

**Abstract.**—Changes in total body energy content of adult (total length ~9 cm, wet mass ~9 g) northern anchovy *Engraulis mordax* were estimated by sampling captive groups swimming at 8.7 and 21.1 cm/s for 12 hours daily. Anchovy were fed euphausiids at rations of 5 and 3.4% of fish wet mass per day (~54 and 37 cal · g fish wet mass<sup>-1</sup> · day<sup>-1</sup>, respectively). Gross energy conversion efficiency increased with ration levels and declined with swimming speed, ranging from 39% to 1%. Dry mass and lipid losses were estimated in fasting fish swimming at the same speeds. Energy losses were 17.6 and 28.2 cal · g fish wet mass<sup>-1</sup> · day<sup>-1</sup> at the slow and fast speeds, respectively. The proportion of food energy used for growth and maintenance metabolism was about 65%. A model derived for adult anchovy metabolism was consistent with observed growth and reproduction rates, and the few measurements of ration and swimming speed in nature.

# Bioenergetics and Growth of Northern Anchovy *Engraulis mordax*

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The incorporation of energy from food into growth and reproduction by northern anchovy *Engraulis mordax* has been roughly quantified. Prey abundance influences the rate of anchovy reproduction during subsequent years, according to time-series analysis (Smith and Eppley 1982). Abundant food probably results in more energy intake and storage. Energy available for growth and reproduction by northern anchovy in the wild has been estimated at 12.8% of energy intake, based on laboratory measurements of gross energy-conversion efficiency (Hunter and Leong 1981). At 12.8% efficiency, the daily ration needed for average growth and reproduction was estimated to be 4-5% of fish wet mass (Hunter and Leong 1981), which is towards the high end of the range of field estimates for engraulids (Blaxter and Hunter 1982). However, food intake and energy demands vary. An energy budget model could help explain and predict the effect of food availability on anchovy growth and reproduction.

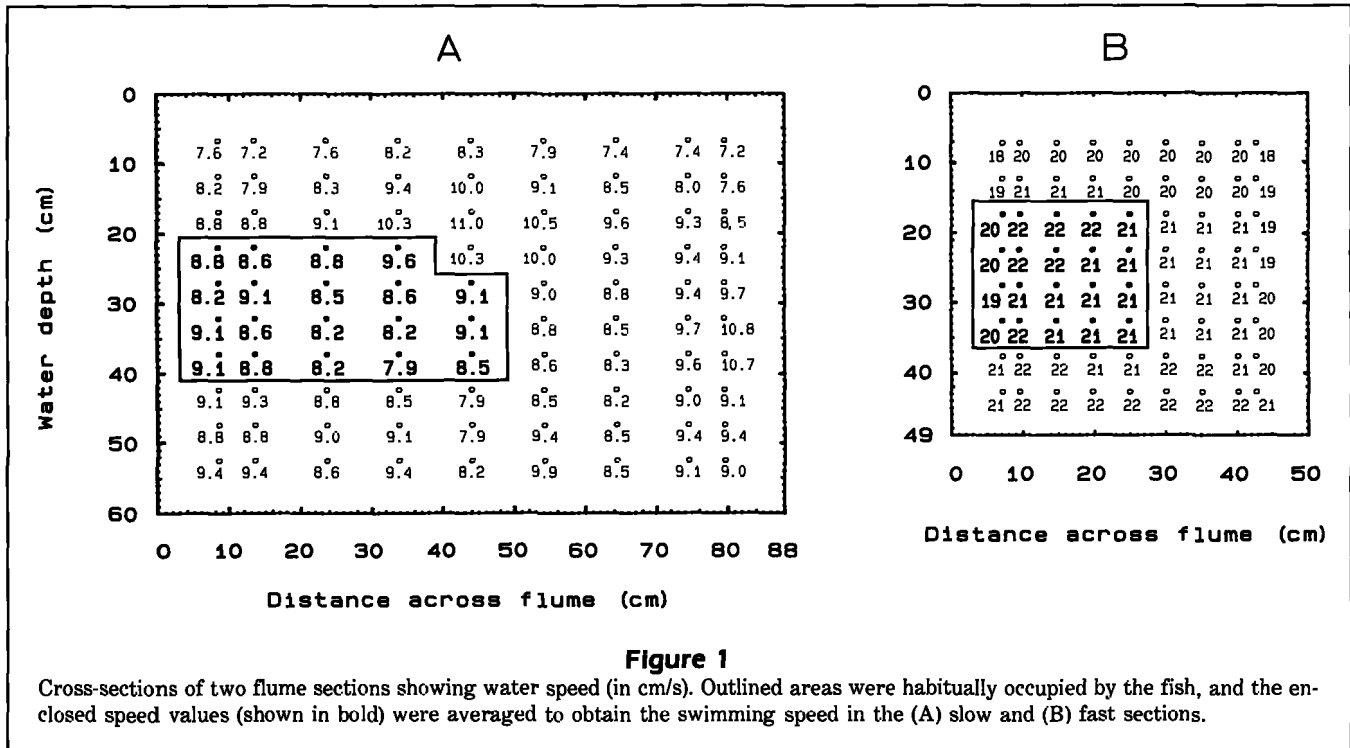
Gross energy-conversion efficiency is the net energy remaining after food assimilation and metabolic losses divided by the total energy consumed as food. Thus, gross energy-conversion efficiency should tend to increase with ration and decrease with increased swimming activity. The impact of swimming activity on clupeoid metabolism has been described for Pacific sardine *Sardinops caerulea* (Lasker 1970), Atlantic menhaden

*Brevoortia tyrannus* (Durbin et al. 1981), and Peruvian anchoveta *E. ringens* (Villavicencio 1981). Estimated metabolic rates of adult northern anchovy (S. Kaupp, R. Lasker, and R. Leong, a table of estimates obtained from J.R. Hunter, Southwest Fish. Sci. Cent., NMFS, NOAA, P.O. Box 271, La Jolla, CA 92037, unpubl. data) are about twice as high as those of its congener, *E. ringens*, at swimming speeds of about 1 body length/s. This difference is not small in relation to the overall energy budget of engraulids; therefore, better estimates of swimming metabolism are needed. The present study measures the energy expended for metabolism by northern anchovy at different swimming speeds, examines the effect of ration and metabolic rate on gross energy-conversion efficiency, and derives a model for adult anchovy metabolism.

## Methods

### The flume

Juvenile and adult northern anchovy ranging from 2 to 7 g wet mass were purchased from live-bait dealers in February 1984 and acclimated to laboratory conditions for 2-4 months prior to being transferred to an open flume for exercising the fish. Procedures for keeping live anchovy are described in Leong (1971) and Hunter and Leong (1981). Fish were fed 0.09 g Biomet trout pellets per fish per day until the study began.



The open flume was composed of two connected sections, the second section narrower and shallower than the first, resulting in a more rapid flow. The first section (the slow section) measured 244 × 88 × 60 cm (1290 L), and the second (the fast section) measured 244 × 50 × 49 cm (600 L). A 20 hp pump at the downstream end of the flume recirculated about 50 L/s of seawater through a feed pipe back to the upstream end of the flume. Water flowed through a tapered expansion section packed with gratings to even the flow. The whole flume was inside a 15,000 L tank. Fresh filtered seawater was added to the recirculating water in the flume at a rate of 20–30 L/minute. Temperature was maintained at 16.5–17.5°C.

Cross-sectional current profiles in each section were measured with a Marincio B-10 ducted impeller current meter. Baffles upstream from each section were adjusted to make the current profiles as uniform as possible, and gratings at the ends of each section confined the fish. Anchovy acclimated to the flume occupied habitual areas within the two sections (Fig. 1). The current measurements in these areas were averaged to estimate swimming speed. The pump was operated 12 hours daily during “daylight”; the photoperiod was 13L:10D with half-hour “dawn” and “dusk” periods.

Fish were anesthetized with quinaldine prior to transfer to the flume. During transfer, the fish were sorted and selected by size. A greater number were put

in the larger (slow) flume section to make fish density similar in both sections. Initially 1600 and 1000 fish were put into the slow and fast sections, respectively. The 12-hour swimming regime was built up over 8–10 days and then maintained for 2–3 weeks for each treatment.

### Treatments

Three levels of energy intake—high, zero, and low rations (in that order)—were imposed at two swimming speeds, making a total of six treatment combinations (Table 1). At each ration level, slow- and fast-speed treatments were applied concurrently in the two flume sections. The initial stock of fish was enough for the high- and zero-ration treatments. The flume was restocked for the low-ration treatments, but the number of laboratory-acclimated fish available was low (Table 1).

Starting 8–10 days before the treatments began, food type was changed to commercially obtained frozen euphausiids (species not identified). Anchovy were fed thawed euphausiids for 1 hour (high ration) or 0.5 hour (low ration) during the end of the daily swimming period. Food placed in 15 L containers of water above the flume flowed into perforated tubes (2.5 cm diameter, 0.6 cm perforations) stretched across the front of the two sections. Screens were temporarily inserted

**Table 1**

Summary of feeding levels in sequence of application, 12-hour enforced speeds, average fish mass, and estimated daily rations for the six treatments using the northern anchovy *Engraulis mordax*.  $N_c$  = initial number of fish in each flume section at the start of each treatment,  $N$  = total number killed for samples (number of samples in parentheses), and  $D$  = percentage of fish that died.

Feeding level	Treatments		$N_c$	$N$	$D$ (%)	Wet mass of food per fish* (g/day)	Fish mass (g)		Corrected daily ration** (% wet mass)	Ration energy (cal · g fish wet mass <sup>-1</sup> · day <sup>-1</sup> )
	Speed (cm/s)						Wet	Dry		
High	8.7		1392	331 (4)	39	0.443	9.02	2.40	5.06	55.7
	21.1		674	184 (4)	49	0.442	9.83	2.57	4.73	52.0
0	8.7		469	291 (5)	8	0	8.86	2.68	0	0
	21.1		131	86 (3)	27	0	9.32	2.96	0	0
Low	8.7		416	298 (4)	16	0.227	6.82	1.92	3.42	37.6
	21.1		177	111 (2)	37	0.285	8.67	2.66	3.38	37.2

\* Average from daily amounts dispensed and equations in Figure 2.

\*\* Corrected for gastric evacuation (cf. Equation 4 in text).

to prevent food in one section from passing to the other. Uneaten food collected on the screens was weighed.

Rations were chosen to match the high ration (4–5%) estimated by Hunter and Leong (1981), and a lower ration (3%) in the middle of the range of field estimates (Blaxter and Hunter 1982). The zero ration was included so that metabolism could be estimated from the loss of body energy.

Preliminary estimates of rations were made from the net mass of food dispensed and the number of fish in each treatment (Table 1). Preliminary ration estimates were calibrated based on the amount of food in stomachs after feeding, corrected for gastric evacuation. To estimate the gastric evacuation rate, 15–24 fish were killed and stomach contents weighed once per hour for 7 hours on the seventh day of the first treatment.

### Removing and counting fish

A sample of fish (Table 2)\* was collected in one sweep of a large dipnet at the beginning and end of each treatment, and every 4–7 days during five of the six treatments. In the low-ration, fast-speed treatment there were enough fish only for the initial and final samples. At least 20 fish were planned for each sample, but the number of fish netted was sometimes lower, or much higher (Table 2)\* because the sample was taken quickly to avoid disturbing the fish.

The standard length of sampled fish, their wet mass, and the wet mass of stomach contents were measured.

A subset of about 20 fish from each sample and the combined stomach contents from 9 samples were dried for 6 days at 55°C, cooled in desiccators, and weighed.

A census was kept on the number of fish in each section of the flume based on rapid counts of the fish transferred to the flume, minus removals due to sampling and mortality. Dead fish were collected and measured each day. The initial counts were accurate to within 10% of the total number collected at the end of the treatments. A corrected census, figured from the total counts, was used in the final calculations.

### Data analysis

Within each treatment, trends in sample means (i.e., length) or calculated values (i.e., kcal/fish) were expressed as slopes in relation to elapsed time by using linear regression (method of least squares). When only two samples were collected in a treatment, the difference over time was calculated. The significance of slopes, differences between initial and final sample means, and differences between values estimated from regression (i.e., log of dry mass) were evaluated with  $t$ -tests.

Apparent growth trends in some treatments were corrected to account for high mortality of fish smaller than the treatment mean. If there was no significant change in length (e.g., in zero-ration treatments), then no correction for mortality was made and length was assumed to be constant. An approximation of the bias in group mean length caused by mortality each day was calculated as the difference between the apparent mean length of the group each day ( $L_A$ ) and the mean length calculated by including the dead fish collected that day,

\* In the zero-ration treatments, sample size was the same as the number dried (Table 3).

**Table 2**

Increase in standard length (95% confidence intervals in parentheses) with time during the four feeding treatments and the correction for size-specific mortality.  $N_C$  = number of fish in each flume section before the first sample,  $N$  = sample size,  $N_S$  = stomach content sample size, and NA = not applicable.

Ration (cal·g <sup>-1</sup> ·day <sup>-1</sup> )	Speed (cm/s)	Day	$N_C$	$N$	$N_S$	Mean length (mm)	Apparent growth	Mortality bias	Actual growth
							in length	(mm/day)	in length
High 55.7	Slow 8.7	0	1392	101	0	88.1 (±1.2)			
		7	1160	168	157*	90.1			
		14	773	29	29	95.4			
		21	556	33	33	91.0 (±2.5)	0.202 (±0.569)	0.155	0.047
High 52.0	Fast 21.1	0	674	99	0	88.9 (±1.1)			
		7	489	33	33	91.8			
		14	327	22	22	95.4			
		21	187	30	30	94.1 (±2.5)	0.277 (±0.324)	0.244	0.033
Low 37.6	Slow 8.7	0	416	75	24	84.4 (±1.1)			
		7	319	78	24	84.1			
		14	212	70	24	85.5			
		20	126	75	24	86.0 (±1.3)	0.092 (±0.099)	0.023	0.069
Low 37.2	Fast 21.1	0	177	52	24	93.9 (±1.7)			
		16	59	59	24	92.9 (±1.7)	-0.063	NA	0

\*Total of 8 samples (Fig. 3) collected 0-7 hours after feeding ( $N_S$  = 23, 21, 19, 16, 24, 15, 15, and 24, respectively).

Daily bias =

$$L_A - \left[ \frac{(L_A N_C) + (L_M N_M)}{N_C + N_M} \right] \text{ mm/day,} \quad (1)$$

where  $N_C$  was the number of fish in the treatment group at the end of each day,  $N_M$  was the number of dead fish that day, and  $L_M$  was the mean standard length of the dead fish that day. The  $L_A$  was calculated from a regression of sample mean lengths on elapsed time over the course of the treatment. The slope of this regression ( $L_A$  on elapsed time) was the apparent growth (Table 2), which was corrected by the average of the daily biases to estimate the actual increase in fish length.

Fish mass was estimated from corrected length using log-log regressions of dry mass on standard length for each sample. The regression estimate for each sample was calculated by assuming that length increased at the corrected rate for that treatment.

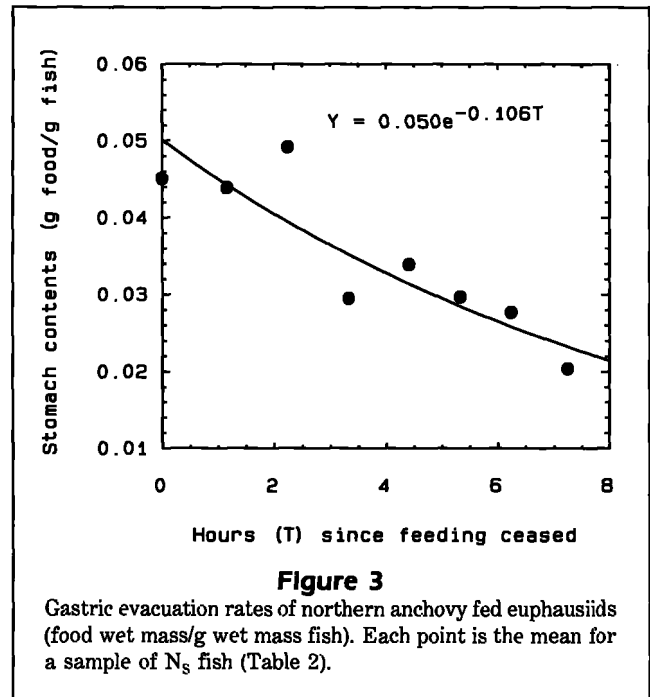
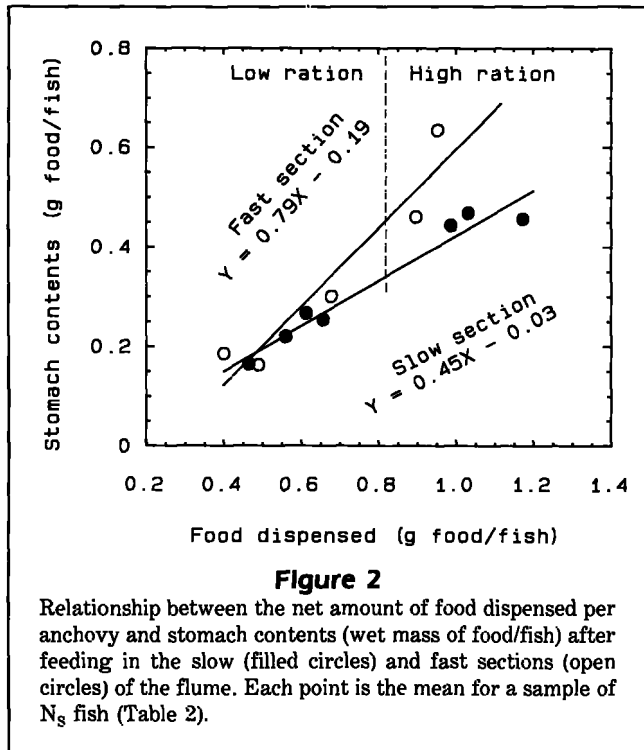
From each sample, a subset of four fish, chosen to best match the estimated length and dry mass of the sample, was analyzed for fat content by using Soxhlet extraction with chloroform-methanol (2:1). Fat content of food removed from stomachs was also measured. Total energy content of fish and food was estimated from published values (Brett and Groves 1979, Hunter

and Leong 1981) for heat of combustion. The rate of energy loss or gain in each treatment was calculated as the regression slope of fish energy content in each sample versus elapsed time.

## Results

### Rations

Anchovy stomach contents from 12 samples (Table 2) were weighed immediately after feeding. The average amount of food in the stomachs was less than (but correlated with) the net amount of food that was dispensed per fish (Fig. 2). The difference was too large to be due to the rate of gastric evacuation. A portion of the food passed through gaps in the bottom of the flume sections and into the surrounding tank. Recirculation of this food was prevented by screens. Regressions of stomach contents on food dispensed (Fig. 2) suggested that a greater proportion of the food dispensed was eaten in the high-ration, fast-speed treatment than in the other treatments. Although the regressions were not significantly different, they were used to estimate stomach contents separately for each speed on days when stomach contents were not sampled. The average of the resulting daily estimates was calculated for each treatment (Table 1).



Evacuation of the food from the stomach was slow (Fig. 3). The absence of an immediate decline in stomach contents after feeding suggested a gastric pause or coprophagy, although this result may be due to sampling errors. The following regression (using a semilog transformation) of mean stomach contents ( $Y$  in grams food/gram fish) versus elapsed time ( $T$  in hours after feeding stopped) describes the data from eight hourly samples (Table 2, Fig. 3):

$$\log_e Y = -2.995 - 0.106 T \quad (N 8, r^2 0.81). \quad (2)$$

Taking the antilog

$$Y = 0.05 e^{-0.106 T} \text{ g food / g fish}, \quad (3)$$

the actual amount of food consumed ( $C_T$ ) between the initiation and cessation of feeding was estimated (Elliott and Persson 1978) as

$$C_T = \frac{[S_T - (S_0 e^{-dT})] rT}{1 - e^{-dT}} \text{ g food}, \quad (4)$$

where  $S_T$  was the amount of food found in stomachs at the cessation of feeding, and  $d = 0.106$  (from Equation 3). No food was in the stomachs at the initiation of feeding ( $S_0 = 0$ ). For 1 hour of feeding,  $C_T$  equaled  $1.054 S_T$ , and for 0.5 hour of feeding,  $C_T$  equaled  $1.027 S_T$ . Thus, only a slight correction of mean stomach content estimates was needed to calculate the rations (Table 1).

The water content of food (euphausiids) averaged 78.4% ( $N 9$ ,  $SD 1.7\%$ ); therefore, dry mass averaged 21.6% of wet mass. The fat content of the food averaged 21.8% of dry mass ( $N 3$ ,  $SD 3.6$ ). S. Kaupp (NMFS Southwest Fish. Sci. Cent., P.O. Box 271, La Jolla, CA 92037, pers. commun., March 1984) found that the average protein content of euphausiids (species not identified) was 43.5% of dry mass ( $N 25$ ,  $SD 0.20$ ). The remaining dry mass (24.7%) was estimated to consist of ash and chitin in roughly equal amounts, since Lasker (1966) found that molts and ash each made up about 10% of dry mass in *Euphausia pacifica*. Assuming 9.2 kcal/g for fat, 5.65 kcal/g for protein, and 4.1 kcal/g for carbohydrate (Brett and Groves 1979), the total caloric content of the food was

$$\left[ \frac{21.8}{100} 9.2 \frac{\text{kcal}}{\text{g dry}} \right] + \left[ \frac{43.5}{100} 5.65 \frac{\text{kcal}}{\text{g dry}} \right] + \left[ \frac{12.4}{100} 4.1 \frac{\text{kcal}}{\text{g dry}} \right] = 5.09 \frac{\text{kcal}}{\text{g dry food}}$$

and

$$\left[ 5.09 \frac{\text{kcal}}{\text{g dry food}} \right] \left[ \frac{21.6 \text{ g dry}}{100 \text{ g wet food}} \right] = 1.1 \frac{\text{kcal}}{\text{g wet food}}$$

### Growth in length

Final mean length was significantly higher than the initial mean length in all feeding treatments except the low-ration, fast-speed treatment (*t*-test,  $P \leq 0.05$ ; Table 2). However, the slopes of the regressions describing the apparent rates of growth (in length) were not significantly different from zero, because of the variation

not explained by growth or selective mortality. The fish schooling in the flume may have sorted themselves by size so that the dipnet frequently caught a sample containing larger- or smaller-than-average fish. The coefficient of variation of length in each sample ranged from 5 to 7%. The low number of samples would make this an important source of error.

**Table 3**

Regressions of the natural log of dry mass ( $\log_e Y$ ) on the log of standard length ( $\log_e X$ ) estimated from actual growth (cf. Table 2), and measures of fat content ( $N = 4$ ) used to estimate dry mass, total energy, caloric growth, and energy loss during the six treatments. Estimates in brackets assume no increase in length; 95% confidence limits in parentheses.  $N$  = number of fish dried.

Treatment	Day	$N$	Regression equation	Length (mm)	Log of dry mass from regression	Dry mass (g)	Fat content (%)	Total energy (kcal)
High ration, slow speed								
	0	25	$\log_e Y = 3.861 \log_e X - 16.664$	89.04	0.668 ( $\pm 0.091$ )	1.95	36.7	11.70
	7	32	$\log_e Y = 5.241 \log_e X - 22.814$	89.36	0.732	2.08	39.8	12.87
	14	19	$\log_e Y = 4.679 \log_e X - 20.333$	89.69	0.705	2.02	40.9	12.61
	21	23	$\log_e Y = 4.605 \log_e X - 19.784$	90.02	0.939 ( $\pm 0.059$ )	2.56	43.9	16.30
				[89.04]	[0.888 ( $\pm 0.059$ )]	[2.43]		
High ration, fast speed								
	0	24	$\log_e Y = 5.524 \log_e X - 23.943$	88.68	0.832 ( $\pm 0.078$ )	2.30	41.7	14.39
	7	23	$\log_e Y = 3.893 \log_e X - 16.587$	88.91	0.883	2.42	43.7	15.38
	14	24	$\log_e Y = 5.193 \log_e X - 22.467$	89.14	0.851	2.34	43.8	14.89
	21	20	$\log_e Y = 4.574 \log_e X - 19.611$	89.37	0.939 ( $\pm 0.056$ )	2.56	44.8	16.42
				[88.68]	[0.903 ( $\pm 0.060$ )]	[2.47]		
Low ration, slow speed								
	0	24	$\log_e Y = 4.515 \log_e X - 19.493$	84.06	0.515 ( $\pm 0.062$ )	1.67	38.4	10.16
	7	24	$\log_e Y = 4.839 \log_e X - 20.856$	84.54	0.616	1.85	41.1	11.51
	14	24	$\log_e Y = 5.485 \log_e X - 23.712$	85.02	0.657	1.93	39.2	11.83
	20	24	$\log_e Y = 5.539 \log_e X - 24.050$	85.44	0.586 ( $\pm 0.066$ )	1.80	40.5	11.15
				[84.06]	[0.496 ( $\pm 0.067$ )]	[1.64]		
Low ration, fast speed								
	0	41	$\log_e Y = 3.352 \log_e X - 14.245$	93.4	0.963 ( $\pm 0.032$ )	2.62	46.4	17.02
	16	49	$\log_e Y = 3.906 \log_e X - 16.733$	[93.4]	[0.988 ( $\pm 0.047$ )]	*[2.62]	46.8	17.07
No food, slow speed								
	0	19	$\log_e Y = 4.587 \log_e X - 19.767$	92.52	1.000 ( $\pm 0.076$ )	2.72	46.2	17.38
	4	24	$\log_e Y = 4.975 \log_e X - 21.499$	do.	1.025	2.79	47.6	17.96
	8	23	$\log_e Y = 5.293 \log_e X - 23.041$	do.	0.923	2.52	44.2	15.76
	12	21	$\log_e Y = 4.838 \log_e X - 21.016$	do.	0.888	2.43	45.1	15.36
	16	24	$\log_e Y = 5.611 \log_e X - 24.716$	[92.52]	[0.914 ( $\pm 0.063$ )]	[2.49]	43.1	15.56
No food, fast speed								
	0	21	$\log_e Y = 3.553 \log_e X - 14.947$	93.48	1.176 ( $\pm 0.064$ )	3.24	45.2	20.97
	6	23	$\log_e Y = 4.903 \log_e X - 21.210$	do.	1.039	2.83	46.8	18.57
	12	42	$\log_e Y = 3.542 \log_e X - 15.066$	[93.48]	[1.007 ( $\pm 0.051$ )]	[2.74]	46.1	17.82

\* Assumed no change in dry mass since the difference was not significant.

Estimates of actual growth (in length), as corrected for mortality (Table 2), appeared similar to those for 1- to 2-year-old anchovy in nature based on otolith increments (Spratt 1975), but were lower than those measured by Hunter and Leong (1981) in the laboratory. No increase in length was indicated during the low-ration, fast-speed treatment, so no correction was made for mortality. The most rapid length increase (0.069 mm/day) was estimated for the group with the smallest mean size (Table 2). This group underwent the low-ration, slow-speed treatment yet appeared to have a faster rate of growth (in length) than did the high-ration, slow-speed group. This might suggest that the increase in length was size-dependent and somewhat independent of the net energy surplus.

Mortality was highest during the high-ration treatments and lowest in the low-ration and fasting treatments, especially at slow speed (Table 1). Fish bumped into the gratings between flume sections during feeding, which may have led to a high rate of injuries resulting in death. The size bias in mortality might have resulted from large fish being less often injured by the gratings. However, the treatment with the smallest sized fish (low-ration, slow-speed) had one of the lowest mortality rates.

### Dry mass

Estimates of fish dry mass for each sample were obtained from mass-on-length regressions (Table 3) by using length estimates corrected for mortality in three feeding treatments (Table 2) and assuming no length change in the other treatments. In all but one case, the final dry mass estimates were significantly greater (high- and low-ration treatments) or lower (zero-ration treatments) than the initial estimates ( $t$ -test,  $P < 0.05$ ). In the zero-ration treatments, the loss of dry mass was more than twice as rapid in the fast-speed treatments as it was in the slow-speed treatments (Table 3). Dry mass increased about four times more rapidly during the high-ration treatments than during the low-ration treatments, and dry mass increased more than twice as rapidly during slow-speed treatments as during fast-speed treatments at both rations. Dry mass did not change significantly between the initial and final estimates when fish were fed the low ration and swam at the fast speed, so growth was assumed to be zero (Table 3).

In three feeding treatments (Table 3) the increases in mass were dependent on estimated increases in length. Although realistic, the corrected length increases (Table 2) may not have been accurate. Therefore, conservative estimates of mass increases in the feeding treatments were calculated by assuming that there was no increase in length (Table 3). A signifi-

cant length-specific increase over initial dry mass was found in the slow-speed, high-ration treatment.

### Caloric growth and gross conversion efficiency

Fat content (Table 3) increased substantially during the high-ration treatments, wherein about 70% of the increase in dry mass was fat. Fat increased about twice as much in the high-ration, slow-speed treatment as in the high-ration, fast-speed treatment. No strong trends in percent fat were found in the low-ration treatments.

The average percent fat of each sample was used to calculate mass of fat and fat-free dry mass per fish. Then the total fish energy content for each sample was calculated (Table 3) by assuming heat of combustion values equal to 29 kcal/g for fat-free dry mass and 9.227 kcal/g for fat (Hunter and Leong 1981).

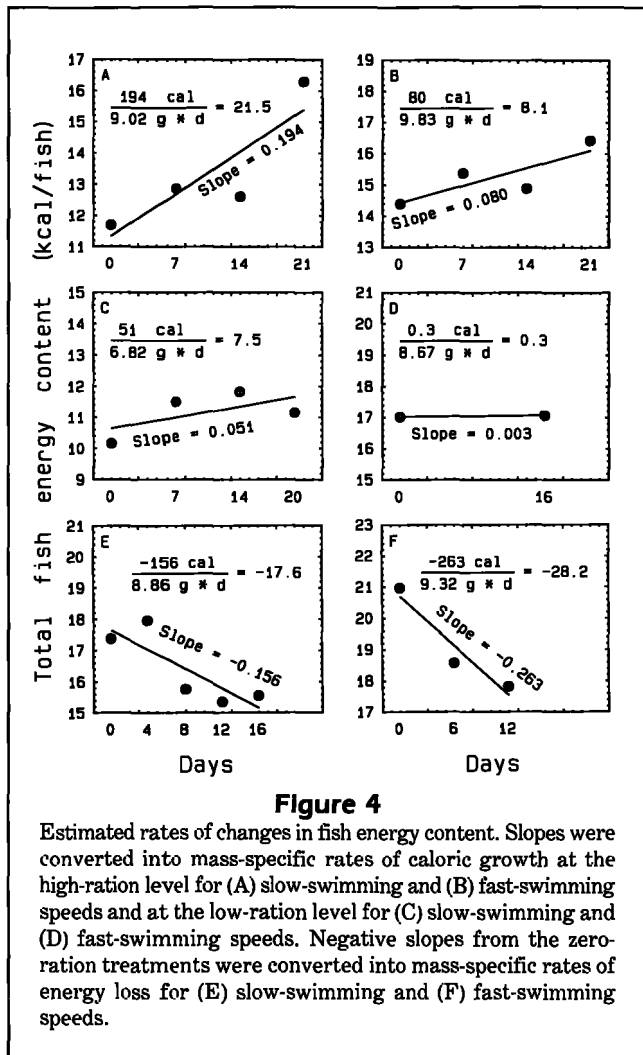
The trends in total energy content from all of the treatments (Fig. 4) were consistent with a simple energy budget in which more food energy taken in (R), or less energy required for metabolism (Q), results in more energy available for reproduction (S), growth (G), and fat storage (F):

$$R = Q + X + I + S + G + F \text{ cal.} \quad (5)$$

Components of the energy budget that were not individually estimated were excretion (X) and digestive losses (I). No spawning occurred during the experiments, although gonad mass changed. In the following analyses, changes in gonad and somatic mass were combined as overall growth (B) and fat storage (F). Metabolism was separated into maintenance metabolism ( $Q_M$ ) and the metabolism associated with extracting usable energy from food (SDA). Ninety percent of the energy losses during starvation were assumed to be respired ( $Q_M$ ), with excretion accounting for the remainder. This is consistent with estimates of endogenous excretion given by Durbin and Durbin (1981, 1983). The "metabolizable fraction" of fasting energy losses has been assumed to be as little as 80% (Brett 1973) for energy derived from body protein. In the present study, about one-third to one-half of the calories lost during fasting were derived from protein.

Energy losses during fasting were greatest during the fast-speed treatment ( $28.2 \text{ cal} \cdot \text{g fish wet mass}^{-1} \cdot \text{day}^{-1}$ )\*\* and lowest during the slow-speed treatment ( $17.6 \text{ cal} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$ , Fig. 4). Growth (in  $\text{cal} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$ ) was greater at both speeds when rations (R) were high than when they were low (Fig. 4). At both

\*\* Hereafter the unit of mass ( $\text{g}^{-1}$ ) refers to fish wet mass.



**Figure 4**

Estimated rates of changes in fish energy content. Slopes were converted into mass-specific rates of caloric growth at the high-ratio level for (A) slow-swimming and (B) fast-swimming speeds and at the low-ratio level for (C) slow-swimming and (D) fast-swimming speeds. Negative slopes from the zero-ration treatments were converted into mass-specific rates of energy loss for (E) slow-swimming and (F) fast-swimming speeds.

feeding levels, caloric growth was greater in the slow-speed than in the fast-speed treatments. In each treatment, energy utilization (in  $\text{cal} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$ ) not accounted for by maintenance metabolism ( $Q_M$ ) and caloric growth ( $B + F$ ) was a relatively constant fraction of the energy consumed:

	Ration (R)	- Growth (B + F)	- Maintenance ( $Q_M$ )	=	Excretion (X)	+ Digestive losses (I)	+ SDA	
High ration, slow speed:	55.7	- 21.5	- 0.9(17.6)	=		20.1		= 0.36 R
High ration, fast speed:	52.0	- 8.1	- 0.9(28.2)	=		18.5		= 0.36 R
Low ration, slow speed:	37.6	- 7.5	- 0.9(17.6)	=		14.3		= 0.38 R
Low ration, fast speed:	37.2	- 0.3	- 0.9(28.2)	=		11.5		= 0.31 R
								Mean 0.35 R

About 35% of the food energy was lost through excretion (X), digestive losses (I), and SDA, so the energy budget Equation (5) may be simplified as

$$R = (B + F + Q_M) / 0.65 \text{ cal} \cdot \text{g}^{-1} \cdot \text{day}^{-1}. \quad (6)$$

Observed gross conversion efficiency (K) was calculated by dividing caloric growth ( $B + F$ ) by ration (R). Gross conversion efficiency predicted by the energy budget approximation (Equation 6) was

$$K = \frac{R - (0.35 R) - Q}{R} \text{ (dimensionless)}. \quad (7)$$

The model closely matched the observed gross conversion efficiencies:

	Gross conversion efficiency (%)	
	Observed	Equation (7)
High ration, slow speed:	39	37
High ration, fast speed:	16	16
Low ration, slow speed:	20	23
Low ration, fast speed:	1	-3

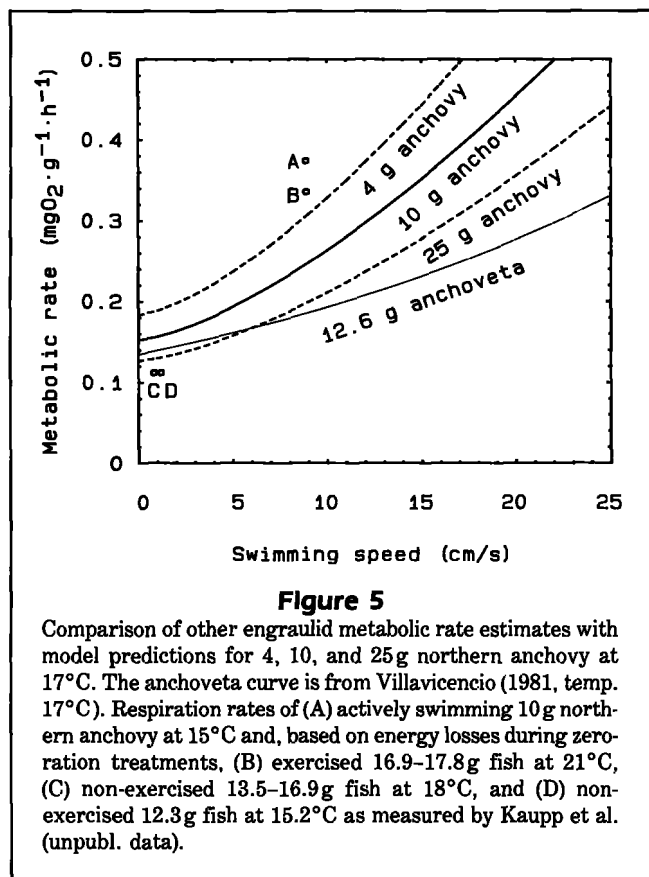
These results indicate that a simple energy budget model, assuming a loss of 35% of the food energy due to X, I, and SDA, explains increased growth with increased ration and decreased growth with increased activity.

## Discussion

### Gross conversion efficiencies

The energy budget approximation (Equation 7) implies that gross conversion efficiency is reduced by low ration and high activity. This was supported by the lower





K values in treatment combinations with low ration or high speed compared with the high-ration, slow-speed treatment. Contrarily, K values in the high-ration, slow-speed treatment were much higher than the 12.8% reported by Hunter and Leong (1981) for northern anchovy even though the fish in the present study were exercised and fed smaller rations. Hunter and Leong (1981) fed fish 124 cal · g<sup>-1</sup> · day<sup>-1</sup> of semi-dry, pelleted trout food (the caloric equivalent of a ration of 16% of wet body mass/day in copepods). At very high rations, the proportion of food energy lost to X, I, and SDA may increase (Paloheimo and Dickie 1966, Brett 1979, Brett and Groves 1979), causing K to decline.

The euphausiids used for food and the rations (Table 1) in the present study were similar to the zooplankton rations of 1.4–4.9% observed in nature (Blaxter and Hunter 1982). So, although X, I, and SDA vary with food composition (Elliott 1976b, Brett and Groves 1979, Tandler and Beamish 1979 and 1980) and may increase at ration levels higher than those in nature, the energy budget generalizations in Equations (6) and (7) should be applicable to adult anchovy in the wild.

The observed range of gross conversion efficiencies (1–39%) extended higher than the range reported for

clupeoids (7–13.5%, Takahashi and Hatanaka 1960, De Silva and Balbontin 1974, Hunter and Leong 1981, Blaxter and Hunter 1982). However, gross conversion efficiencies this high are found in many juvenile fishes (60% Hatanaka and Takahashi 1956, 34% Elliott 1976a, 10–25% Brett and Groves 1979). The importance of different results in such studies is difficult to judge, because of differences in the assumptions, expressions (percentages of mass or energy), experimental conditions (size, maturity, temperature, activity), and the rarity of error estimates.

### A model for adult anchovy metabolism

A model for anchovy metabolism was derived by using the estimates from the present study, data on closely related species, and general principles relating swimming speed and metabolism to fish size. The model required estimates of (1) standard metabolism, (2) swimming metabolism, (3) the effect of fish size on standard and swimming metabolism, and (4) the effect of temperature. These estimates are provided in the following sections.

**Standard metabolism** Standard metabolism was estimated by extrapolating to zero swimming speed from the rates estimated at two speeds. An exponential relationship (Brett 1964) was assumed,

$$Q_M = ae^{bV} \text{ cal} \cdot \text{g}^{-1} \cdot \text{day}^{-1}, \quad (8)$$

where the metabolic rate exclusive of SDA ( $Q_M$ ) consists of standard metabolism ( $Q_0 = a$ ) increased by a factor ( $e^{bV}$ ) for the cost of swimming, where V is swimming speed. The energy losses measured in the present study resulted from fish exercising half the time and resting half the time, so

$$Q_M = [0.5 (ae^{bV})] + [0.5 (a)] \text{ cal} \cdot \text{g}^{-1} \cdot \text{day}^{-1}. \quad (9)$$

The metabolic rate estimates ( $Q_M = 0.9 \times 17.6 = 15.8$ , and  $0.9 \times 28.2 = 25.4 \text{ cal} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$ ) from the two exercise levels ( $V = 8.7$  and  $21.1 \text{ cm/s}$ , respectively) were substituted for  $Q_M$  and V in Equation (9). The resulting simultaneous equations were solved, and  $Q_0$  was calculated to be  $12.1 \text{ cal} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$  at  $V = 0$ . Assuming an oxycaloric equivalent of 3.24 cal/mg O<sub>2</sub> (Elliott and Davison 1975), the standard metabolic rate was  $0.156 \text{ mg O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ . Assuming the same metabolizable fraction (0.9) and oxycaloric equivalent, energy losses of  $9.7 \text{ cal} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$  at the lowest activity levels measured by S. Kaupp et al. (unpubl. data,) amounted to  $0.112 \text{ mg O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ . The standard metabolism of 12.6 g anchoveta at 17°C (Villavicencio 1981) was  $0.135 \text{ mg O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ . These values (Fig. 5)

were similar to the estimate of  $Q_M$  in the present study.

**Swimming metabolism** Standard metabolism ( $Q_0 = 12.1 \text{ cal} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$ ) subtracted from the  $Q_M$  estimates for fish at the two speeds left 3.7 and 13.3  $\text{cal} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$ , respectively, for the metabolic cost of swimming ( $Q_V$ ) for 12 hours a day at 8.7 and 21.1 cm/s. On an hourly basis,  $Q_V$  amounted to 0.308 and 1.11  $\text{cal} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ , respectively. A linear fit to log-transformed estimates of  $Q_V$  versus log-transformed  $V$  indicated that

$$Q_V = (0.0137 V^{1.44}) \text{ cal} \cdot \text{g}^{-1} \cdot \text{h}^{-1}. \quad (10)$$

For extrapolating beyond the range of measurements, a power function makes a good model for swimming metabolism, because mechanical principles and empirical evidence (Ware 1978, Wu and Yates 1978) indicate that thrust and drag in swimming fish are power functions of speed.

**Effect of fish size** Fish size was not manipulated in the present study, so size effects could not be quantified from the results. However, reviews (Winberg 1956, Brett and Groves 1979) of results from a large number of studies have led to the generalization that the mass exponent of standard metabolism in fishes is close to 0.8. The corresponding mass-specific exponent (-0.2) combined with the estimate of  $Q_0$  from the present study results in this model,

$$\begin{aligned} Q_0 &= 18.8 M^{-0.2} \text{ cal} \cdot \text{g}^{-1} \cdot \text{day}^{-1} \\ &= 0.783 M^{-0.2} \text{ cal} \cdot \text{g}^{-1} \cdot \text{h}^{-1}, \end{aligned} \quad (11)$$

where  $M$  is anchovy wet mass ( $\sim 9 \text{ g}$  in the present study).

The effect of fish size on the cost of swimming can be modeled by expressing speed relative to length so that the cost of swimming at the normalized speed is the same for any size of fish. The cost of swimming in sockeye salmon *Oncorhynchus nerka*, obtained by subtracting standard metabolism from total metabolism of 8–54 cm salmon swimming at speeds of 13–143 cm/s (Brett 1965), can be accurately described by a power function of the Reynolds number (Wu and Yates 1978). The Reynolds number combines fish length, speed, and kinematic viscosity. A similar way of expressing this relationship, which matches Brett's (1965) results (at 15°C) extremely closely, is

$$Q_V = 8.7934 \left[ \frac{V}{L^{0.64}} \right]^{1.71} \text{ mg O}_2 \cdot \text{kg}^{-1} \cdot \text{h}^{-1}. \quad (12)$$

Thus, for different sizes of sockeye salmon, the cost of swimming is the same when speed ( $V$ ) divided by fish length ( $L$  in cm) to the 0.64 power is the same. This relationship is also reflected in length exponents (0.5–0.7) for endurance speed in fishes (Bainbridge 1962, Hunter 1971). Note that dividing  $V$  by  $L$  (body lengths/second) does not normalize speed with respect to swimming cost or endurance. For anchovy, the present study assumed that the length exponent for normalized speed was 0.6. Then, from Equation (10)

$$Q_V = 0.095 \left[ \frac{V}{L^{0.6}} \right]^{1.44} \text{ cal} \cdot \text{g}^{-1} \cdot \text{h}^{-1}, \quad (13)$$

and the cost of swimming in anchovy can be estimated for any size and swimming speed.

**Effect of temperature** Anchovy metabolic rates were estimated at only one temperature (17°C) in the present study, but the effect of temperature on engraulid anchovy metabolism was estimated for Peruvian anchoveta (Villavicencio 1981) at 14–20°C. These data indicated an increase of 78% in total respiration rate over a change of 6°C. Applying this intensity of temperature effect to the model would amount to

$$Q' = 2.046 Q e^{0.0959 T} \text{ (in any units)}, \quad (14)$$

where  $Q$  is the metabolic rate (in any units) at 17°C, and  $T$  is the ambient temperature (°C). However, short-term temperature acclimation periods in the laboratory (Villavicencio 1981) may result in greater metabolic rate changes than in the long term in nature. Estimates from Equation (14) should be viewed skeptically, until better estimates of the effect of temperature on anchovy metabolism can be found.

### Evaluation of the model

Estimates of maintenance metabolism ( $Q_M = Q_0 + Q_V$ ) from the model (Equations 11 and 13) for 4, 10, and 25 g northern anchovy at 17°C were compared with other data on engraulids (Fig. 5), assuming an oxygen equivalent of 3.24 cal/mg  $\text{O}_2$  (Elliott and Davison 1975). Oxygen consumption of northern anchovy swimming at about 9 cm/s in an annular respirometer was 0.38 mg  $\text{O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$  (Kaupp et al. unpubl. data). The rate of energy loss in fasting northern anchovy swimming in a flume at about 9 cm/s was 29.3  $\text{cal} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$  or 0.34 mg  $\text{O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$  (Kaupp et al. unpubl. data, energy loss multiplied by 0.9, the metabolizable fraction). These data were about twice as high as the tunnel respirometry data on anchoveta (Villavicencio 1981) swimming at 9 cm/s (Fig. 5). The model

predicts metabolic rates in the middle of this range, indicating that it may provide reasonable estimates for engraulid metabolism.

To use the model to estimate ration, the energy required for standard metabolism (Equation 11) and the cost of swimming (Equation 13 converted to  $\text{cal} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$ ) plus the energy needed for growth or reproduction, are multiplied by 1/0.65 (from Equation 6) to account for X, I, and SDA. The result is the daily food energy requirement. Similarly, 65% of food energy minus standard and swimming metabolism gives the surplus available for growth and reproduction at that level of food intake and activity.

Hunter and Leong (1981) estimated the food energy requirements of 1-year-old anchovy (wet mass 10.3 g, length 10.3 cm) at  $33.8 \text{ cal} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$  (copepods at 4% of wet mass/day). According to the model in the present study, X, I, and SDA remove  $11.8 \text{ cal} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$ , and standard metabolism (Equation 11) is  $11.8 \text{ cal} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$ . Supposing 1-year-old anchovy swim at 12 cm/s for 12 hours each day, this costs  $0.45 \text{ cal} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$  (Equation 13), or 5.4 cal/g. If they swim at 2 cm/s for the other 12 hours, this costs another 0.4 cal/g, making the total swimming cost  $5.8 \text{ cal} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$ . Subtracting all these costs from the ration energy leaves  $4.4 \text{ cal} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$ , which Hunter and Leong (1981) estimated to be enough for normal growth plus 20 spawnings per year.

Is this level of swimming activity realistic? Using sonar tracking and Doppler shift analysis, Holliday (1977) measured a relatively uniform swimming speed averaging 45 cm/s over a 40-minute interval for what were thought to be northern anchovy about 14 cm long (25 g). To swim for 12 hours a day at this speed, while maintaining normal growth and spawning 20 times per year, 3-year-old anchovy (Hunter and Leong 1981) would require a ration of 7.7% of body weight per day. However, 3 hours a day at this speed, with the rest of the day at 3 cm/s, would allow for the same growth and reproduction on a ration of only 4%.

It appears that anchovy growth rates in nature and the estimate of spawning 20 times per year (Hunter and Leong 1981) are consistent with the current study's model predictions for anchovy swimming at speeds and consuming rations similar to those observed in nature. Three aspects of the model were determined by experiment: (1) A constant proportion of food energy is available for metabolism and growth, (2) metabolism increases with swimming speed, and (3) gross energy conversion efficiency is a function of ration level and activity. The model should be useful in estimating the effect of changing food abundance on spawning frequency and growth, particularly as more measurements of activity become available.

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