PREY SIZE SELECTIVITY AND FEEDING RATE OF LARVAE OF THE NORTHERN ANCHOVY, *ENGRAULIS MORDAX* GIRARD

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ABSTRACT

A series of laboratory feeding experiments was conducted with larvae of the northern anchovy, *Engraulis mordax*, at 10, 20, 30, and 40 mm SL. The larvae were fed wild zooplankton in high (100 prey/liter) and low (10 prey/liter) concentrations. The 10-mm larvae consumed primarily rotifers, probably because of their past feeding history. The 20-40-mm larvae tended to select large copepods at high concentrations, and medium and large copepods at low concentrations. The ability of late larvae to select the largest prey available is similar to the foraging behavior of adult anchovies reported by previous workers. The foraging of 40-mm larvae was probably restricted by the size of the experimental tanks.

Feeding rates as a function of larval size and prey concentration were estimated and compared to a conservative estimate of basal metabolic costs. Only 20- and 30-mm larvae feeding at 100 prey/liter consumed enough food to grow at rates similar to those observed in the sea, which indicates that even late larvae require somewhat concentrated patches of food.

RESUMEN

Una serie de experimentos de alimentación en laboratorio se llevó a cabo con larvas de anchoveta del norte, *Engraulis mordax*, de 10, 20, 30, y 40 mm (largo estándar). Las larvas fueron alimentadas con concentraciones altas (100 presas/litro) y bajas (10 presas/litro) de zooplancton silvestre. Las larvas de 10 mm consumieron principalmente rotíferos, probablemente debido a su historial de alimentación previo. Las larvas de 20 a 40 mm LS seleccionaron principalmente copépodos grandes a altas concentraciones, y copépodos medianos y grandes a concentraciones bajas. La habilidad de las larvas maduras para escoger las presas disponibles más grandes es similar al comportamiento depredador de las anchovetas adultas de acuerdo a lo informado por otros investigadores. La predación de las larvas de 40 mm probablemente fue restringida por el tamaño del tanque experimental.

Las tasas de alimentación fueron calculadas como función del tamaño larvario y de la concentración de presas y fueron comparadas con una estimación de los costos en metabolismo basal. Sólo las larvas de 20 a 30 mm, quienes consumieron 100 presas por litro, se alimentaron lo suficiente como para crecer a tasas similares a las observadas en el mar. Esto indica que incluso las larvas maduras requieren la presencia de sus presas concentradas en "manchas."

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INTRODUCTION

In order to understand the factors affecting recruitment and year-class strength, scientists have done much research on the early life history of the northern anchovy, *Engraulis mordax* Girard. The rationale behind this work has been that year-class strength may be determined by the growth and mortality rates of larvae in the first month of life (5-15 mm SL), especially during the transition from the yolk-sac stage to planktivorous feeding (Lasker 1975). However, correlation of the densities of early larvae (less than 15 mm SL) with the strength of the subsequent year class has shown that only exceptionally small recruitment can be predicted, not medium or large recruitment (Smith 1981). Smith and Lasker (1978) note that an increase of an order of magnitude occurred in the anchovy population between 1951 and 1969, while the annual average daily production of 20-day-old larvae remained relatively constant. From this observation it is apparent that variations in survival during the late larval phase (20-35 mm SL, ca. 1-3 months old) are also important in determining recruitment (Smith 1985). The late larval and juvenile stages are presently the least understood phases of *E. mordax*.

Feeding and growth characteristics of northern anchovy show gradual changes from early to late larval stages. Northern anchovy larvae of all sizes feed by visually mediated biting (Blaxter and Hunter 1982). Filter feeding begins only after metamorphosis (35-40 mm SL). As a larva grows, it requires more food of a larger size to maintain a given rate of growth. However, there seems to be no further increase in food size after larvae reach about 12 mm SL, even though the mouth width, and therefore the size of particles ingestible, continues to increase (Hunter 1981). In the field, there are far more food particles of the size taken by first-feeding larvae (50-100 μm) than there are of larger particles needed by older larvae (ca. 200 μm and larger) (Arthur 1977; Hunter 1981). The maximum

naupliar biomass in waters of the California Current occurs at a naupliar width of about 70 μm (Arthur 1977). Measurements of the standing stocks of pelagic organisms indicate that there is approximately equal biomass over logarithmically equal size ranges (Sheldon et al. 1977); in other words, the number of organisms decreases exponentially as size of organisms increases linearly (Vlymen 1977).

Jack mackerel larvae inhabiting the same general environment as the anchovy are able to secure increasingly larger food particles as they grow (Arthur 1976). This suggests that factors other than mouth size, such as the relatively slow swimming speed of engrauliid larvae, may limit the size of food captured by *E. mordax* (Hunter 1981). Late larvae are thought to continue to feed on smaller prey and to take larger copepods when available, although this apparently has not been examined in either field-caught or laboratory-reared larvae larger than 20 mm SL (Arthur 1976; Hunter 1981).

Methot (1981) reports that late larvae grow at a slower rate (0.30-0.35 mm/day) than early larvae (0.47-0.70 mm/day) or early juveniles (0.40-0.60 mm/day). The ratio between weight and length seems similar during all stages (Methot 1981); therefore, the reason for slower length-specific growth during the late larval stage may lie in feeding ecology, energetic requirements, and assimilation efficiency. Methot (1981) suggests that the decline in growth through the late larval period may be due to the inability of larvae to find and capture large particles.

Here I present the results of laboratory experiments conducted with *E. mordax* larvae fed wild zooplankton to determine how prey-size selectivity and feeding rates differ between larvae of various sizes that are feeding on different densities of prey. The results are used to infer whether larvae can obtain enough food at the experimental prey concentrations to meet metabolic and growth requirements.

METHODS

Larvae of *Engraulis mordax* were reared from eggs at 18°C in the laboratory at the Southwest Fisheries Center, La Jolla, California, using the methods presented by Hunter (1976). Larvae were fed the dinoflagellate *Gymnodinium splendens*, the rotifer *Brachionus plicatilis*, and the harpacticoid copepod *Tigriopus californicus*, all reared in the laboratory.

Wild zooplankton for the feeding experiments was collected in Mission Bay from October 25, 1984, to February 21, 1985. Collections were made from a skiff, with 0.5-m ring nets of 64-μm and 333-μm nylon mesh. The nets were fitted with solid cod ends. The two nets were towed sequentially for 5 minutes each at approximately 1 m/sec, and the catches from six sets of tows were combined. The most abundant organisms collected were calanoid copepods of the genus *Acartia*. Also common were the cyclopoid copepods *Corycaeus* spp. and *Oithona* spp., and the harpacticoid copepod *Euterpina acutifrons*. Gastropod veligers and rotifers were occasionally abundant.

Experimental Design

The experimental design was orthogonal, with two main factors—larval length (10, 20, 30, and 40 mm SL) and prey concentration (10/liter and 100/liter). The larval lengths were chosen to cover the entire larval life in this species. The prey concentrations were chosen to approximate high and low average densities of microzooplankton prey sampled in areas inhabited by anchovy larvae in the California Current (Arthur 1977). Each combination of factors and levels was replicated twice. Only two tanks were available for experiments; therefore, experiments with the two prey concentrations were done simultaneously for a particular size of fish. The size-composition of wild plankton varied between experiments because of natural variations in the plankton collections. The order of experiments was randomized so that any seasonal change in plankton composition was interspersed among sizes of larvae.

Experimental Procedure

One to three days before an experiment, I transferred 20-30 reared larvae to each experimental tank. The experimental tanks were as similar as possible to the rearing tanks in construction (400-liter, 1.2-m-diameter, black fiberglass), aeration, lighting, and temperature. Larvae were starved and acclimated for 1-3 days, depending on size, until guts were empty and behavior seemed normal.

Fresh plankton was collected each morning (0800-1200 hrs), and experiments were conducted in the afternoon (1400-1800 hrs). Immediately before the experiment, I stopped the aeration. I then added the appropriate amount of plankton to create the target concentration. To determine the actual concentration and distribution of prey in each tank, I took samples with plexiglas tubes (7-cm diameter) lowered onto rubber stoppers that had been placed on the bottom before I added plankton. Sample volume ranged from 500-750 ml, depending on the volume of water in the tank. I preserved five replicate samples in 5% buffered Formalin for later enumeration. I used size-frequency data from samples in the high-density tank (100/liter) to determine size-frequency in the low-density tank (10/liter). Pilot studies indicated a coefficient of variation between replicate samples of 8%-74%.

I measured swimming speed for two 10-minute periods before and after plankton was added. To measure the speed, I randomly selected an individual fish, and then, with the aid of 1-cm and 3-cm grid patterns on the bottom of the tank, estimated the distance the fish traveled in 2 seconds. The number of fish observed in 10 minutes ranged from 35 to 142. I converted speeds into body lengths/sec, using the mean standard length of the fish in each tank.

I terminated the experiments after 30-60 minutes by anesthetizing all fish with MS_{222}, at a concentration of 0.1 g/l. This was done to prevent the larvae from defecating or regurgitating their gut contents during handling (June and Carlson 1971). After 10 minutes, I collected fish with a dip net as quickly as possible, and preserved them in 10% buffered Formalin for later measurement and enumeration of gut contents. Duration of the experiments was assumed to be less than the time required for larvae to fill their guts at the experimental prey concentrations or to defecate prey ingested during the experiment (G. Theilacker, pers. comm.).

Laboratory Analyses

All prey items were identified in three categories: nauplii, copepods (including copepodites and adult copepods), and others. I measured items across the maximum width, excluding appendages. Initially I grouped the measurements into 50-μm size categories, and later regrouped them into five categories for data analysis: nauplii (< 150 μm wide), small copepods (< 100 μm wide), medium copepods (100-300 μm wide), large copepods (> 300 μm wide), and others (predominantly rotifers < 200 μm; also gastropod and bivalve veligers).

Plankton samples were stained with Biebrich scarlet, and counted in either a settling chamber with an inverted microscope at 50-100×, or a Plexiglas counting dish under a dissecting microscope at 25-50×. In the settling chamber, some plankters were found in the supernatant after the settling period of 12-15 hr. I estimated the percentage of error (i.e., the proportion of plankters not settling completely) from 20 samples; it averaged 15.1% for nauplii and copepods. There was no significant size-bias in the error factor. All counts made with settling columns were subsequently corrected.

I examined the guts of ten larvae from each experiment (except for one experiment with 10-mm larvae, when only eight larvae were available). I measured the fish (SL), and dissected the guts in glycerin. I teased out the gut contents with fine needles, and stained them with Chlorazol Black E in lactic acid and ethyl alcohol (Judkins and Fleminger 1972). All prey items were counted and measured under a compound microscope.

I determined the live length of each fish by using the shrinkage correction factors of Theilacker (1980) for 10 min of net treatment followed by preservation in 10% Formalin. Shrinkage rates due to MS_{222} and net treatment were similar. For 10-mm larvae, the shrinkage from 10 min in 0.1 g/l MS_{222} followed by Formalin preservation was 13.1% ($n = 20$), compared to 15% from 10 min of net treatment followed by Formalin preservation (Theilacker 1980).

Gut contents and plankton data were converted from numbers of prey to dry weight, taking into account the size-frequency of prey by 50-μm width classes before the data were combined into the five larger prey classes for analysis. The width-specific volumes of copepods and nauplii were calculated from ocular micrometer measurements of the length, width, and depth, assuming nauplii to be ellipsoids, and copepods to be ellipsoids (cephalothorax) plus cylinders (abdomen). I determined volume-to-width relationships for nauplii [ln volume = −14.20 + 3.08 (ln width), $r^2 = 0.902$, $n = 42$] and copepods [ln volume = −13.56 + 3.02 (ln width, $r^2 = 0.993$, $n = 75$]. The width-specific dry weight of fresh, mixed-species copepod samples was determined following the methods of Theilacker and Kimball (1984). I rinsed samples with isotonic ammonium formate solution (3.4%), sorted them into 50-μm size classes, and dried them overnight on glass slides at 60°C. I prepared 14 slides, each containing from 3 to 95 individuals, depending on the size of copepods. Following drying, samples were removed from the slides and weighed on a Cahn electrobalance. I determined the dry-weight-to-volume relationship by linear regression with intercept set equal to 0 [dry weight = 0.19 (volume), $p < .001$, $n = 14$], and used the relationship to calculate dry weights of nauplii and copepods from their volume. The dry weight used for the prey category "others" was the average for rotifers < 200 μm wide (0.30 μg) given by Theilacker and Kimball (1984).

Data Analyses

Prey-size selectivity was determined using the alpha index (α) (Chesson 1978). I chose this index because it allows comparisons of selectivity between experiments with different prey compositions (Chesson 1983), and also because it is possible to test the apparent selectivity against a random model (Manly 1974). The index is calculated as:

$$\alpha_i = \frac{r_i/p_i}{\sum_{i=1}^{m} r_i/p_i}$$

where m = number of prey types = 5
r_i = proportion of prey type i consumed
p_i = proportion of prey type i available.

p_i was assumed to be constant for the duration of each experiment; i.e., the initial prey concentration was assumed to be not significantly depleted by larvae feeding during the experiment. r_i was determined from gut content analyses.

I calculated the alpha index for each of the five prey categories, for each larva that fed during experiments. The values so obtained were not suitable for parametric statistical analyses, because the variances remained heterogeneous after arc sine transformation. Therefore, I examined the median values and the quartiles above and below the median. The observed values are compared with the value expected if feeding was random on all categories of prey ($\alpha = 1/m = 0.20$).

In order to compare feeding rates between sizes of larvae at the target concentrations, I fitted feeding-rate data for each 10-mm size class of larvae to a log-linear multiple regression model:

$$\ln(\text{rate} + 1) = \ln(a) + b_1(\text{SL}) + b_2(\text{concentration})$$

I backtransformed the resulting estimates, taking into account the variance of the regression, and calculated 95% confidence limits (Beauchamp and Olson 1973).

I calculated the metabolic and growth requirements using the following values and assumptions:

1. Larvae fed at the estimated mean feeding rates throughout a 12-hr feeding day.

2. Daily minimum metabolic requirement (24 hr) was calculated from the following model presented by Theilacker[1] for anchovy larvae at 15.5°-16°C:

$$Q = 4.269\, W^{0.697}$$

where Q = metabolic rate in μl O_2/day
W = fresh dry weight in mg

and converted to μg prey material using the following factors: 0.00463 cal/μl O_2 and 4.9×10^{-3} cal/μg, for copepod prey (Theilacker and Kimball 1984).

3. Assimilation efficiency was 70% for larvae of all sizes, a rough extrapolation from Theilacker's results.[2]

4. Weight-specific growth rates of larvae in the sea were taken from Methot (1981). The surface temperatures reported in that study (generally representative of anchovy spawning areas) ranged from 13° to 19°C, with the mode at approximately 15°-16°C.

5. Fresh dry weights were calculated from the formula in Hunter (1976) for 10-30-mm larvae, and from unpublished data of Hunter for 40-mm larvae.

RESULTS AND DISCUSSION

The target and actual larval lengths and prey concentrations are given in Table 1, along with the feeding incidence (% of larvae with one or more prey in gut). Because 10-mm larvae did not feed at 10 prey/liter, I tested them at 100 and 1000 prey/liter. Feeding incidence tended to increase with both larval length and prey concentration; similar results have been reported for other species of fish larvae (Houde and Schekter 1980).

Swimming Activity

The mean swimming speed, measured as body lengths/sec (bl/s), in each experiment is shown in Table 2, along with t-tests of the equality of means before feeding (after 1-3 days of food deprivation) and during feeding. For 10-mm larvae, mean speed was always less than 1 bl/s, and showed no changes with the addition of food. My results contrast with those of a previous study in which anchovy larvae from 4-8 days old (< 6 mm SL) swam slower when inside a dense patch of food cells (up to 260 cells/ml) than when outside such a patch (Hunter and Thomas 1974). The difference in these results could be because the "patches" created by adding food in my experiments were 3 to 4 orders of magnitude less dense than those used by Hunter and Thomas.

For 20-40-mm larvae, mean swimming speed ranged from 0.6 to 3.3 bl/s and tended to increase during feeding (9 of 11 t-tests with $p < .10$). However, there was no difference in the relative increase in speed during feeding between high and low prey concentrations; i.e., larvae did not swim faster while feeding on high prey concentrations (Table 2).

Prey Selectivity

The mean proportion of various prey types consumed by various sizes of larvae at high and low concentrations is compared to the mean available size composition in Figure 1. The 10-mm larvae consumed primarily rotifers (the "others" category), although they consumed some nauplii and copepods at 1000 prey/liter. The 20-40-mm larvae tended to consume a higher proportion of nauplii at low concentrations than at high concentrations, and higher proportions of medium and large copepods at high concentrations than at low concentrations. Medium copepods (100-300 μm wide) formed the largest proportion (50%-80%) of prey consumed, both by numbers and by weight for 20-40-mm larvae at both concentrations.

[1]Theilacker, G.H. MS. Feeding ecology and growth energetics of larval northern anchovy, *Engraulis mordax*.
[2]Ibid.

TABLE 1
Comparison of Target Values for Standard Length of Northern Anchovy Larvae and Prey Concentrations with the Mean Values for Two Experiments

Target		Actual			
SL (mm)	Conc. (no./liter)	SL (mm)	Conc. (no./liter)	Conc. (μg./liter)	Feeding incidence (%)
10	100	10.2 (1.8)	278.1 (61.0)	148.1 (25.5)	77.8
	1,000		1,173.0 (148.8)	969.2 (53.6)	72.2
20	10	22.2 (2.2)	36.9 (16.4)	23.6 (13.2)	50.0
	100		92.2 (19.8)	64.6 (10.5)	95.0
30	10	28.4 (3.0)	19.5 (9.5)	9.0 (3.7)	85.0
	100		127.3 (18.7)	92.9 (42.7)	100.0
40	10	43.0 (5.0)	10.2 (0.4)	7.9 (4.3)	100.0
	100		166.0 (58.5)	264.9 (165.9)	100.0

Standard deviation is shown in parentheses below mean values.

TABLE 2
Mean Swimming Speed (Body Lengths/Sec) of Northern Anchovy Larvae Before and During Feeding Experiments, and Results of t-Tests of the Equality of Means

		Swimming speed (body lengths/sec)			
SL (mm)	Prey conc.	Before	During	t	*p*
10	Low	0.8 (0.3)	0.8 (0.3)	0	ns
	High	0.8 (0.3)	0.7 (0.3)	1.5	>.10
	High	0.5 (0.4)	0.5 (0.4)	0	ns
	Low	0.7 (0.4)	0.7 (0.4)	0	ns
20	Low	0.6 (0.4)	1.8 (1.2)	−10.2	<.001
	High	1.3 (1.2)	2.0 (0.9)	−5.2	<.001
	Low	1.2 (0.6)	2.3 (1.1)	−6.9	<.001
	High	1.5 (1.2)	1.9 (1.1)	−1.9	<.10
30	Low	2.6 (1.2)	3.0 (1.4)	−1.8	<.10
	High	3.3 (0.9)	2.2 (0.7)	8.7	<.001
	Low	2.3 (1.1)	2.1 (0.8)	−1.2	>.20
	High	1.3 (0.6)	1.6 (0.6)	−2.9	<.001
40	Low	1.4 (0.8)	1.6 (0.6)	−1.8	<.10
	High	1.2 (0.5)	1.9 (0.5)	−9.1	<.001
	High	1.0 (0.4)	2.7 (0.6)	−18.2	<.001

Standard deviation is shown in parentheses after each mean. The number of observations for each mean ranged from 35 to 142.

The alpha indexes of selectivity are presented in Figure 2, and compared to the random feeding value of 0.20. The 10-mm larvae were highly selective for rotifers. This could have been influenced by two factors. First, there was a large proportion of rotifers in the tank during the experiment. The rotifers came both from the plankton used for the experiment (collected by chance during a rotifer bloom) and from the rearing tanks when the fish were transferred. Before the experiments began, I attempted to remove the transferred rotifers using an air-lift pump, but was not entirely successful. The second factor was the larvae's lack of experience with wild zooplankton as food. The 10-mm larvae were accustomed to eating cultured rotifers, and may have been unable to adjust to wild plankton in the time allowed by the experiment. However, in the field, anchovy larvae select prey smaller than the largest they are capable of ingesting (Arthur 1976). In the laboratory, herring larvae (12-19 mm SL) selected wild zooplankton narrower than the widest available and ingestible during feeding experiments, even though they were accustomed to wild zooplankton as food during rearing (Checkley 1982). The fact that 10-mm anchovies ate more medium copepods at 1000/liter than at 100/liter suggests that they were better able to capture

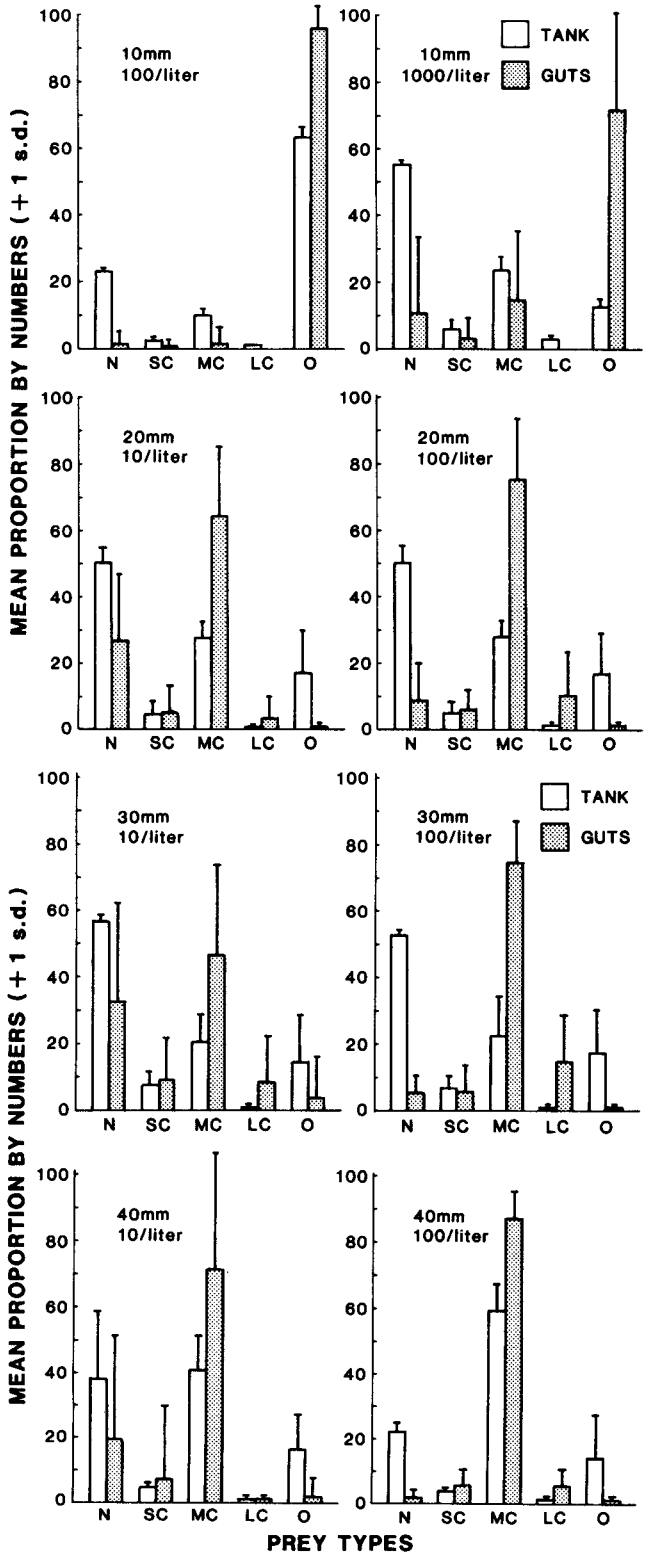

Figure 1. Comparisons of the proportions of various prey types consumed versus the proportions available to northern anchovy larvae of 10, 20, 30, and 40 mm SL, feeding at high and low prey concentrations. Mean values for two experiments are indicated by bars, with 1 standard deviation shown by a line above each bar. Prey types are abbreviated as follows: N, nauplii < 150 μm wide; SC, small copepods < 100 μm wide; MC, medium copepods 100-300 μm wide; LC, large copepods > 300 μm wide; and O, others (mainly rotifers < 200 μm wide, and gastropod and bivalve veligers).

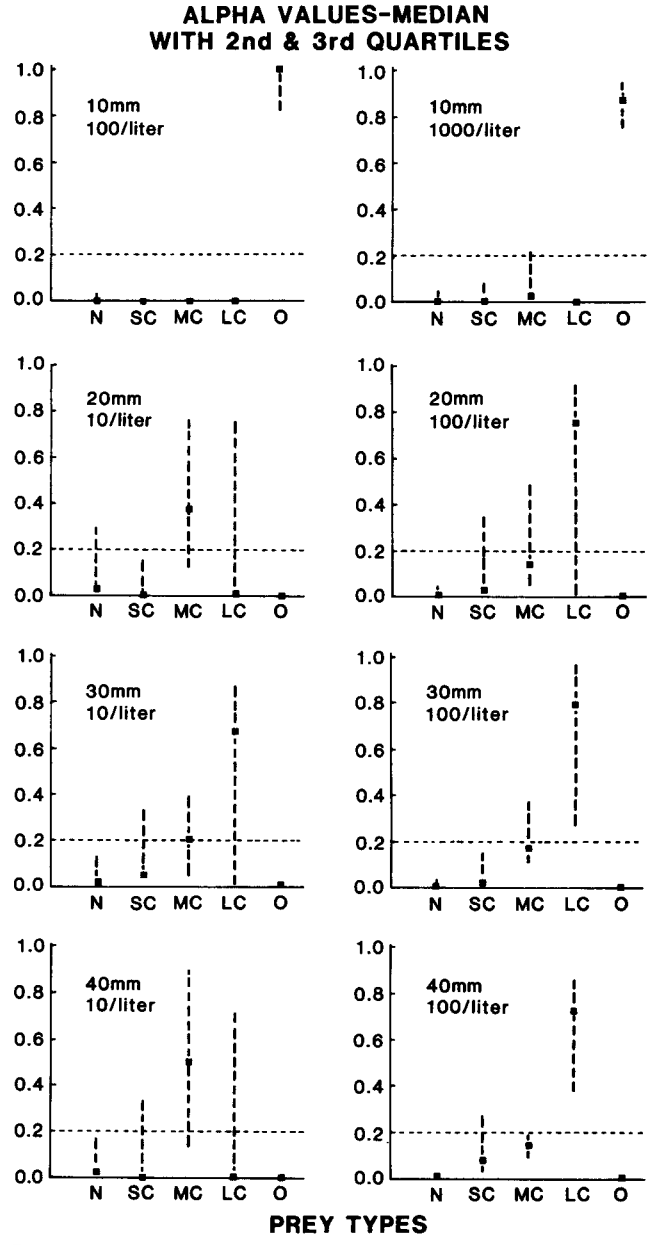

Figure 2. Values of the alpha index of selectivity for each prey type, size of northern anchovy larvae, and prey concentration. The median value from two experiments (number of fish = 20) is shown by the square symbol, with the quartiles above and below the median indicated by the vertical dashed lines. The random feeding value (α = 0.20) is shown by the horizontal dashed line on each graph. The prey types are abbreviated as in Figure 1.

larger prey at high density, regardless of previous experience. The larger larvae (20-40 mm) had all been previously exposed to wild plankton as an occasional food source in the rearing tanks.

The 20-40-mm larvae tended to select large copepods at high concentrations, and to select medium and large copepods at low concentrations. There is obviously much individual variation in selectivity. No clear pattern of difference in selectivity or size composition of prey consumed appears to exist between 20-, 30-,

and 40-mm larvae; all tended to select the largest prey available. Adult northern anchovy in the Southern California Bight showed similar selectivity for the largest prey available while feeding in schools on a variety of plankton assemblages of prey genera and sizes overlapping those used here (Koslow 1981).

There was some indication that the 20-40-mm larvae may have significantly reduced the concentration of larger prey during some experiments, but this depletion was not quantified. Such a violation of the assumption of constant p_i would tend to make the alpha values presented here an underestimation of the actual degree of selectivity (Chesson 1978, 1983; Manly 1974).

Feeding Rates

Estimated feeding rates (Figure 3), given both as numbers per minute and as dry weight per minute, were calculated from multiple regression equations describing feeding rate as a function of larval size and prey concentration for each 10-mm size class (Table 3). Feeding rate was higher at 100/liter than at 10/liter for all sizes of larvae. At 100 prey/liter, 40-mm larvae consumed 1.5-2 times more items than did 20- and 30-mm larvae. However, in terms of dry weight of prey consumed/min, 40-mm larvae consumed less than did 30-mm larvae, indicating that 40-mm larvae ate more small prey than did 30-mm larvae. This may be because the experimental tank was small relative to the searching abilities of 40-mm larvae, and because 40-mm larvae apparently depleted the tank of large copepods during the experiment.

Metabolic and Growth Requirements

The results of the calculations of food consumed and metabolic costs are presented in Table 4. For all sizes of larvae at all concentrations (except 20-mm larvae at 10/liter), larvae ingested enough food to meet their basal metabolic needs. However, the consumption rates used here are probably somewhat high for two reasons: (1) feeding rates were measured during the first 30-60 minutes of feeding after a period of starvation, and were thus higher than an average 12-hour rate (Hunter 1972); and (2) feeding rates were measured at 18°C, whereas minimum metabolic requirements and field growth rates are more representative of larvae at 15°-16°C.

Nevertheless, estimated growth rates as a percentage of body weight are compared with the weight-specific growth rates of field-caught larvae (Methot 1981) to determine if larvae could grow at observed rates at the prey concentrations tested (Table 4). Neither 10-mm nor 40-mm larvae could grow at field growth rates at any of the food concentrations tested, but I do not believe the results for these two size classes are reliable.

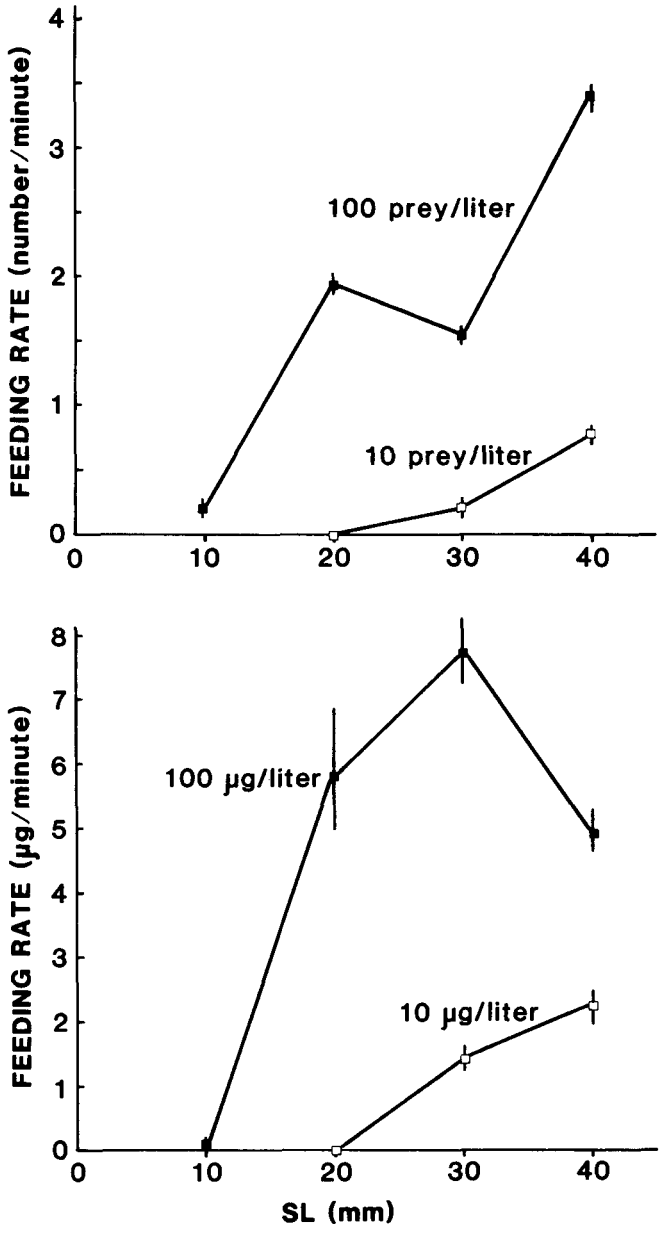

Figure 3. Estimated feeding rates of northern anchovy larvae of various sizes at two standardized prey concentrations. Rates are expressed as numbers of prey per minute and as weight of prey consumed per minute. The 95% confidence limits are indicated by vertical lines through each estimate.

The feeding of 10-mm larvae was probably not typical, because prior feeding was only on rotifers. Foraging of 40-mm larvae was probably affected by tank size.

According to the estimates, the 20- and 30-mm larvae would consume enough food to grow at observed rates at prey concentrations of 100/liter, but not at 10/liter. Thus, even late larvae (20-30 mm), which are able to select large prey, may require somewhat concentrated patches of food. On the other hand, 100 prey/liter is substantially lower than estimated food densities required for survival and growth in past studies (Hunter 1981), and is in keeping with the more recent

TABLE 3
Parameters for Multiple Linear Regression Equations* Describing Feeding Rate (ln rate + 1) in Relation to Larval Length (x_1) and Prey Concentration (x_2) for Northern Anchovy Larvae

SL (mm)	b_1	(Standard error)	b_2	(Standard error)	ln a	mult. r^2	F	p
Numbers of prey per minute								
10	−0.006	(0.012)	−0.7E-4	(0.5E-4)	0.243	0.107	1.97	0.16
20	0.025	(0.032)	0.013	(0.002)	−0.815	0.472	16.53	0.00
30	−0.015	(0.022)	0.008	(0.001)	0.491	0.556	23.18	0.00
40	−0.014	(0.017)	0.010	(0.001)	0.900	0.749	55.30	0.00
20-40	0.016	(0.005)	0.010	(0.001)	−0.463	0.666	116.64	0.00
Weight of prey per minute								
10	−0.002	(0.004)	−0.2E-4	(0.2E-4)	0.076	0.067	1.18	0.32
20	0.130	(0.041)	0.022	(0.004)	−3.032	0.557	23.25	0.00
30	0.052	(0.035)	0.014	(0.002)	−1.040	0.546	22.28	0.00
40	−0.037	(0.026)	0.007	(0.001)	2.282	0.664	36.62	0.00
20-40	0.002	(0.008)	0.008	(0.001)	0.556	0.528	65.31	0.00

*Model: $\ln(\text{rate} + 1) = \ln a + b_1x_1 + b_2x_2$

literature for larvae in general (Houde and Schekter 1980; Munk and Kiorboe 1985).

The prey concentrations used here were chosen to approximate high and low densities of prey suitable for *E. mordax* larvae in the field. Arthur (1977) states that the usual densities in areas where most anchovy larvae are found are about 1.5-4 copepodids/liter and about 13-30 nauplii/liter. The highest concentrations he reported from several studies in California Current waters were 36 copepodids/liter and 195 nauplii/liter. There are many difficulties in estimating field concentrations of appropriate-size prey on spatial scales relevant to larvae, especially because both prey sizes and foraging ranges change as larvae grow. Such estimates involve significant problems in sampling and data interpretation, since no single type of zooplankton gear adequately samples the entire size range of prey at one time and place, and different types of gear integrate densities over different scales—e.g., water bottles on a scale of decimeters (Owen 1981), pumps and nets over meters to kilometers (Beers and Stewart 1967; Arthur 1977). The prey distribution used in my experiments was skewed toward larger prey, with most experiments offering about 40% copepodids and adult copepods (range 30%-60%). This is about four times as many copepodids as larvae would normally encounter in the wild (Arthur 1977; Sheldon et al. 1977).

TABLE 4
Bioenergetic Estimates for *Engraulis mordax* Larvae Feeding at Two Prey Concentrations, Calculated for a 24-hr Period, with a 12-hr Feeding Period

SL (mm)	Dry weight (mg)	Metabolic requir. (μg)	Prey conc. (μg/l)	Consump. (μg)	Growth potential* (μg)	Growth body wt. (%)	Field growth (%)
10	0.316	1.808	100	43.2	28.4	9.0	15-20
			1,000	28.8	18.4	5.8	
20	4.185	10.941	10	0		—	8-9
			100	4,183.2	2,917.3	69.7	
30	31.930	45.102	10	1,015.2	665.5	2.1	5-6
			100	5,400.0	3,734.9	11.7	
40	105.82	103.95	10	1,641.6	1,045.2	1.0	3-4
			100	3,715.2	2,496.7	2.4	

*calculated as consumption × assimilation efficiency − metabolic requirement.

In conclusion, these experiments indicate that feeding ability of northern anchovy larvae changes most dramatically between 10 and 20 mm SL. By 20 mm, the larvae's size selectivity is functionally similar to that of adults, in that larvae are capable of selecting the largest prey available over the range of sizes normally encountered. Koslow (1981) calculates that a spawning stock of 1.32-2.35 $\times$ 10^6 anchovies in the Southern California Bight would consume 10% to more than 100% of the secondary production available in the area. This implies that growth rates of late larvae may be limited by (1) intraspecific competition for large prey items with adults, (2) low prey concentrations, and (3) the stochastic interaction of these two factors.

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