeding ecology and growth energetics of larval northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 85:213–228.

Theilacker, G. H., and K. Dorsey.
1980. Larval fish diversity, a summary of laboratory and field research. *In* Workshop on the effects of environmental variation on the survival of larval pelagic fishes, p. 105–142. Intergov. Oceanogr. Comm. Workshop Rep. No. 28., UNESCO, Paris.

Theilacker, G. H., and A. S. Kimball.
1984. Comparative quality of rotifers and copepods as foods for larval fishes. Calif. Coop. Oceanic Fish. Invest. Rep. 15:80–86.

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

Yamashita, Y.
In press. Defecation of larval Japanese anchovy *Engraulis japonica* due to net sampling. Bull. Tohoku Reg. Fish. Res. Lab., No. 52.

Yoklavich, M. M., and K. M. Bailey.
1989. Growth of larval and juvenile walleye pollock from Shelikof Strait, Gulf of Alaska, as determined from daily increments in otoliths. Proc. Int. Pollock Symp., Nov. 14–16, 1988, Anchorage, AK., p. 241–251. Alaska Sea Grant Program, Univ. Alaska, Fairbanks.