FEEDING ECOLOGY AND GROWTH ENERGETICS OF LARVAL NORTHERN ANCHOVY, *ENGRAULIS MORDAX*

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ABSTRACT

The relation between prey consumption and gross growth efficiency was determined for first-feeding northern anchovy, *Engraulis mordax*, fed rotifers for 2 weeks. Larval length- and weight-specific daily consumption, given as prey numbers, dry weight, and caloric value, were less for the 2/mL rotifer diet and gut residence time was longer, resulting in a higher gross growth efficiency (0.46) than the 25/mL rotifer diet (0.37). Daily percent increases in dry weight for northern anchovy fed rotifers were 15% at the low density and 21% at the high density. Northern anchovy grew the most, 23% per day, when fed 2/mL copepods, but their length-specific weight was less than those fed on the rotifer diets. Equations for the rotifer and copepod diets are given for calculating growth in length and weight, size-specific stomach contents related to feeding period, and daily food consumption based on empirically determined gastric evacuation rates. Respiration was measured directly and indirectly, by using a starvation analysis to measure the caloric equivalent of metabolism; results from both methods agreed. A power equation was used to express metabolism as a function of dry weight. Estimates of gross growth efficiencies showed that larval northern anchovy may exhibit a high growth rate or a high efficiency, but not both at the same time. Information also is given on increase in size of prey selected as northern anchovy larvae grow.

Measurements of gross-growth efficiency (calories of growth/calories consumed) of fishes are a good indicator of the adequacy of their diet and state of health (Brett and Groves 1979). Generally a favorable environment for larval fish growth can be inferred by using information on growth efficiencies as related to prey densities. A high-growth efficiency is the result of efficient assimilation of food energy for growth, with relatively little energy lost as feces or used in respiration.

A wealth of information is available on larval northern anchovy, *Engraulis mordax*. Research has been directed toward understanding the factors that affect their survival, yet no information exists on the growth efficiency of larval northern anchovy.

Larval northern anchovy have been cultured in the laboratory, and their growth and survival on wild plankton (Kramer and Zweifel 1970; O'Connell and Raymond 1970) and on cultured foods (Lasker et al. 1970; Theilacker and McMaster 1971; Hunter 1976) have been described and compared with their growth in the field (Methot and Kramer 1979). Incubation times, yolk absorption and the onset of feeding (Lasker 1964; Lasker et al. 1970), feeding success and swimming behavior (Hunter 1972) and their ability to withstand starvation (Hunter 1976; Theilacker and Dorsey 1980) have been studied. Here I describe how variations in prey density affect consumption, growth, and gross growth efficiencies and compare my results to those on other larval fishes.

MATERIALS AND METHODS

The rationale for my experimental design was to avoid known problems that affect interpretation of results of energetic studies. Mainly I determined gut contents directly, which gives a measure of individual variability, rather than by controlling prey level in the tank and estimating feeding by difference in prey numbers over time. To obtain more precise fresh dry weight values for these small larvae, I grouped them by size class to increase the measured weight. I converted the number of prey eaten to width-specific and species-specific fresh dry weights and caloric values, thus precluding problems inherent with feeding rate estimations that use preserved sample weights and/or average prey weights. Because gastric evacuation depends on feeding rates, I conducted the evacuation experiments with actively feeding larvae. In addition, I compared and validated traditional oxygen uptake measurements with a starvation analysis used to estimate the caloric equivalent of metabolism.

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Larval Rearing

Northern anchovy eggs were spawned by administering hormone injections to a brood stock held at the Southwest Fisheries Center (Leong 1971). Larvae raised from the eggs were kept in 100 L circular, black polypropylene tanks at constant temperature (15.5°C) and photoperiod (12 h/12 h). In this study, I varied the prey type and density. At the onset of feeding, northern anchovy larvae have small mouths that restrict their feeding to small prey (Hunter 1977). Thus for the initial feeding (day 3) all larvae were fed *Gymnodinium splendens*, a naked dinoflagellate having a width of about 50 μm (Lasker et al. 1970), and 2 days later the larvae were fed larger prey. Because it is impossible to quantify the caloric input from *Gymnodinium* directly (digested cells cannot be counted), the experiments began on day 5 when the larger prey could be removed from the fish stomachs, counted, measured, and subsequently expressed as caloric input.

Experimental Design

I conducted five experiments. In the first experiment, rotifers, *Brachionus plicatilis*, at a density of 35/mL were fed for 20 days, and the number of prey eaten was determined. The size of the rotifers was not measured in this initial experiment, but in subsequent experiments, widths of prey eaten were measured. In the second and third experiments, rotifers were offered at densities of 2 and 25/mL respectively for 14 days. In the fourth experiment, copepods, *Tigriopus californicus*, nauplii and copepodites were fed to larvae at a density of 2/mL (usually 1 nauplius and 1 copepodite/mL) for only 9 days instead of 14 days because of problems with the copepod culture. In the fifth experiment, larvae were fed copepods at 0.2/mL for 12 days without the initial addition of *Gymnodinium*. (Mortalities were high on this low density copepod diet, and data are few; high mortalities are consistent with results reported by O'Connell and Raymond [1970] for northern anchovy raised on a similar diet. The addition of a *Chlorella* bloom to this diet improves survival of northern anchovy [Moffatt 1981].)

To estimate larval growth as the increase in standard length, SL, and dry weight, W, larvae were pipetted individually onto a slide and measured while alive. Larvae were then rinsed in distilled water and, to ensure dependable mean dry weight determinations, grouped by size class onto a clean slide. Larvae <5 mm were grouped by 0.2 mm size class, and those >5 mm were grouped by 0.3 mm size class. Numbers of larvae per group ranged between 2 and 12; the larger the larval weight, the fewer larvae I grouped together. After drying to a constant weight at 60°C (Lovegrove 1966), larvae were removed from the slides by using a single-edged razor blade and weighed on a Cahn electrobalance to ±2 μg.

Feeding

To estimate feeding rates and daily consumption, each prey item removed from the larva's gut was counted and its width measured. Width is the dimension that limits a fish larva's selection of prey (Beyer 1980; Hunter 1981). Prey defecated onto the slide were included in the total number eaten. Gut contents in dry weight were determined by summing the width-specific weights of the prey eaten each day. I used the width-specific fresh dry weights and caloric values for *Brachionus* and *Tigriopus* given by Theilacker and Kimball (1984) and reproduced here in Table 1.

Because northern anchovy larvae eat continuously, asymptotic curves ($c = C_{max} \times (1 - e^{-kt})$) were used to describe food intake, i.e., the relation between observed gut contents c and time t, where C_{max} is the asymptotic gut contents (contents in gut at steady state after filling) and k is the instantaneous rate of gut filling. Using Marquardt's algorithm for fitting nonlinear models, parameters C_{max} and k were estimated for 0.5 mm length classes (Table 2). Fish with empty stomachs were included in this analysis because all fish were used in the growth estimates. Daily mean gut contents $\bar{c}$ were calculated by integrating the area beneath

TABLE 1.—Width-specific dry weight and caloric value of rotifers, *Brachionus plicatilis*, and copepods, *Tigriopus californicus*[1].

Prey	Width class μm	Per individual: Dry weight μg (SE)	Per individual: Volume × 10^6 μm	Per individual: Caloric value × 10^{-3} cal
Brachionus plicatilis (4.4 cal/mg)				
Rotifers	74.3-109.7	0.10 (0.01)	0.65	0.44
	109.8-146.7	0.22 (0.04)	1.73	0.97
	146.8-183.8	0.41 (0.06)	2.96	1.80
	183.9-195.0	0.47 (0.08)	3.99	2.07
Tigriopus californicus (4.9 cal/mg)				
Nauplii	74.3-109.7	0.04 (0.01)	0.20	0.20
	109.8-146.7	0.13 (0.01)	0.55	0.64
	146.8-183.8	0.25 (0.01)	1.17	1.23
	183.9-195.0	0.38 (0.00)	1.77	1.86
Copepodites	146.8-183.8	0.63 (0.15)	3.38	3.09
	183.9-221.0	1.20 (0.26)	6.21	5.88

[1]From Theilacker and Kimball 1984, table 2.

TABLE 2.—Estimates of the asymptotic gut contents (C_{max}) and instantaneous rate of gut filling (k) for northern anchovy (n) fed several diets[1].

Diet	Prey level per mL	SL (mm)	n	Prey number C_{max}	Prey number k	Prey weight µg C_{max}	Prey weight µg k
Rotifers[2]	35	4.00	89	6.16	0.33		
		5.00	236	9.90	0.32		
		6.00	131	11.91	1.13		
		7.00	219	15.92	3.73		
		8.00	159	28.33	3.78		
		9.00	171	46.36	2.56		
		10.00	89	52.22	1.72		
Rotifers	25	4.25	58	[3]15.55	0.12	1.80	0.29
		4.75	69	7.79	0.67	2.12	0.67
		5.25	54	12.93	0.62	2.36	0.83
		5.75	35	14.01	0.64	2.92	0.58
		6.50	28	16.97	1.96	3.31	3.76
		8.00	32	27.80	1.84	6.68	1.61
Rotifers	2	4.25	33	7.44	0.35	0.50	0.18
		4.75	19	4.97	1.61	1.35	0.98
		5.25	18	8.86	1.29	2.42	0.73
		8.00	16	9.94	1.30	4.00	0.88
Copepods[4]	2	4.25	21	1.54	1.27	0.08	0.49
		4.75	63	4.89	0.42	0.52	0.37
		5.25	44	4.45	0.45	0.94	0.57
		5.75	32	3.86	0.41	1.15	1.49
		[5]6.25	31	4.94	1.01	1.99	0.88
		8.00	14	7.22	1.30	3.66	0.66

[1]Includes zero gut contents; observed gut contents c at time t = $C_{max} \times (1 - e^{-kt})$.
[2]Prey width not measured.
[3]87% rotifers <150 µm width.
[4]Fish eating *Gymnodinium* exclusively were removed to estimate C_{max} and k.
[5]Copepod concentration <0.1/mL.

the curves and dividing by the 12-h feeding period.

Equations were derived for each diet from the relation of C_{max} and k with fish size and duration of feeding; these equations allow the calculation of gut contents c at time t for all fish lengths between 4 and 8 mm. The parameters (Table 3) were found using the derivative-free nonlinear regression program (BMDPAR) by Biomedical Computer Programs (BMDP, 1981).

Daily consumption F_w was estimated using a modification of an equation for consumption developed by Stauffer (1973) and discussed by Elliott and Persson (1978) and Jobling (1981), $F_w = rt + C_{12}$, where r is the µg evacuated per hour calculated as mean gut contents $\bar{c}$ divided by the empirically determined rate of gastric evacuation (see Evacuation Rates), t is the duration of feeding, and C_{12} is the dry weight of the food remaining in the stomach at the end of the 12-h feeding period.

Growth

Length data for all feeding treatments were fit to exponential growth curves, SL = $l_0 e^{kt}$ where l_0 is length at hatching, k is the instantaneous growth rate and t is the age. Length-weight data were fit to a power equation where weight $W = a(\mathrm{SL})^b$; parameters for the growth equations are given in Table 4.

TABLE 3.—Parameters for equation[1] relating observed gut contents c in µ g dry weight at time t to standard length (SL) of northern anchovy fed three diets.

Diet	Age	n	P_1	(SD)	P_2	(SD)	P_3	(SD)	P_4	(SD)
Rotifers										
25/mL	5-14	280	−1.90	(0.70)	0.51	(0.18)	0.57	(0.16)	0.29	(0.03)
2/mL	5-14	103	—	—	[2]0.69	—	0.33	—	0.326	—
Copepods										
2/mL	5-9	171	2.84	(0.88)	−0.39	(0.12)	[3]1.26	[3](0.75)	1.18	(0.10)

[1]$c = p_3 e^{p_4 \mathrm{SL}(1 - e^{-(p_1 + p_2 \cdot \mathrm{SL})t})}$.
[2](P_1 + P_2) fixed at 0.69, the mean k from Table 2; asymptotic standard deviations could not be computed because k was held constant.
[3]× 10^{-3}.

TABLE 4.—Parameters for northern anchovy growth equations where SL is standard length in mm, W is weight in µg, and t is age in days.

Diet	Age (d)	Age length $\mathrm{SL} = l_0 e^{kt}$ n	l_0	(SD)	k	(SD)	Length-weight $W = a(\mathrm{SL})^b$ n	a	(SD)	b	(SD)
Rotifers											
25/mL	5-14	280	3.06	0.05	0.06	0.001	253	0.197	0.040	3.16	0.11
2/mL	5-14	103	3.14	0.07	0.05	0.002	84	0.379	0.030	2.80	0.04
Copepods											
2/mL	5-9	138	3.06	0.15	0.07	0.010	109	0.297	0.097	2.88	0.20

Metabolism

I determined metabolic rates for the larvae, which ranged in age from first-feeding (3 days after hatching) to 25 days using the Winkler technique. I chose the Winkler technique where large vessel volumes could be used and there was no need to shake the vessels during the experiment, as required for manometric techniques. Pearcy et al. (1969) found no differences between Winkler and Warburg estimates of oxygen consumption. Oxygen consumption was estimated at 16°C during 18-23 h experimental periods with a 12 h light-dark cycle. The respiration vessels were attached to a large, slowly rotating wheel. Young larvae, 0.02-0.14 mg dry weight were tested in 40 mL vessels in groups of 10-50, while larvae older than 16 days (larger than 0.14 mg) were tested individually in 60-150 mL vessels. All fish tested had empty guts. Data were not used when mortalities occurred during the experiment.

To express metabolism (Q) as a function of dry weight, I used a nonlinear regression to fit a power equation to the data (see parameters for Model 1 in Table 5). The data points were weighted by their sample size (n = 10-50). The Model 1 fit was unsatisfactory for the whole size range, presumably because each data point for the young larvae (n = 72) was a group mean, and the model was significantly weighted toward the young larvae, causing it to overestimate oxygen consumption for the few large larvae (n = 17). Because the experimental technique differed (i.e., respiration was measured for groups of young larvae or individual older larvae), I also fitted two separate curves. These curves (Model 2) gave a good fit to the data (Table 5); the Model 2 equation for younger larvae was used in the present study.

An alternate approach for estimating metabolic requirements is to starve larvae of known size (weight), determine the size-specific weight loss, and convert the weight loss to calories. This approach eliminates the need to restrict larval swimming activity in a respiration vessel. Presumably the weight loss in caloric units would equal the loss due to metabolic costs, excluding the metabolic cost of attacking prey. Using this approach, I fed control northern anchovy larvae ad libitum on *Gymnodinium* and *Brachionus* and starved the test larvae; both groups were maintained in 100 L rearing tanks at 15.5°C. Live standard length and dry weight of groups of the same length were measured daily, as described earlier in this Methods section, for 10-50 larvae sampled daily from each treatment.

I calculated the caloric equivalent of northern anchovy tissue using the caloric values given by Hunter and Leong (1981) for fat-free anchovy tissue, 4.129 cal/mg, and for anchovy lipid, 9.227 cal/mg. For example, northern anchovy larvae weighing 25 μg contained 6 μg of lipid (unpubl. data: John Hakanson, UCSD, Scripps Institution of Oceanography); using the above caloric equivalents for 19 μg of fat-free tissue and 6 μg of lipid yields 5.36 cal/mg as the energy equivalent of anchovy tissue. In a 20-d laboratory experiment, Hakanson found that lipid weight appeared to increase proportionally with anchovy weight, thus the caloric content of anchovy tissue would be approximately constant for the age range studied. Lipid content seems to be lower in older northern anchovy larvae. The only other information I found was for 40-60 d-old northern anchovy where the caloric content averaged 4.9 cal/mg (unpubl. data: John Hunter, Southwest Fisheries Center). I used 5.4 cal/mg as the caloric value of anchovy tissue for larvae between 5 and 14 days of age.

TABLE 5.—Parameters for equation $Q = aw^b$ where Q is metabolic rate in μL O_2/h for northern anchovy and w is their fresh dry weight.

Model	N	Size group (mg dry wt) w	Parameters a(SE)	b(SE)
1	89	0.02-2.70	[1]3.844 ± 0.100	0.858 ± 0.029
2	72	0.02-0.14	2.897 ± 0.344	0.834 ± 0.057
2	17	0.14-2.70	4.269 ± 0.325	0.697 ± 0.107

[1]The sum of the residuals in Model 1 does not equal zero, thus the program calculation of SE's is biased.

Evacuation

Gut clearance times were determined for actively feeding fish of various ages fed the rotifer and copepods diets. Larvae were transferred from the 100 L rearing tank to a 10 L test tank. Because northern anchovy larvae are sensitive to handling, handling was restricted to one transfer. Transferred larvae were kept in the test tank for 18 hours prior to an evacuation experiment because injured larvae usually die within 8-10 hours after transfer. First, larvae were fed a low concentration of prey that had been dyed with National Fast Blue (Laurence 1971). After larvae had filled their guts, eating most of the dyed prey, a known density of undyed prey was added. Larvae were sampled at 5-min intervals, and the time required for them to void their guts of the dyed prey was determined. The number of prey in the full guts was counted and converted to dry weight. Evacuation rates are given as μg prey cleared through the gut per hour. Rates were related to fish size and to prey type.

The timing of the second prey addition was not critical for determining gut clearance rates at high prey densities. But when the timing was not correct for the tests that used low prey concentrations, deciphering the meaning of the gut contents was problematical. Results from most of these low-density tests could not be used.

A series of evacuation experiments also was conducted with nonfeeding northern anchovy that were removed from their food source, rotifers, to filtered seawater.

To reduce the incidence of injury during transfer, I constructed a cylindrical, clear plastic container (15 mm high and 7 mm diameter) with handle and a removable bottom grooved to fit the circumference of the cylinder. Larvae to be transferred were surrounded by the cylinder, and then the bottom was fitted onto the cylinder. The container with fish was transferred and lowered into the test tank. Removing the bottom and slowly raising the cylinder released the fish. Prey that were transferred into the experimental tank with the larvae were removed by an air-lift pump that slowly recirculated water and was screened to prevent the removal of larvae (O'Connell and Paloma 1981).

Growth Efficiency

To determine growth efficiencies, I used the information on growth (Table 4), daily food consumption estimated from the general equations (Table 3) and evacuation rates of 1.15 hours for the high-density rotifer diet and 1.5 hours for the low-density diet. Gross growth efficiency was estimated based on dry weight and on caloric estimates. It is the ratio of growth to ingestion. To estimate assimilation efficiency, I used the information on weight-specific metabolic rates and simply combined the energy of metabolism and growth and divided it by the energy consumed. Assimilated energy lost as feces and urine was not accounted for.

RESULTS

Feeding

Sizes of prey fed to larval northern anchovy in these experiments ranged from 50 μm for *Gymnodinium*, to 74-195 μm for rotifers and copepod nauplii, and 147-221 μm for copepodites. In contrast to larvae fed the rotifer diets, fish offered the copepod diet did not switch from eating *Gymnodinium* at first feeding on day 3 to eating larger prey on day 5. All fish fed copepods and sampled on day 5 contained *Gymnodinium* in their gut, and 96% of these guts were full of *Gymnodinium* (Table 6). By day 7, the number of copepod-fed northern anchovy eating *Gymnodinium* had decreased to 80%, with 10% full. These data reveal that young northern anchovy were unsuccessful at capturing *Tigriopus* nauplii at 1/mL until 7-8 days of age, and because of this behavior and the failure of the copepod culture on day 9, I was unable to quantify daily consumption for northern anchovy fed copepods.

Northern anchovy reared on the low-density (2/mL) and high-density (25/mL) rotifer diets ate only a few *Gymnodinium* cells after day 4. Between rotifer treatments, incidence of feeding on *Gymnodinium* after day 4 was higher for fish fed the low-density diet (Table 6). On day 5, northern anchovy concentrated on eating rotifers in the 75-150 μm size range; between 84 and 97% of the rotifers eaten by larvae sampled from both rotifer treatments were <150 μm width (Table 7). Only 7% of the rotifers available to these larvae were smaller than 150 μm width. Hence on day 5 larvae were selecting small rotifers in higher proportions than were available; in the two treatments, the apparent density of roti-

TABLE 6.—Presence of *Gymnodinium* in guts of larval northern anchovy related to age of larvae and to diet.

	Diets								
	Rotifers 25/mL[1]			Rotifers 2/mL[2]			Copepods 2/mL[3]		
Age (d)	*n*	Incidence (%)[4]	Gut full (%)[5]	*n*	Incidence (%)[4]	Gut full (%)[5]	*n*	Incidence (%)[4]	Gut full (%)[5]
5	21	48	0	29	83	0	27	100	96
6	82	59	0	11	9	0	57	77	16
7	10	10	0	5	0	0	49	80	10
8	75	9	0	0	—	—	5	0	0
9	27	7	0	38	6	0	33	0	0

[1]Apparent density of rotifers <150 μm = 2/mL.
[2]Apparent density of rotifers <150 μm = 0.1/mL.
[3]Apparent density of nauplii <150 μm = 1/mL.
[4]Percent of larvae having *Gymnodinium* cells in guts with rotifers or copepods.
[5]Percent of larvae having guts full with *Gymnodinium* cells.

TABLE 7.—Width frequency of prey eaten by northern anchovy (n) related to their diets and to their age and size.

Age (d)	Rotifers 25/mL[1] Prey composition (%)			Rotifers 2/mL[2] Prey composition (%)			Copepods 2/mL[3] Prey composition (%)		
	n	<150 μm	>150 μm	n	<150 μm	>150 μm	n	<150 μm	>150 μm
5	21	83.5	16.5	29	97.3	2.7	27	88.0	12.0
6	82	11.0	89.0	11	75.0	25.0	57	60.0	40.0
7	10	5.2	94.8	5	38.7	61.3	49	59.0	41.0
8	75	33.1	66.9	0	—	—	5	33.4	56.6
9	27	40.9	59.1	38	12.2	87.8	33	31.8	68.2
Length (mm)									
4.1-4.5	60	49.7	50.3	37	91.4	8.6	21	80.0	20.0
4.6-5.0	77	25.7	74.3	20	23.4	76.6	69	68.3	13.7
5.1-5.5	55	43.9	56.1	23	15.1	84.9	45	57.3	42.7
5.6-6.0	35	36.6	63.4	9	11.8	88.2	30	40.0	60.0
6.1-6.5	23	38.2	61.8	0	—	—	17	36.4	63.6

[1]Apparent density of prey <150 μm = 2/mL.
[2]Apparent density of prey <150 μm = 0.1/mL.
[3]Apparent density of prey <150 μm = 1/mL.

fers <150 μm was equivalent to about 2 and 0.1/mL. In sum, the larvae switched to eating prey >150 μm on day 6 in the high-density rotifer treatment, day 7 in the low-density treatment, and day 8 in the copepod treatment (Table 7). If the analysis is based on larval size instead of larval age, selection for prey >150 μm occurs at 4.6-5.0 mm for northern anchovy fed the rotifer diets and at 5.6-6.0 mm for those fed the copepod diet (Table 7; Fig. 1).

Feeding intensity was highly variable on all diets. The observed stomach contents can differ by as much as a factor of three (Fig. 2) from the predicted stomach contents (C_{max}) used in the feeding models.

At high rotifer densities, northern anchovy filled their guts at a faster rate and consumed more. On average, fish eating the high-density rotifer diet were full within 2 hours, while those eating a low-density diet were full in about 3 hours. Comparing the average observed stomach contents, and excluding empty stomachs, for fish of equal age shows that all larvae eating at the high prey density ate more than their counterparts eating at lower prey densities (Table 8).

Growth

Hunter (1976) showed that the length-weight rela-

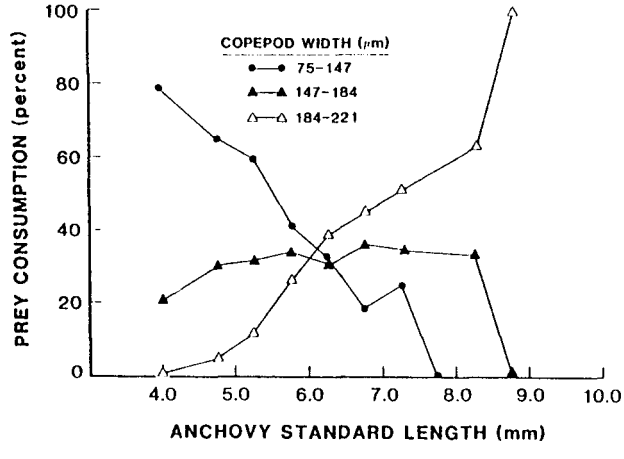

FIGURE 1.—Size of copepod prey eaten by northern anchovy related to fish size. See Table 1 for copepod width classes.

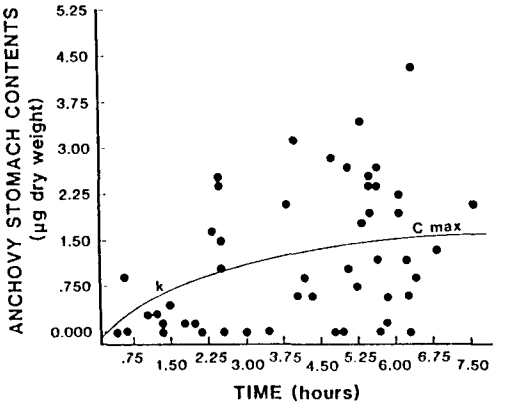

FIGURE 2.—Observed stomach contents of 4.0-4.5 mm northern anchovy fed 25 rotifers/mL, predicted rate of gut filling k and predicted maximum gut content C_{max}. Each point is one larva.

TABLE 8.—Mean dry weight of food (µg) observed in stomachs[1] of northern anchovy (n) related to their age.

Age (d)	Rotifers 25/mL		Rotifers 2/mL		Copepods 2/mL		Copepods 0.2/mL	
	n	µg	n	µg	n	µg	n	µg
5	9	1.75	17	0.60	8	0.18		
6	57	2.23	4	0.27	39	0.55		
7	8	3.56	5	1.41	37	0.67		
8	51	2.10	—	—	3	0.87	1	0.08
9	26	2.99	27	2.60	31	1.88	6	0.78
10	—	—	—	—			9	1.51
11	6	3.60	—	—			9	0.42
12	22	5.14	4	[2]6.39			3	0.90

[1]Average stomach contents (excludes empty stomachs) calculated for t = >3 hours; 3 hours is a reasonable time for northern anchovy to fill guts eating at lowest prey densities tested (see text).
[2]Day 13.

tion for northern anchovy was curvilinear on a log-log plot, and he used a Laird Gompertz model to describe both growth in length and in weight over 75 days. Because I am describing only the first 2 weeks of growth, I used a simpler exponential model (Table 4) which probably should not be used for larvae beyond 2 weeks of age.

Larvae grew at 0.35 mm/day on the copepod diet (k = 0.07) and at 0.33 and 0.25 mm/day on the high- (k = 0.06) and low-density (k = 0.05) rotifer diets (Table 4). On the average, the dry weight of larval northern anchovy was proportional to length to the third power. Depending on diet, the length exponent ranged from 2.80 to 3.16 (Table 4).

Daily percent increases in dry weight for northern anchovy fed the rotifer diets were 15% for larvae fed 2/mL and 21% for larvae fed 25/mL. However, northern anchovy grew the most, 23% per day, on the 2/mL copepod diet. For the three diets tested, daily growth in dry weight as a percent was constant over the size range.

An analysis of covariance was used to test for diet-induced differences in the relation between natural logarithms of length and weight for larval northern anchovy between days 5 and 9 when prey concentrations were controlled. Larvae which fed on copepods were significantly longer and heavier at age than larvae eating rotifers. There were no length or weight differences at age 7 days between the two rotifer treatments (Table 9), but there were differences in growth thereafter. Larvae raised on the two rotifer diets were the same weight at 4.9 mm (30.75 and 33.25 µg; P = 0.3), but larvae raised on copepods weighed less at 4.9 mm (28.54 µg) than larvae fed on the rotifer diets (P = 0.11 and <0.01).

I compared the distribution of my northern anchovy dry weights at length for the rotifer and

TABLE 9.—Effect of diet on northern anchovy standard length (SL) and dry weight (W).

Diet	Density per mL	No. cases[1]	Age = 7 days $\bar{x}$ SL (mm)	$\bar{x}$ W (µg)	Probabilities = SL and = W 1 vs. 2 SL/W	1 vs. 3 SL/W	2 vs. 3 SL/W
1-Rotifers	25	34	4.78	28.36	0.20/0.71	0.00/0.00	0.00/0.00
2-Rotifers	2	14	4.61	27.33			
3-Copepods	2	28	5.28	35.11			

			SL = 4.9 mm $\bar{x}$ W (µg)	Probabilities 1 vs. 2	1 vs. 3	2 vs. 3
1-Rotifers	25	34	30.75	0.30	0.11	0.00
2-Rotifers	2	14	33.25			
3-Copepods	2	28	28.54			

[1]Case numbers contain 2-12 larvae depending on number in group that were weighed.

copepod diets with those in a study by Hunter (1976) where northern anchovy were fed *Brachionus*, 50-100/mL, and copepods, *Tisbe* 0.01/mL, at 17°C and *Gymnodinium* was fed as the first food. The curves show that among experiments there appear to be diet-induced differences in weight at length (Fig. 3).

Metabolism

The caloric equivalent of metabolism for northern anchovy larvae ranging in age from first feeding to 25 days was determined using the relation between the metabolic rate and fresh dry weight (Model 2, Table 5) and by converting the oxygen uptake to calories using an oxycalorific equivalent of 0.00463 cal/μL O_2 (Brett and Groves 1979). I assume the metabolic rate approximates "routine" metabolism.

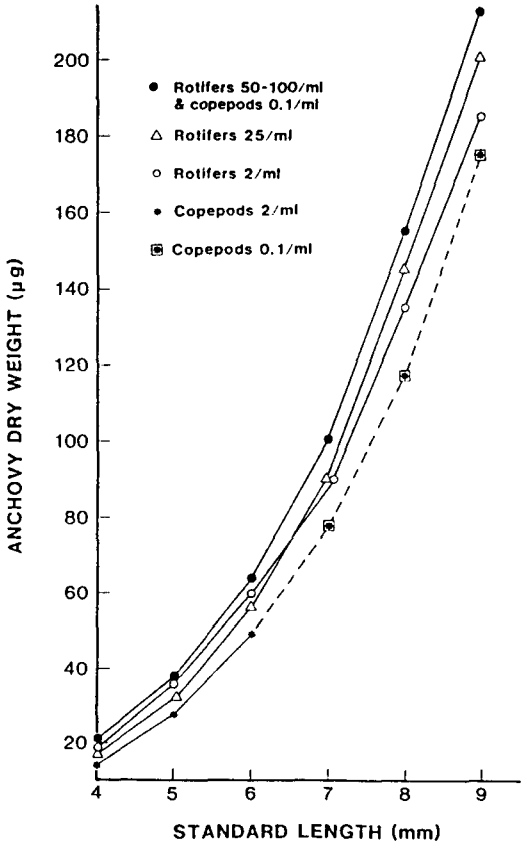

FIGURE 3.—Relation between dry weight and standard length for northern anchovy fed several diets where *Gymnodinium* was the first food.

I also determined the caloric equivalent of metabolism for first-feeding northern anchovy by starving them, determining the weight loss, and converting the loss to calories. Starving larvae lost an average of 10% of their body weight per day for 3 days, after which larvae must have continued to lose weight, but no decrease could be measured (Fig. 4). The time to maximum weight loss was 3-4 days, the time of irreversible starvation for northern anchovy from the onset of feeding (Lasker et al. 1970; Theilacker and Dorsey 1980). Larvae that weighed an average of 0.0211 mg at 3 days of age weighed an average of 0.0148 mg on day 6. The weight loss (0.0063 mg) × 5.4 cal/mg, which is the assumed caloric equivalent for northern anchovy tissue, equals 0.0339 calories, or a metabolic demand of 0.011 cal/day. This value, determined at a slightly lower temperature, corresponds well with the value obtained for first-feeding northern anchovy weighing 0.0211 mg using respiration measurements (0.013 cal/day).

Evacuation Rates

Gut clearance times for northern anchovy larvae appeared to be independent of larval age; however, the weight of food evacuated per hour increased with age because the stomach contents increased. Because the larvae fed at a constant rate after the gut was filled and defecated continuously, the gut clearance rate for actively feeding northern anchovy larvae was constant. The average gut clearance time for anchovy feeding on 25 rotifers/mL was 1.15 hours (SE = 0.13; range 0.7-1.5 hours; n = 6 tests). Reducing the prey density to 2/mL increased the average gut clearance time to 1.5 hours (range 1.2-1.8 hours; n = 2 tests) for the rotifer diet and 2.73 hours (SE = 0.26; range 2.0-3.3 hours; n = 4 tests) for the copepod diet.

Nonfeeding northern anchovy cleared their guts in 2.8-5.8 hours, depending on their size and stomach capacity (2.8 h/4.8 mm; 4 h/6.3 mm; 5 h/7.9 mm; 5.8 h/8.5 mm).

Daily Consumption of Rotifers and Growth Efficiency

Daily consumption was less on the low-density diet and, as a percent of body weight eaten per day, consumption ranged between 31 and 86%, depending on prey concentration and fish size (Tables 10, 11). For both rotifer diets, weight-specific consumption decreased with increasing body weight (Fig. 5).

Gross growth efficiencies were higher for north-

ern anchovy fed the low-density diet (Tables 10, 11). Mean gross-growth efficiency (days 5-14) based on dry weight was 0.30 for the high-density diet and 0.37 for the low-density diet. Based on calories, mean gross-growth efficiencies were 0.37 and 0.46 respectively.

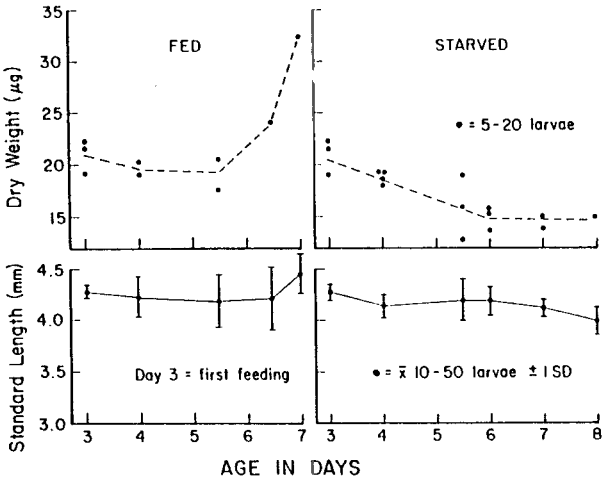

FIGURE 4.—Changes in standard length and weight of fed and starved northern anchovy larvae over time.

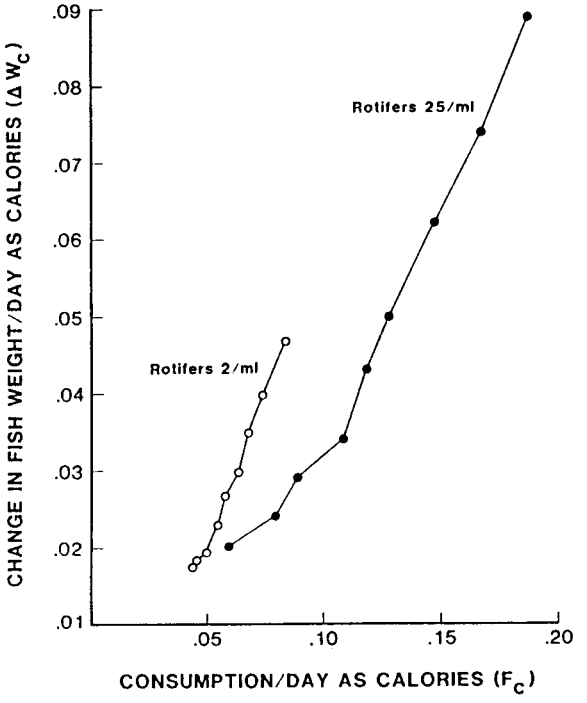

FIGURE 5.—Gross growth efficiencies (W_c/F_c; Tables 10, 11) of northern anchovy fed rotifers at 25/mL and at 2/mL.

TABLE 10.—Estimation of growth efficiency of larval northern anchovy fed rotifers at 25/mL.

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)	(14)	(15)	(16)
					Gut contents		Consumption									
Diet	Age (d)	Standard length (mm)	Dry weight (μg)	Gut clearance rate (μg/h)	Daily mean (μg)	Residual at end of feeding (μg)	Food (μg)	Body weight (%/d)	Calories (cal/d)	Metabolic rate (μL O_2/d)	Metabolic rate (cal/d)	Change in fish weight (μg/d)	Change in fish weight (cal/d)	Gross efficiency	Gross efficiency	Assimilation estimate
	A	l	W	r	$\bar{c}$	C_{12}	F_w	$F_{w/W}$	F_c		Q_m	ΔW	ΔW_c	$\Delta W/F_w$	$\Delta W_c/F_c$	P
Rotifers (25/mL)	5	4.13	17.41	1.03	1.19	1.73	14.14	81	0.06	2.36	0.010	3.71	0.020	0.26	0.33	50.2
	6	4.39	21.12	1.34	1.54	2.00	18.11	86	0.08	2.77	0.012	4.38	0.024	0.24	0.30	44.4
	7	4.66	25.50	1.58	1.82	2.19	21.14	83	0.09	3.24	0.014	5.35	0.029	0.25	0.32	47.5
	8	4.95	30.86	1.80	2.07	2.39	23.99	78	0.11	3.80	0.016	6.31	0.034	0.26	0.31	45.7
	9	5.25	37.17	2.03	2.33	2.61	26.97	73	0.12	4.44	0.019	7.89	0.043	0.29	0.36	51.3
	10	5.58	45.06	2.28	2.62	2.88	30.23	67	0.13	5.21	0.022	9.27	0.050	0.31	0.38	55.6
	11	5.92	54.33	2.55	2.94	3.17	33.82	62	0.15	6.09	0.026	11.48	0.062	0.34	0.41	58.7
	12	6.29	65.80	2.88	3.31	3.53	38.04	58	0.17	7.14	0.031	13.77	0.074	0.36	0.44	61.7
	13	6.68	79.57	3.25	3.74	3.96	42.94	54	0.19	8.37	0.036	16.48	0.089	0.38	0.47	65.7
	14	7.09	96.05	3.68	4.24	4.45	48.67	51	0.21	9.79	0.042					

[1]Hatching = Day 0.

[2]$l_t = 3.06\, e^{0.06t}$; live length.

[3]$W = 0.197\, l^{3.16}$ (on day consumption is estimated); fresh dry weight.

[4]$r = \bar{c}/1.15$ h (see text).

[5]$\bar{c} = \int_0^{12} C_{max}(1 - e^{-kt})/12 \cdot dt$.

[6]$C_{12} = C_{max}(1 - e^{-12k})$.

[7]$F_w = rt + C_{12}$; t = 12 h.

[8]$F_{w/W}$.

[9]$F_c = F_w \times 4.4$ cal/mg (see Table 1).

[10]μL O_2/d = 24 (2.879 $W^{0.834}$) (see Table 5).

[11]Q_m 0.00463 × μL O_2/d; (1 μL O_2 = 0.00463 cal) (see text).

[12]ΔW = weight gained 1 day after consumption estimated.

[13]$\Delta W_c = \Delta W \times 5.4$ cal/mg (caloric estimation for larva) (see text).

[14]$\Delta W/F_w$.

[15]$\Delta W_c/F_c$.

[16]$P = \dfrac{Q_m + \Delta W_c}{F_c}$.

TABLE 11.—Estimation of growth efficiency of larval northern anchovy fed rotifers at 2/mL.

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)	(14)	(15)	(16)
					Gut contents		Consumption									
Diet	Age (d)	Standard length (mm)	Dry weight (μg)	Gut clearance rate (μg/h)	Daily mean (μg)	Residual at end of feeding (μg)	Food (μg)	Body weight (%/d)	Calories (cal/d)	Metabolic rate (μL O_2/d)	Metabolic rate (cal/d)	Change in fish weight (μg/d)	Change in fish weight (cal/d)	Gross efficiency	Gross efficiency	Assimilation estimate
	A	l	W	r	$\bar{c}$	C_{12}	F_w	$F_{w/W}$	F_c		Q_m	ΔW	ΔW_c	$\Delta W/F_w$	$\Delta W_c/F_c$	P
Rotifers (2/mL)	5	4.03	18.77	0.72	1.08	1.23	9.87	53	0.043	2.50	0.012	2.87	0.015	0.29	0.35	67.3
	6	4.24	21.64	0.76	1.15	1.31	10.51	49	0.046	2.83	0.013	3.29	0.018	0.31	0.39	66.6
	7	4.46	24.93	0.83	1.24	1.41	11.33	45	0.050	3.18	0.015	3.60	0.019	0.32	0.38	68.4
	8	4.68	28.53	0.89	1.33	1.52	12.16	43	0.054	3.56	0.016	4.29	0.023	0.35	0.43	74.0
	9	4.92	32.82	0.96	1.44	1.64	13.16	40	0.058	4.00	0.019	5.09	0.027	0.39	0.47	79.3
	10	5.18	37.19	1.05	1.57	1.79	14.35	38	0.063	4.51	0.021	5.57	0.030	0.39	0.48	80.6
	11	5.44	43.48	1.14	1.71	1.94	15.62	36	0.069	5.06	0.023	6.56	0.035	0.42	0.51	85.5
	12	5.72	50.04	1.25	1.87	2.13	17.09	34	0.075	5.68	0.026	7.44	0.040	0.44	0.53	88.3
	13	6.01	57.48	1.37	2.06	2.34	18.82	33	0.083	6.38	0.030	8.69	0.047	0.46	0.57	92.2
	14	6.32	66.17	1.52	2.28	2.59	20.83	31	0.092	7.18	0.033					

[1]Hatching = Day 0.

[2]$l_t = 3.14\ e^{0.05\,t}$; live length.

[3]$W = 0.379\ l^{2.90}$ (on day consumption is estimated); fresh dry weight.

[4]$r = \bar{c}/1.5$ h (see text).

[5]$\bar{c} = \int_0^{12} C_{max}\,(1 - e^{-kt})/12 \cdot dt$.

[6]$C_{12} = C_{max}\,(1 - e^{-12k})$.

[7]$F_w = rt + C_{12}$; t = 12 h.

[8]$F_{w/W}$.

[9]$F_c = F_w \times 4.4$ cal/mg (see Table 1).

[10]μL O_2/d = 24 (2.879 $W^{0.834}$) (see Table 5).

[11]Q_m 0.00463 × μL O_2/d; (1 μL O_2 = 0.00463 cal) (see text).

[12]ΔW = weight gained 1 day after consumption estimated.

[13]$\Delta W_c = \Delta W \times 5.4$ cal/mg (caloric estimation for larva) (see text).

[14]$\Delta W/F_w$.

[15]$\Delta W_c/F_c$.

[16]$P = \dfrac{Q_m + \Delta W_c}{F_c}$.

DISCUSSION

Larval northern anchovy feeding ecology was similar to other larval fishes (Laurence 1977; Haegler and Outran 1978; Werner and Blaxter 1980; Theilacker and Dorsey 1980; Blaxter and Hunter 1982; Eldridge et al. 1982; Houde and Schekter 1981, 1983). As the larval northern anchovy grew they selected increasing larger prey, and on the rotifer diets, their feeding and growth rates increased with increasing concentrations of prey. In addition to the growth response to different prey concentrations, I observed differences in growth due to prey type. Fish grew the fastest on the copepod diet where one-third fewer calories were available than were available in the high-density rotifer diet ($4 \times 10\text{-}2$ vs. $13 \times 10\text{-}2$ cal/mL for prey <150 μm).

Length at age obtained for the first 2 weeks by larvae raised on copepods agreed with previous studies where northern anchovy were fed copepods and *Gymnodinium* was the first food (Kramer and Zweifel 1970; Hunter 1976). However, the larvae raised on copepods did not put on as much weight per unit length as their counterparts fed rotifers and *Gymnodinium*. Between days 5 and 9, the faster growing, copepod-fed larvae had significantly lower size-specific weights, and the weight exponents estimated for the first 2 weeks were lower, 2.9, than for larvae feeding on the high-density rotifer diet, 3.2. Lasker et al. (1970) found an exponent of 3.3 for northern anchovy fed on a high-density veliger and *Gymnodinium* diet.

These weight exponents estimated for northern anchovy are lower than the exponents of about 4 reported for deep-bodied fish larvae (haddock, flounder, cod, and scup; Laurence 1979). Likewise the exponents obtained for Atlantic herring ranged between 3.8 and 4.7 (reviewed by Checkley 1984). Weights of fishes used to estimate the exponents in the other laboratory studies ranged between 20 and 10,000 μg, whereas the northern anchovy weights ranged between 20 and 100 μg. Differences in growth rates occur as larval fish grow (Zweifel and Lasker 1976), and length-weight relations may change over the size range. Additionally, larval morphology is an obvious important component in the length-weight relation, and experimental variables may further complicate the relation. Moksness (1982) reported a low weight exponent of 2.6 for capelin, *Mallotus villosus*, from the field and from a large rearing basin. Both Atlantic herring and capelin larvae are similar in morphology to northern anchovy.

In previous laboratory feeding studies of larval northern anchovy, percent of body weight eaten per day was usually higher than consumption rates, 31-86%, I estimated. Reported values were 126-144% for northern anchovy (Hunter 1972), 197-440% for bigeye anchovy (Chitty 1981), and 20-295% for bay anchovy (Houde and Schekter 1981). Consumption varies with prey concentration and temperature, and the differences may be due to the experimental conditions. In the other studies, temperatures were higher and food concentrations were both lower and higher, with some including *Chlorella* blooms. However, it is likely that the differences are due to use of average food weights in the other studies. First-feeding northern anchovy larvae select small prey (Table 7; Fig. 1), and if average prey weight is larger than those actually being eaten by the larvae, their consumption may have been overestimated. For example, in Table 2, the average full stomach (C_{max}) of 4.25 mm fish (day 4-5) fed 25 rotifers/mL contained 15.55 rotifers while the average 4.75 mm fish (day 5-6) contained 7.79 rotifers. Using the width-specific weights (Table 1), I converted the 15 small rotifers to 1.8 μg and the 8 larger ones to 2.1 μg.

The exponent for the regression relating oxygen consumption to northern anchovy weight was 0.834 for larvae weighing <0.14 mg and 0.697 for larger larvae. Exponents have been reported for larval winter flounder, *Pseudopleuronectes americanus* (0.74; Laurence 1975); larval bay anchovy, *Anchoa mitchilli* (0.8; Houde and Schekter 1983); larval sea bream, *Archosargus rhomboidalis*, and larval lined sole, *Achirus lineatus* (0.838 and 0.942; Houde and Schekter 1983). Brett and Groves (1979) suggested a weight exponent of 0.86 for adult fish. There is considerable variation in respiration rates in the literature, probably depending on experimental conditions. The respiration rates given here for northern anchovy range between 3.1 and 6.9 μL/mg per hour for 0.02-2.7 mg larvae, and they are comparable to rates given for other fishes of similar age and size (reviewed by Theilacker and Dorsey 1980).

The evacuation rates determined here, 1.15-2.73 hours, for actively feeding northern anchovy larvae are comparable to rates of 1-3 hours estimated by Arthur (1976) for field samples. Particle residence time in the gut depended on prey density, prey type, and experimental design, e.g., feeding vs. nonfeeding larvae. Werner and Blaxter (1980) also showed that evacuation rates for herring fed *Artemia* were more rapid at higher prey densities, and because live and undigested prey were defecated, assimilation must have been low at these high prey densities.

Northern anchovy larvae, like herring, are con-

tinuous feeders, and at the high prey concentration, high consumption rates reduced the gut residence time and decreased digestion (assimilation; Tables 10, 11). At the lower prey concentration, the slower digestion time and increase in assimilation was not sufficient to compensate for the reduced consumption, and daily increase in weight, 15%, was less than the weight increase on the high-density diet, 21%. This result is similar to that in the recent study on assimilation by Pacific herring larvae fed *Brachionus* and *Artemia* (Boehlert and Yoklavich 1984). Using radioisotope tracers, Boehlert and Yoklavich found decreased assimilation at high food densities, but overall the larvae had a greater total energy gain at the high food densities because the higher food consumption more than compensated for the decreased assimilation.

Assimilation estimates, given here for northern anchovy larvae, fed two rotifer diets, averaged 53 and 79% and are somewhat higher than rates of 39-68%, depending on prey density, given by Boehlert and Yoklavich (1984) for Pacific herring. The assimilation estimates for northern anchovy larvae may not be reliable because the estimate assumes that weight-specific metabolic rates of fish fed both diets were equal. In addition, I made no attempt to correct for activity or to partition the portion of food assimilated into parts lost as feces and urine. Buckley and Dillman (1982) developed a technique to measure nitrogenous wastes of larval flounder. Assimilation efficiencies of 65-75% are commonly used in calculations of larval fish growth efficiencies (Ware 1975).

Estimates of gross growth efficiencies are not compromised by the above concerns. Larval northern anchovy gross-growth efficiencies increased with age, indicating that an increasing fraction of the calories consumed was translated into growth (Tables 10, 11). It is unrealistic that growth efficiencies would continue to increase. Brett and Groves (1979) suggested that for older fish growth rates become asymptotic with time. Growth efficiencies given here (24-46%) are consistent with growth efficiencies reported for other larval fish species (14-41% in Theilacker and Dorsey 1980) fed 1,000 or more prey per liter; reported efficiencies are high and extremely variable.

Direct observations of larval stomach contents showed that some rotifer-fed larvae fed at three times the average rate (C_{max}; Fig. 2). These fish may be the successful ones that survive in the field. Their high feeding rates would yield faster growth through the vulnerable larval stage. Feeding intensity also was highly variable for larvae eating copepods (Fig. 6), but the average number of copepods eaten was less than the average number of rotifers eaten (Table 2).

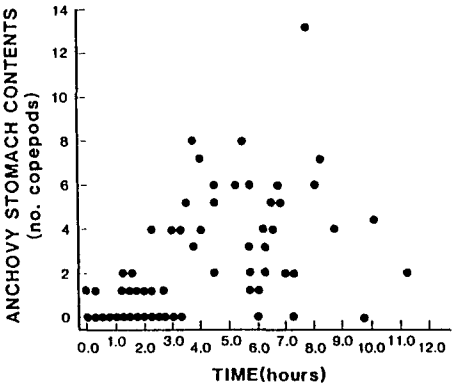

FIGURE 6.—Number of copepod nauplii observed in stomachs of 4.0-5.0 mm northern anchovy fed 2 copepods/mL. Each point is one larva.

Northern anchovy raised on copepods ate mainly *Gymnodinium*, augmenting their diet with copepod nauplii (Table 12). The stomachs of 96% of the 5-d-old larvae were full with *Gymnodinium* cells (Table 6). Fish were obtaining 60-90% of their daily caloric intake from *Gymnodinium*. This is evident by comparing the daily caloric intake (F_c) for day 5-6 larvae of equal size or weight that were fed copepods (Table 12) with those fed rotifers (Tables 10, 11). Consumption of 2-4 cells/minute can account for this energy input (4.2×10^{-5} cal/*Gymnodinium* cell [Vlymen 1977]), and successful feeding acts of this magnitude have been directly observed by Hunter (1981). Lasker and Zweifel (1978) developed a model (a modified version of Vlymen's [1977] model) to describe survival at sea in areas of various concentrations and proportions of large and small prey and concluded that large prey made very little contribution to survival of first-feeding larvae when sufficient (40 mL) small prey were available. As observed here, the ingestion of 10-20 copepod nauplii/day in addition to small *Gymnodinium* cells resulted in a growth rate of 0.35 mm/day, which is comparable to a rate of 0.37 mm/day reported for wild northern anchovy of similar age (Methot and Kramer 1979), and lends additional credence to Lasker and Zweifel's (1978) hypothesis that survival of northern anchovy depends on patchy (layered) distributions of small, abundant prey like *Gymnodinium*.

For all diets, an equivalent number of small prey,

TABLE 12.—Estimate of caloric input from copepods eaten by northern anchovy.

Diet	Age (d) [1]	Standard length (mm) [2]	Dry weight (μg) [3]	Gut clearance rate (μg/h) [4]	Gut contents, Daily mean (μg) [5]	[6]	Consumption [7]	[8]	[9]
							Copepods (μg)	Body weight (%/d)	Copepods (cal/d)
	A	*l*	*W*	*r*	$\bar{c}$ est	$\bar{c}$ obs	F_w	$F_{w/w}$	F_c
Copepods	5	4.34	20.35	0.07	0.19	0.16	1.07	05	0.0052
2/mL	6	4.66	24.99	0.10	0.28	0.30	1.55	06	0.0076
and	7	4.99	30.43	0.15	0.41	0.43	2.26	07	0.0111
Gymnodinium	8	5.36	37.39	0.23	0.62	0.68	3.44	09	0.0169
	9	5.75	45.77	0.35	0.96	1.08	5.32	12	0.0261

[1]Hatching = Day 0.
[2]$l_t = 3.06\ e^{0.07t}$.
[3]$W = 0.297\ l^{2.86}$.
[4]$r = \bar{c}$ est/2.73 h (see text).
[5]Estimated using equation in Table 3.
[6]Average stomach contents calculated for t = >3 h; includes empty stomachs.
[7]$F_w = 12\ r + \bar{c}$ est.
[8]% body weight eaten/d as copepods.
[9]Calories/d, copepods; $F_w \times 4.9$ cal/mg (Table 1).

Gymnodinium cells, was available and the concentration of large prey was varied. Availability of large prey of a suitable size in the copepod diet was 10 times the number available in the low-density rotifer diet. Because 4 mm (day 5) larvae fed copepods ate mainly *Gymnodinium*, and those fed the low-density rotifer diet ate mainly rotifers (Tables 2, 6), copepods nauplii must be more difficult to catch than rotifers, and consequently larvae consumed the more abundant *Gymnodinium* cells. Larvae which consume prey as they are encountered, rather than choosing a diet that maximizes the energy gained per unit foraging time, have been labelled "number maximizers" as opposed to "energy maximizer" in the parlance of Griffiths (1975) and Hughes (1979). Additional evidence that points to northern anchovy feeding as "number maximizers" is that, when prey of the proper size were available, their feeding rates paralleled prey abundance (Tables 10, 11).

The energy budget I calculated for northern anchovy fed rotifers at two concentrations gives information on their growth requirements that can be translated to growth requirements in the field. My data support Boehlert and Yoklavich's (1984) and Checkley's (1984) conclusions that larval fish may exhibit a high growth rate or a high growth efficiency, but not both at the same time. Boehlert and Yoklavich studied Pacific herring, which are 2-4 times the weight of northern anchovy, but like anchovy feed continuously, and found that as consumption increased, the total amount of food assimilated continued to increase despite a decrease in the efficiency of the assimilation. Checkley studied Atlantic herring and found that the gross growth efficiencies of Atlantic herring increased with increasing consumption, but he showed that the relation was peaked, and by incorporating results from the literature for other species, he also described a decrease in growth efficiency at high consumption for larval fishes.

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