

Reprinted from: SPATIAL PATTERN IN PLANKTON COMMUNITIES (1978)
Edited by John H. Steele
Book available from: Plenum Publishing Corporation
227 West 17th Street, New York, N.Y. 10011

GROWTH AND SURVIVAL OF FIRST-FEEDING NORTHERN ANCHOVY LARVAE
(*ENGRAULIS MORDAX*) IN PATCHES CONTAINING DIFFERENT PROPORTIONS
OF LARGE AND SMALL PREY

Reuben Lasker and James R. Zweifel

National Marine Fisheries Service, NOAA
Southwest Fisheries Center
La Jolla, California 92038

INTRODUCTION

As early as 1914, Hjort proposed that differential mortality of first-feeding larvae due to variable feeding conditions could be the cause of extreme variations in year class strength of fish. Tests of this simple attractive hypothesis have given equivocal results at best. With regard to clupeid larvae, on the average, there is usually not enough food available for the larvae to survive, considering the amount of water a larva is capable of searching and its inefficiency in capturing food when it first starts to feed (Hunter, 1972). With the sampling gear currently used (pumps and plankton nets*), it is still difficult to establish whether any body of water can support enough larval fish survival to ensure the establishment of a robust year class. To do so, however, would be a first step toward defining criteria for successful recruitment, a recognized need in all fisheries research today (Gulland and Boerema, 1973). The success of pelagic fish in their environment has prompted fishery scientists to postulate that there have to be suitable concentrations of food organisms in space and time (patches) to provide for larval feeding and that Hjort's hypothesis is still viable and should be rigorously tested.

The significance of food aggregations for larval fish can only be assessed if we know important features of larval feeding

*Both kinds of gear sample a lot of water and tend to give results which average numbers of organisms over depths or distances and consequently obscure fine-scale patchiness of larval fish food.

behavior. Although we know relatively little about the behavior of most fish larvae, it is possible now, with at least one species, *Engraulis mordax*, to assemble the pertinent behavioral data as a result of some recent intensive laboratory and field investigations. Two recent papers by Lasker (1975 and 1978) have provided evidence for the aggregation of properly sized food particles in the habitat of the first-feeding larval anchovy off California. He found that stability of the water column in the upper 30 meters appeared to be the key condition required for larval anchovy food organisms to aggregate in densities high enough to exceed the threshold for the feeding stimulus of first-feeding Northern anchovy larvae. Disruption of this stability was caused by vigorous storms or by upwelling along the coast, both resulting in a dilution of the microplankton needed for feeding and, by inference, excessive mortality of any larvae which needed to feed immediately after these events occurred. In addition, the work of Hunter (1972, 1976, 1977), Hunter and Sanchez (1976), Arthur (1976, 1978), Lasker (1964), Lasker *et al.* (1970) and Vlymen (1974, 1977) provide us with a background of behavioral and physiological information on the larvae of the northern anchovy, *Engraulis mordax*. The interest in anchovies goes beyond their importance in the California Current ecosystem; anchovies contribute to some of our largest fisheries, and, indeed, when the Peruvian anchovy fishery was at its peak, the anchovy catch made up 25% of the entire world fish catch.

These studies suggest that patchiness, which results in relatively high concentrations of larval anchovy food, is a major factor in the survival of clupeid larvae, although, as we will illustrate, high concentrations alone cannot be the sole criterion for survival. Other factors, such as the nutritive value and digestibility of the food, size of the food particle, food selection by the larva, learning by the larva, and a variety of other behavioral modalities, have to be taken into consideration if one is to predict whether a particular feeding regime will be favorable to larval anchovies. In this investigation, we consider the naive*, first-feeding anchovy larva presented with food on the first day it is capable of feeding. Patchiness obviously provides higher absolute concentrations of food particles than is usually found in the anchovy larva's environment. We attempt to show here that high food concentrations characteristic of patches in the sea, which appear to provide abundant food in the normal foraging distance of the larva, may still not be sufficient to provide for larval

*The term naive encompasses both the concept of non-selectivity of prey and a pattern of search based upon the random walk ('the blundering idiot' model, Murdie, 1971).

anchovy growth and survival on the first day of feeding. Because of the rapid development of learning in larvae and the increase in success of capture and selectivity, we have chosen to analyze only the first day of feeding by anchovy where learning has not had the opportunity to develop. However, we believe this modeling technique can be extended to assess growth and survival in older larvae as well.

LARVAL ANCHOVY BEHAVIOR AND FOOD DISTRIBUTION

A first-feeding larval anchovy is dependent for food on a very local scale. Its swimming and feeding behavior has been studied by Hunter (1972) in great detail. The pertinent results from his study relative to the capture of food is that feeding appears to be entirely visual and that, at first feeding, success of prey capture ranges from 10-30% of the micro-, phyto- and zooplankters attacked by the larva (Figure 1).

From laboratory and field work, Lasker (1975) showed that there is a critical threshold concentration of food particles for gut-filling by first-feeding anchovy larvae. At the prevalent oceanic temperature, 13-14°C in the anchovy's spawning ground, Lasker found that about thirty 40-50 μm particles/ml, were needed in the larva's immediate environment to stimulate feeding and gut filling. This is remarkably similar to prey concentrations which are determined from Vlymen's (1977) computer simulation for meeting the larva's energetic needs on the first day of feeding. In the laboratory, however, other factors for successful feeding are apparent and can modify these threshold concentrations. These were listed by Lasker (1975) as follows.

Particle Size at First Feeding Appears to be Critical

We know from the stomach content work on larval anchovies by Arthur (1976) as well as from investigations by Rojas de Mendiola (1974) on the larva of the Peruvian anchovy *E. ringens*, that these larvae can capture and eat particles as large as 100 μm in smallest dimension when they first begin to feed, but that the usual diet contains smaller particles with a minimum size ingested from 25 μm , and nauplii with an average width of 68 μm . Arthur (1976) mentions that about 20% of the food found in very early-stage anchovy larvae were "unidentified spheres ... probably of plant origin" but mostly, he and other workers describe copepod eggs and nauplii as dominant identifiable foods found in the larval intestine. For example, during the first few days of feeding, stomach contents revealed 43% of ingested particles were copepod nauplii; at 9 days of age, when the larva is 6 mm long, 68% of the food particles found are copepod

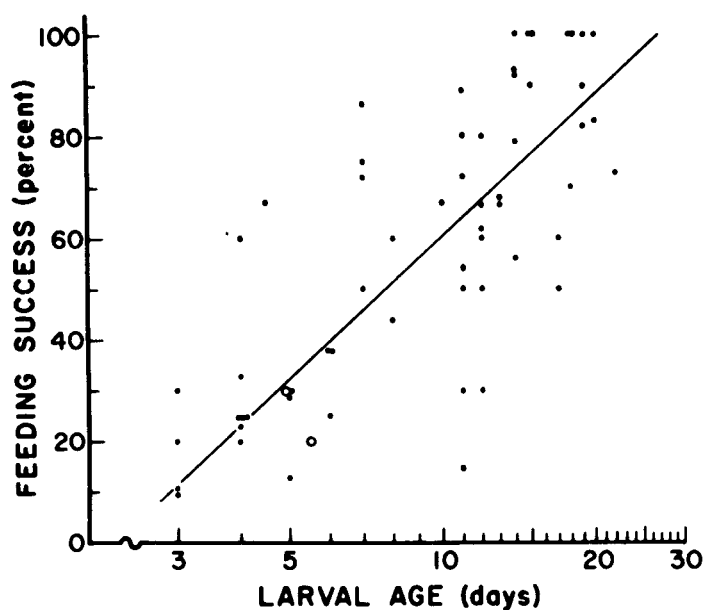


Figure 1. Feeding success (percent of attacked prey captured) of anchovy larvae of various ages fed *Brachionus*. Larval age is plotted on log scale, equation for line is percent success = $93.2 (\log \text{ age}) - 33.30$. Two open circles, larvae fed *Gymnodinium* (from Hunter, 1972).

nauplii and at 14 days (ca. 8 mm long), 91% were nauplii*. Doubling the diameter of a spherical particle increases its volume 8 times. In the environment of the anchovy larva, this difference can have a profound effect on the feeding larva. For example, when feeding

*Gut content studies suffer from the uncertainty that particles found may be there because they could not be digested. However, the particle sizes actually ingested are pertinent in the following discussion.

on small particles, the anchovy larva must capture (according to Hunter) approximately 230 forty-micron diameter particles a day. If the capture efficiency on the first day of feeding is 10%, the larva must attack 2,300 particles. However, the capture and digestion of a single 80 μm particle provides energy at least equivalent to 8 forty-micron particles. Large particles, however, are not captured with as high an efficiency as small ones and this lower efficiency is related to mouth size (Hunter, 1977). Hunter (1977) also shows that when the anchovy larva reaches 6 mm in size (approximately 9 days of age), its metabolism has reached a level whereby it cannot survive on small particles alone. Thus, in any analysis of the feeding environment, consideration of both particle size and particle concentration seems to be essential.

The Number of Particles Per Unit Volume in the Anchovy
Larva's Environment Must be Above a Minimum Concentration

Hunter (1977) evaluated two methods available for determining the food density requirements for survival of anchovy larvae using a simple searching model as well as laboratory density experiments. His conclusions were that laboratory density experiments yield higher food density requirements for survival of anchovy larvae than simple searching models, but that the former suffer from the possible existence of larval density dependent interactions and that the small experimental tank volume may limit the searching capacity of the larva. While the searching model is not affected by these variables, it is grossly affected by errors in the parameters and the assumptions required by the model.

Using laboratory-spawned, first-feeding anchovy larvae as a bioassay of sea water aboard ship, Lasker (1975) showed that gut filling by a first-feeding anchovy larva in natural water at 13-14°C only occurs when a density of about 30 forty-to-fifty micron particles/ml is present at first feeding. He verified this with laboratory experiments. As the larva grows and becomes a more efficient feeder, the number of particles per unit volume needed for feeding is less because the animal increases the size of the particles it takes and begins to ignore smaller ones. At least for first-feeding larvae, the results obtained by Lasker give a reasonable estimate of the minimum density of 40-50 μm particles required for first feeding by anchovy larvae. Vlymen (1977) has demonstrated, through a prey concentration random walk model and a Markov chain prey attack model, that there is a quantitative connection between the growth of a larva and geometric arrangement of prey in its environment. He concludes from his model that survival after the first day of feeding can be achieved at particle concentrations of between 14 and 32 forty-micron particles/cm³ in a geometrically structured patchy environment with patches having

a particle concentration of 32 particles/cm³ and an interpatch region having concentrations 14 particles/cm³. The radius of the patches, and the interpatch region used in Vlymen's simulation, are in centimeters, a scale which is not routinely sampled in the sea.

The Kind of Food Organism Determines Larval Survival and Growth

Scura and Jerde (1977) showed in a number of laboratory experiments that first-feeding Northern anchovy larvae will ignore and fail to feed on particles less than 20 μ m in diameter. These included diatoms, whether single or in chains, and microflagellates, e.g., *Dunaliella* or *Tetraselmis*. Diatoms are rarely reported from gut content studies of anchovy larvae. In the event a particle is large enough to be seen and eaten by an anchovy larva, the nutritional and caloric content of the particle must be sufficiently high in the aggregate to provide for metabolism and growth. Lasker *et al.* (1970) also showed that there was a striking difference between the ability of various microzooplankton to support larval anchovy growth and survival. For example, veliger larvae of some snails supported no anchovy larva growth or survival, while the dinoflagellate *Gymnodinium splendens* and the rotifer *Brachionus plicatilis* could be used to rear the animal (Hunter, 1976). The dinoflagellate *Prorocentrum* does not support growth, as Scura and Jerde (1977) have shown, nor does the dinoflagellate *Gonyaulax polyedra*. *Prorocentrum* may simply be too small and not have enough calories per cell; but *Gonyaulax*, a larger cell, can be captured in great quantity by the larva and, although smaller than *Gymnodinium*, might have been expected to support growth and survival, but did not do so in laboratory experiments.

PROBABILITIES OF ENCOUNTER AT DIFFERENT DENSITIES

In this section, we suggest an approach which, when coupled with field information on the distribution of proper-sized food particles for first-feeding anchovy larvae, may provide a tool with which to determine the extent and goodness of fit of anchovy larvae feeding grounds. With this information, it may be possible to predict whether recruitment will be successful from any particular spawning.

Important features of anchovy larvae behavior have been pointed out above. The most important of these, for purposes of this discussion, are the threshold concentrations for feeding, the number

of strikes a first-feeding larva makes in a day*, the percent success with which it can capture food, and the maximum size particle it can successfully ingest at first feeding. Although usually there is a hyperbolic distribution of particle size in ocean water with the largest particles being fewest in number (Vlymen, 1977), often in the environment of these larvae we find patches containing two or more specific size classes of particles together, e.g., copepod nauplii and dinoflagellates. As a first-feeding anchovy larva swims among these particles, it encounters the most prevalent organism most frequently and captures at least 10% of those at which it strikes. If the animal attacks a nauplius twice the diameter of a dinoflagellate in a hunting series and manages to capture it, the nauplius can provide as much as an order of magnitude more energy than the smaller particle on which it was feeding. Therefore, the feeding behavior of an individual anchovy larva is constrained by a) the concentration and kind of prey which will stimulate a feeding attack; b) the prey distribution; c) the physical and physiological limitation on the number of possible attacks; and d) the gut volume.

In the first analysis shown below, Vlymen's (1977) computer growth model** for Northern anchovy larvae is used with some modification to simulate a random distribution of two size ranges of particles, 45-55 μm and 95-105 μm in diameter. Therefore, on the first day of feeding, the larva is faced with a locally homogeneous environment containing a random selection of particles suitably sized for ingestion. The concentrations of the particles (Table 1) are such that they encompass the range for these sizes found by surveys in the Southern California Bight, the major spawning and feeding ground of the Northern anchovy. When one does this, concentrations of the two particles can be found that provide for metabolism at least, and growth when these concentrations are exceeded. This analysis assumes that the placement of large particles in the feeding queue of small particles is random, with the results given as the average growth rate for the population of first-feeding anchovy larvae on the first day.

*Hunter and Thomas (1974) have shown that the rate of larval anchovy feeding increases with increasing food density. Strike rates of anchovy larvae can be as high as 10 per minute, but usually average 4 to 5 per minute. We use 10 strikes per minute in this simulation model.

**Some of the terminology employed (e.g., size specific capture rates) is more general than actually required for this paper. The mathematics and notation used were chosen in order to simplify the adaptation of Vlymen's work and in anticipation of further work on the same topic.

Table 1

Analysis of average growth in millimeters of anchovy larvae for the first day of feeding in varying concentrations of organisms in two size ranges: 45-55 and 95-105 μm at 14.0°C, a 10% capture success rate and random distribution. Energy per each small particle is 4.236×10^{-5} cal. and for each large particles is 4.523×10^{-4} cal. based on caloric content of *Gymnodinium splendens* (Vlymen, 1977) and a copepod nauplius, respectively (Lasker, 1965).

Concentrations of 45-55 μm particles/ml	Concentrations of 95-105 μm particles/ml					
	0.00	0.001	0.01	0.1	1.0	10.0
0.0	-0.08	-0.08	-0.08	-0.08	-0.08	-0.02
1.0	-0.08	-0.08	-0.08	-0.08	-0.08	-0.01
10.0	-0.08	-0.08	-0.08	-0.08	-0.07	-0.01
20.0	-0.07	-0.07	-0.07	-0.07	-0.07	-0.01
30.0	-0.07	-0.07	-0.07	-0.07	-0.06	0.00
40.0	-0.06	-0.06	-0.06	-0.06	-0.06	0.00
50.0	-0.06	-0.06	-0.06	-0.06	-0.05	0.01
60.0	-0.05	-0.05	-0.05	-0.05	-0.05	0.01
70.0	-0.05	-0.05	-0.05	-0.05	-0.04	0.01
80.0	-0.04	-0.04	-0.04	-0.04	-0.04	0.02
90.0	-0.04	-0.04	-0.04	-0.04	-0.03	0.02
100.0	-0.04	-0.04	-0.04	-0.03	-0.03	0.02
200.0	-0.03	-0.03	-0.03	-0.03	-0.02	0.01
300.0	-0.03	-0.03	-0.03	-0.03	-0.02	0.00

If the larva could attack all prey in its visual field, the expected number of captures, N_c , would be the product of the number N of potential attacks (excursions), the probability of attack PA , the probability $PS(S)$ of actually selecting organisms of size S (in this analysis $PS(S)=1$), the relative frequency $R(S)$ of organisms of size S in the prey distribution and the probability of capture $PC(S)$, i.e., where $E(N_c)$ is the average number of prey captured,

$$E(N_c) = N PA \sum_{s=l}^u PS(S) R(S) PC(S)$$

where $N \leq N_{max}$, and $\sum_{s=l}^u$ indicates a summation over all sizes of acceptable or available prey.

Vlymen's (1977) model corrects the attack and capture rates for delays between each. In other words, once an attack is made, there is a finite time before the next attack. This is taken into consideration in programming the survival and growth of anchovy larvae feeding on different sized particles; the attack probabilities are calculated as defined in the program diagrammed in Figure 2.

The expected volume V_c of captured organisms will be

$$E(V_c) = N PA \sum_{S=\lambda}^u PS(S) R(S) PC(S) V(S)$$

where $N \leq N_{max}$

$$V_c \leq V_{max}$$

When $V(S)$ is the volume of organisms of size S , the gross energy return GE_c will be

$$E(GE_c) = N PA \sum_{S=\lambda}^u PS(S) R(S) PC(S) CAL(S)$$

where $CAL(S)$ is the calories per organism of size S and

$$N \leq N_{max}$$

$$V_c \leq V_{max}$$

$$S_1 = 45-55 \text{ } \mu\text{m}; S_2 = 95-105 \text{ } \mu\text{m}$$

$$N_{max} = 10 \text{ strikes/min} = 600/\text{hr.} = 7200/12\text{-hr. day}$$

$$PC(S) = \text{constant for any length}$$

$$PS(S_1) = PS(S_2) = 1$$

$N PA$ is calculated from Vlymen (1977) and is a function of total concentration

$$TC = C_1 + C_2 \text{ where } C_1 = 1, 10, 20, 30, 40, 50, 60, 70, 80,$$

$$90, 100, 200, \text{ and } 300/\text{ml and}$$

$$C_2 = 0.001, 0.01, 0.1, 1.0 \text{ and } 10.0/\text{ml.}$$

$$R(S_1) = \frac{C_1}{TC}, R(S_2) = \frac{C_2}{TC}$$

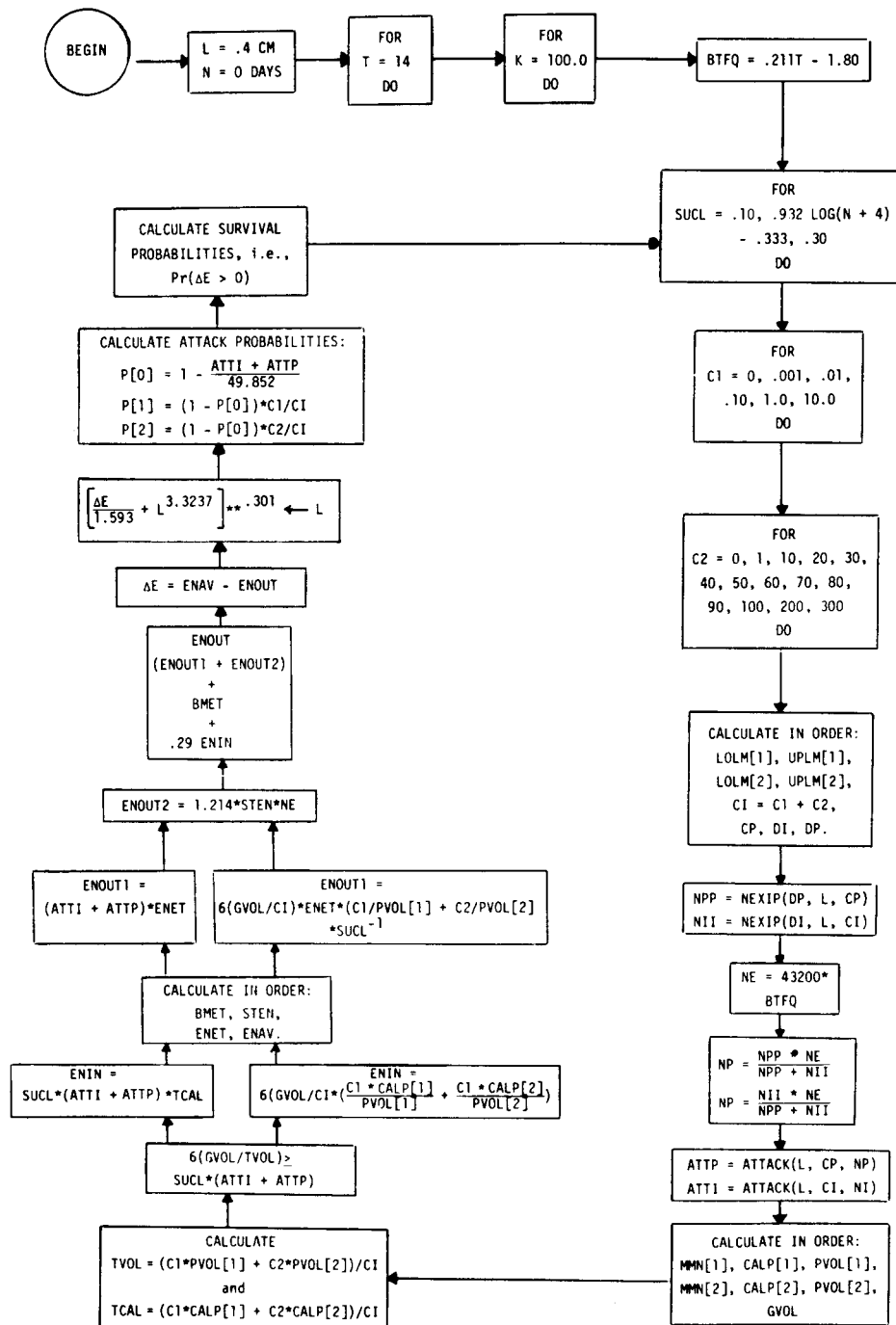


Figure 2. Program modified after Vlymen (1977) for determining survival and growth of first-feeding larval anchovy in various food concentrations. Notation after Vlymen (1977) follows:

L = larval anchovy length, 4 mm
N = 0, first day of feeding
T = 14.0°C
K = dispersion coefficient of 100.00, i.e. random distribution of prey
BTQ = temperature dependent excursion frequency
SUCL = age dependent success of capture function
C1 = concentration of small prey
C2 = concentration of large prey
LOLM = lower prey concentration limits
UPLM = upper prey concentration limits
CI = interpatch concentration
CP = intrapatch concentration
DP = patch diameter
DI = intrapatch distance
NEXIP (D,L,C) = number of steps required to traverse distance D in
concentration of food particles C by larva of length L
NPP = NEXIP (DP,L,CP) = number of excursions a larva of length L will
require to traverse a patch of radius DP and
concentration CP
NII = NEXIP (DI,L,C1) = number of excursions a larva of length L will
require to traverse an interpatch of radius DI
and particle concentration C1
NE = number of excursions in 12 hours of foraging
NP = proportion of total daily foraging excursions spent in patches,
and NI = in between patches
ATTACK (L,C,N) calculates the number of attacks on prey made by an anchovy
larva of length L with N excursions in prey concentration C; NI,
attacks between patches; NP, attacks in patches
CALP = caloric value of particles
MMN = size of particles
PVOL = volume of particle
GVOL = maximum gut volume of larva of length L
TVOL = total volume of particles eaten
TCAL = total calories of particles eaten
SUCL*(ATT1+ATTP) = particles successfully attacked
NE = number of excursions; excursions at night = 0.214 NE
STEN = energy per excursion
ENIN = energy in, or daily ration of calories
ENOUT1 = energetic debt of attacks
ENOUT2 = energetic debt of 24 hours of swimming, i.e. 1.214*NE*STEN
BMET = temperature and length dependent basal metabolic debt for 24 hours
ENAV = available energy or 0.48 ENIN
ENET = energy of attack = 3 STEN
0.29 ENIN = energy cost for mechanical processing of food
P[0] = probability of no attack
P[1] = probability of attack on small particle
P[2] = probability of attack on large particle

This simulation implies that the total number of particles in the larva's environment governs the frequency of strikes. The larger particles, even at their highest concentration, are ingested randomly (non-selectivity). Technically, despite the highest concentrations of the largest particles (e.g., nauplii), these must be taken very infrequently if the concentration of small particles is so high that the larger particles rarely show up in the feeding queue. Therefore, it is not the absolute concentration of the large particles that govern their capture by the larva, but rather their concentration relative to the larger number of small particles in the larval environment. Tables 1, 3 and 5 show the results of this simulation. A full discussion of these results is given in the following section.

A second analysis (Tables 2, 4 and 6) is based upon the same random arrangement of large particles among small particles, but

Table 2

Analysis of percent survival of anchovy larvae after the first day of feeding in varying concentrations of organisms in two size ranges: 45-55 and 95-105 μm at 14.0°C and random distribution. Attack rate is 10 per minute and success of capture is 10%. Energy per each small particle is 4.236×10^{-5} cal. and for each large particle is 4.523×10^{-4} cal. based on caloric content of *Gymnodinium splendens* (Vlymen, 1977) and a copepod nauplius, respectively (Lasker, 1965).

Concentrations of 45-55 μm particles/ml	Concentrations of 95-105 μm particles/ml					
	0.00	0.001	0.01	0.1	1.0	10.0
0.0	0.0	0.0	0.0	0.0	0.0	31.0
1.0	0.0	0.0	0.0	0.0	0.0	30.0
10.0	0.0	0.0	0.0	0.0	0.0	34.7
20.0	0.0	0.0	0.0	0.0	0.0	41.1
30.0	0.0	0.0	0.0	0.0	0.0	47.5
40.0	0.0	0.0	0.0	0.0	0.0	54.1
50.0	0.0	0.0	0.0	0.0	0.0	60.2
60.0	0.0	0.0	0.0	0.0	0.0	66.2
70.0	0.0	0.0	0.0	0.0	0.0	71.6
80.0	0.0	0.0	0.0	0.0	0.0	76.6
90.0	0.0	0.0	0.0	0.0	0.1	81.0
100.0	0.0	0.0	0.0	0.0	0.5	84.7
200.0	0.1	0.1	0.1	0.1	1.4	62.9
300.0	0.1	0.1	0.1	0.1	0.7	40.5

Table 3

Analysis of average growth in millimeters of anchovy larvae for the first day of feeding in varying concentrations of organisms in two size ranges: 45-55 and 95-105 μm at 14.0°C, a 20% capture success rate and random distribution. Energy per each small particle is 4.236×10^{-5} cal. and for each large particle is 4.523×10^{-4} cal. based on caloric content of *Gymnodinium splendens* (Vlymen, 1977) and a copepod nauplius, respectively (Lasker, 1965).

Concentrations of 45-55 μm particles/ml	Concentrations of 95-105 μm particles/ml					
	0.00	0.001	0.01	0.1	1.0	10.0
0.0	-0.08	-0.08	-0.08	-0.08	-0.07	0.07
1.0	-0.08	-0.08	-0.08	-0.08	-0.07	0.07
10.0	-0.07	-0.07	-0.07	-0.07	-0.05	0.08
20.0	-0.06	-0.06	-0.06	-0.05	-0.04	0.09
30.0	-0.04	-0.04	-0.04	-0.04	-0.03	0.10
40.0	-0.03	-0.03	-0.03	-0.03	-0.02	0.11
50.0	-0.02	-0.02	-0.02	-0.02	-0.00	0.12
60.0	-0.01	-0.01	-0.01	-0.01	0.01	0.13
70.0	0.00	0.00	0.00	0.01	0.02	0.14
80.0	0.02	0.02	0.02	0.02	0.03	0.15
90.0	0.03	0.03	0.03	0.03	0.04	0.15
100.0	0.04	0.04	0.04	0.04	0.05	0.16
200.0	0.06	0.06	0.06	0.06	0.07	0.13
300.0	0.06	0.06	0.06	0.06	0.06	0.10

the results are given in percent survival. Survival probabilities are calculated from the frequencies with which the 49,852 excursions (made by a larva in a 12-hour day) would end in an attack. Vlymen (1977) has assumed that "awareness" or conditions for an attack will occur when the number of particles within the visual field, K , is ≥ 1 and calculated this probability to be:

$$PA = Pr(K \geq 1) = 1 - e^{(-\lambda V_{pr})}$$

where V_{pr} is the volume of the visual field = $0.0159L^3$ where L , the length of the larva, is in centimeters and λ is concentration in number of prey per milliliter. The condition necessary for survival is that the energy balance $\Delta E \geq 0$; the available energy is calculated from the actual intake of N_1 small particles and N_2 large particles when food is limiting or from the maximum digestible volume of food estimated to be 6 * gut volume in a 12-hour day.

Table 4

Analysis of percent survival of anchovy larvae after the first day of feeding in varying concentrations of organisms in two size ranges: 45-55 and 95-105 μm at 14.0°C and random distribution. Attack rate is 10 per minute and success of capture is 20%. Energy per each small particle is 4.236×10^{-5} cal. and for each large particle is 4.523×10^{-4} cal. based on caloric content of *Gymnodinium splendens* (Vlymen, 1977) and a copepod nauplius, respectively (Lasker, 1965).

Concentrations of 45-55 μm particles/ml	Concentrations of 95-105 μm particles/ml					
	0.00	0.001	0.01	0.1	1.0	10.0
0.0	0.0	0.0	0.00	0.0	0.0	98.6
1.0	0.0	0.0	0.00	0.0	0.0	98.7
10.0	0.0	0.0	0.00	0.0	0.0	99.6
20.0	0.0	0.0	0.00	0.0	0.4	99.9
30.0	0.0	0.0	0.00	0.0	5.4	99.9
40.0	0.1	0.1	0.1	0.4	29.8	99.9
50.0	14.1	14.1	15.3	22.1	72.2	99.9
60.0	80.5	80.5	80.4	83.4	95.8	99.9
70.0	99.5	99.5	99.5	99.5	99.8	99.9
80.0	99.9	99.9	99.9	99.9	99.9	99.9
90.0	99.9	99.9	99.9	99.9	99.9	99.9
100.0	99.9	99.9	99.9	99.9	99.9	99.9
200.0	99.9	99.9	99.9	99.9	99.9	99.9
300.0	99.9	99.9	99.9	99.9	99.9	99.9

To simulate the conditions needed for survival (as opposed to average growth shown in Tables 1, 3 and 5), the following conditions must be met by the model: a) the energy balance is such that $\Delta E \geq 0$ (in Vlymen's notation $ENIN-ENOUT$), and b) the available energy is the smaller of either of two quantities, $ENIN = 0.48 [N_1 \text{ CAL}(S_1) + N_2 \text{ CAL}(S_2)]$ (i.e., the actual catch) or when food is not limiting,

$$ENIN = \frac{6 * \text{gut volume}}{C_1 + C_2} \left[\frac{C_1 \text{ CAL}(S_1)}{V(S_1)} + \frac{C_2 \text{ CAL}(S_2)}{V(S_2)} \right].$$

For any realization k of a trinomial, the relative frequency $f(N_{0,k}, N_{1,k}, N_{2,k})$ of obtaining $N_{0,k}$, $N_{1,k}$ and $N_{2,k}$ attacks on particles is

Table 5

Analysis of average growth in millimeters of anchovy larvae for the first day of feeding in varying concentrations of organisms in two size ranges: 45-55 and 95-105 μm at 14.0°C, a 30% capture success rate and random distribution. Energy per each small particle is 4.236×10^{-5} cal. and for each large particle is 4.523×10^{-4} cal. based on caloric content of *Gymnodinium splendens* (Vlymen, 1977) and a copepod nauplius, respectively (Lasker, 1965).

Concentrations of 45-55 μm particles/ml	Concentrations of 95-105 μm particles/ml					
	0.00	0.001	0.010	0.1	1.0	10.0
0.0	-0.08	-0.08	-0.08	-0.08	-0.06	0.12
1.0	-0.08	-0.08	-0.08	-0.08	-0.06	0.12
10.0	-0.07	-0.07	-0.07	-0.06	-0.04	0.13
20.0	-0.06	-0.05	-0.05	-0.05	-0.03	0.14
30.0	-0.03	-0.03	-0.03	-0.03	-0.01	0.16
40.0	-0.01	-0.01	-0.01	-0.01	0.01	0.17
50.0	0.00	0.00	0.00	0.00	0.02	0.18
60.0	0.02	0.02	0.02	0.02	0.04	0.19
70.0	0.03	0.03	0.03	0.04	0.05	0.20
80.0	0.05	0.05	0.05	0.05	0.07	0.22
90.0	0.06	0.06	0.06	0.06	0.08	0.23
100.0	0.08	0.08	0.08	0.08	0.09	0.24
200.0	0.11	0.11	0.11	0.11	0.11	0.19
300.0	0.11	0.11	0.11	0.11	0.11	0.16

$$f(N_{0,k}, N_{1,k}, N_{2,k}) = \frac{N!}{N_{0,k}! N_{1,k}! N_{2,k}!} P_0^{N_{0,k}} P_1^{N_{1,k}} P_2^{N_{2,k}}$$

where N = total number of excursions made by the larva (obtained from tail beat frequencies),

$N_0 = N - N_1 - N_2$ is the number of excursions in which no attacks have been made,

P_1 = probability of attack on small particles,

P_2 = probability of attack on large particles, and

$P_0 = 1 - P_1 - P_2$ is the probability of no attacks.

Table 6

Analysis of percent survival of anchovy larvae after the first day of feeding in varying concentrations of organisms in two size ranges: 45-55 and 95-105 μm at 14.0°C and random distribution. Attack rate is 10 per minute and success of capture is 30%. Energy per each small particle is 4.236×10^{-5} cal. and for each large particle is 4.523×10^{-4} cal. based on caloric content of *Gymnodinium splendens* (Vlymen, 1977) and a copepod nauplius, respectively (Lasker, 1965).

Concentrations of 45-55 μm particles/ml	Concentrations of 95-105 μm particles/ml					
	0.00	0.001	0.01	0.1	1.0	10.0
0.0	0.0	0.0	0.0	0.0	0.0	99.9
1.0	0.0	0.0	0.0	0.0	0.0	99.9
10.0	0.0	0.0	0.0	0.0	0.3	99.9
20.0	0.0	0.0	0.0	0.0	7.2	99.9
30.0	0.0	0.0	0.1	0.6	43.1	99.9
40.0	31.0	31.0	31.9	42.3	87.7	99.9
50.0	97.1	97.1	97.1	97.4	99.5	99.9
60.0	99.9	99.9	99.9	99.9	99.9	99.9
70.0	99.9	99.9	99.9	99.9	99.9	99.9
80.0	99.9	99.9	99.9	99.9	99.9	99.9
90.0	99.9	99.9	99.9	99.9	99.9	99.9
100.0	99.9	99.9	99.9	99.9	99.9	99.9
200.0	99.9	99.9	99.9	99.9	99.9	99.9
300.0	99.9	99.9	99.9	99.9	99.9	99.9

The probabilities $P_0 + P_1 + P_2 = 1$ and the attacks plus no attacks equal total number of excursions, i.e., $N_0 + N_1 + N_2 = N$.

To estimate survival over the first day of life, all $f(N_{0,k}, N_{1,k}, N_{2,k})$ must be determined to satisfy

$$.48 (N_{1,k} C_1 + N_{2,k} C_2) > ENOUT \text{ when } N_{1,k} V_1 + N_{2,k} V_2 \leq 6 * \text{gut volume}$$

or

$$\frac{.48 (N_{1,k} C_1 + N_{2,k} C_2) 6 * \text{gut volume}}{N_{1,k} V_1 + N_{2,k} V_2} > ENOUT$$

where $N_{1,k} V_1 + N_{2,k} V_2 > 6 * \text{gut volume}$.

In addition, since the maximum strike rate is 10/minute, we must impose the finite restriction that $N_1 + N_2 \leq 12 \text{ (hrs.)} \times 60 \text{ (min/hr)} \times 10 \text{ (strikes/min)} = 7200$.

Although all of the $N(N-1)$ possible outcomes have a finite probability of occurrence, the number of calculations can be significantly reduced by considering only outcomes in the ranges:

$$N P_0 - m \sqrt{N P_0 (1-P_0)} < N_{0,k} < N P_0 + m \sqrt{N P_0 (1-P_0)}$$

$$N P_1 - m \sqrt{N P_1 (1-P_1)} < N_{1,k} < N P_1 + m \sqrt{N P_1 (1-P_1)}$$

$$N P_2 - m \sqrt{N P_2 (1-P_2)} < N_{2,k} < N P_2 + m \sqrt{N P_2 (1-P_2)}$$

where $N_{2,k} = N - N_{0,k} - N_{1,k}$ and where m represents the number of standard deviations and can be made as large as necessary. In this calculation, $m=4$ so that the probability of any outcome falling outside the range will be negligible except for the very lowest particle densities; i.e., for estimating survival of say $<0.01\%$.

The probabilities P_0 , P_1 and P_2 are determined as follows:

$$P_0 = 1 - (ATTI + ATTP)/49,852 \quad (\text{Figure 2})$$

where P_0 is the probability of no attacks and

$1 - P_0$ is the probability of attack on either large or small particles, and $ATTI + ATTP$ is the total number of attacks.

$$\text{Then } P_1 = (1 - P_0) \left(\frac{C_1}{C_1 + C_2} \right)$$

$$\text{and } P_2 = (1 - P_0) \left(\frac{C_2}{C_1 + C_2} \right)$$

where C_1 = concentration of small particles,

C_2 = concentration of large particles.

RESULTS OF SIMULATED FEEDING BY FIRST-FEEDING ANCHOVY LARVAE

Minimum survival by first-feeding anchovy larvae to a second day of feeding depends on threshold concentrations of small particles and not on the presence or absence of large particles. From Tables 2, 4 and 6, large particles can be seen to enhance survival, but even in the highest concentration of large particles ever recorded from the Northern anchovy larva's environment, about 0.3/ml, and with capture success set at the highest level possible (30%), anchovy larvae can neither grow nor survive the first day of feeding on a diet of large particles alone. A probable food environment that the larva encounters is a proportion of small to large food particles of 30:0.1 or 30:0.01 per milliliter. At 30 small particles per milliliter, no anchovy larvae will survive the first day (Table 6). Only when large particles become prevalent at this low concentration of small particles, i.e., when there are between 0.01 and 0.1/ml or 10 to 100 per liter, is there a small increase in survival, although average growth remains negative. However, the difference in growth and survival is striking when the larva has in its immediate environment 40 small particles per milliliter instead of 30. Survival in this instance is increased to 31% and large particles make little difference even in concentrations as high as 0.1 per milliliter. Above 0.1 per milliliter (100/L) of large food particles, survival becomes greatly enhanced as long as 40 small particles per milliliter are also present. At concentrations greater than 10/ml, the distance of a first-feeding larva from its nearest possible food item is within its perceptive field, 2.7 mm (Hunter, 1972). The distance at 30 and 40 particles per milliliter are 1.78 to 1.62 mm, respectively (Gallagher and Burdick, 1970). This may be a critical range for the larva.

It is clear from the simulation of a 10% capture success rate shown in Tables 1 and 2 that under virtually all concentrations and combinations of food, a concentration of nauplii not yet seen in the sea, 10/ml (10,000/L), is needed to insure reasonable survival to the second day of feeding. At 20 and 30% capture rates, there is good agreement with the experimental data of O'Connell and Raymond (1970) who found that there was good survival of young anchovy larvae at naupliar concentrations of 4000/L, also abnormally high when compared to concentrations found in the ocean.

P. E. Smith (personal communication) believes that survival after the first day of feeding, as deduced from field collections, can be as high as 75%. This value is encountered in this simulation in concentrations of prey frequently found in the sea in dinoflagellate blooms (i.e., where small particles are between 40 and 50/ml) and emphasizes the importance of spatial and temporal aggregations of food patches in the larva's environment.

When the capture success rate is low (10%, Tables 1 and 2), this increases the negative aspect of having large numbers of small particles available to the larva. It is evident that the larva is so occupied by attacks on energy-poor particles and that it rarely encounters and cannot capture enough large, energy-rich particles at this low capture success rate to survive or grow through the first day of feeding.

Tables 3 and 4 illustrate the results of an intermediate capture success rate, 20%. Positive growth is only achieved when 70-80 small food particles per milliliter are available (Table 3) and there is very little to be gained by having large particles in the environment unless they are in hundreds per liter. Survival (Table 4) is achieved at much lower concentrations of small particles with the critical value about 50/ml. Survival enhancement by large food particles occurs in this simulation when 10-100/L of these are present coincidentally with the larger number of smaller particles.

THE RELATION BETWEEN PHYTOPLANKTON AND ZOOPLANKTON SPATIAL DISTRIBUTION AND LARVAL ANCHOVIES IN THE SEA

It is logical to inquire to what extent the concentrations of small and large food particles needed for adequate survival and growth of first-feeding anchovy larvae are found in the Northern anchovy spawning ground during the spawning season, December through March.

Phytoplankton

In 1974, Lasker (1975) found that chlorophyll maximum layers occasionally contained particle densities which could provide good feeding for first-feeding anchovy larvae. For example, in a series of stations along the California coast near Los Angeles, the densities of the dinoflagellate *Gymnodinium splendens* induced feeding by first-feeding anchovy larvae (on shipboard) at concentrations from 34 to more than 300 per milliliter. *Gymnodinium* was present as an apparently continuous patch which extended along the coast approximately 100 kilometers. An important observation was that stormy conditions were found to disrupt these layers and reduce the minimum densities below threshold levels for larval anchovy first feeding.

In a later study, Lasker (1978) reported on an extensive survey made along the California and Baja California coasts in 1975 where he sought to detect areas of anchovy spawning where particle densities were above minimum thresholds for first-feeding larval anchovy. He found a remarkable patch of the dinoflagellate

Gonyaulax polyedra extending from at least Point Conception to the Mexican border, a distance of 300 kilometers. The seaward extent of this very large patch ranged from a few kilometers in December 1974 to 40 kilometers in January 1975; the latter extending across the Southern California Bight from the mainland shore to the Channel Islands.

The vertical distribution of dinoflagellate patches has been studied from time to time. Sharp chlorophyll maxima coincide with dinoflagellate maxima but, with current sampling gear, these patches seem to be many meters thick. However, Kiefer and Lasker (1975) analyzed the vertical migration of *Gymnodinium splendens* populations and got very sharp chlorophyll maxima only 1 to 2 meters thick (Figure 3). Visual sightings of dinoflagellate blooms at the surface often give the familiar red or rust color of a "red tide." In 1976, the rich Peruvian upwelling system experienced a vast bloom of *Gymnodinium splendens* which became so dense in some places that hydrogen sulfide was produced when the organisms died. In Peru this phenomenon is known as "aguaje" and extended from Pimental to Matarani, a distance of 2,000 kilometers, in a more or less continuous patch (B. Rojas de Mendiola and J. Valdivia of the Instituto del Mar del Peru, personal communication).

In 1975, when *Gonyaulax polyedra* was the dominant particle in the feeding size range of first-feeding anchovy larvae and *Gymnodinium splendens* similarly dominated the Peruvian upwelling system, it is tempting to speculate that *Engraulis mordax* first-feeding larvae ate *Gonyaulax* in numbers off California while the Peruvian anchovy first-feeding larvae, *Engraulis ringens*, were eating *Gymnodinium*. In the former, because of the poor nutritional value of *Gonyaulax*, a poor year class would have been expected while in the latter we would have expected to see a good year class. Complicating the *Gonyaulax* situation in 1975, however, was the fact that a massive upwelling in the midst of the anchovy spawning season destroyed the patches of *Gonyaulax* and in fact severely reduced particle concentrations below the threshold needed for gut filling and metabolic needs of first-feeding larvae. Indeed, the 1975 year class of the Northern anchovy was very poor compared to other years (Sunada, California Department of Fish and Game, personal communication) while the Peruvian anchovy showed a resurgence from previous low levels in its 1975 year class. While these are at present only single observations, they suggest that it may be worthwhile to investigate both particle densities and distribution and nutritional content of larval anchovy food to forecast whether a recruitment will be successful or not. Microzooplankton concentrations never exceeded 30 per liter in hundreds of samples taken during 1974 and 1975 in the California studies described above.

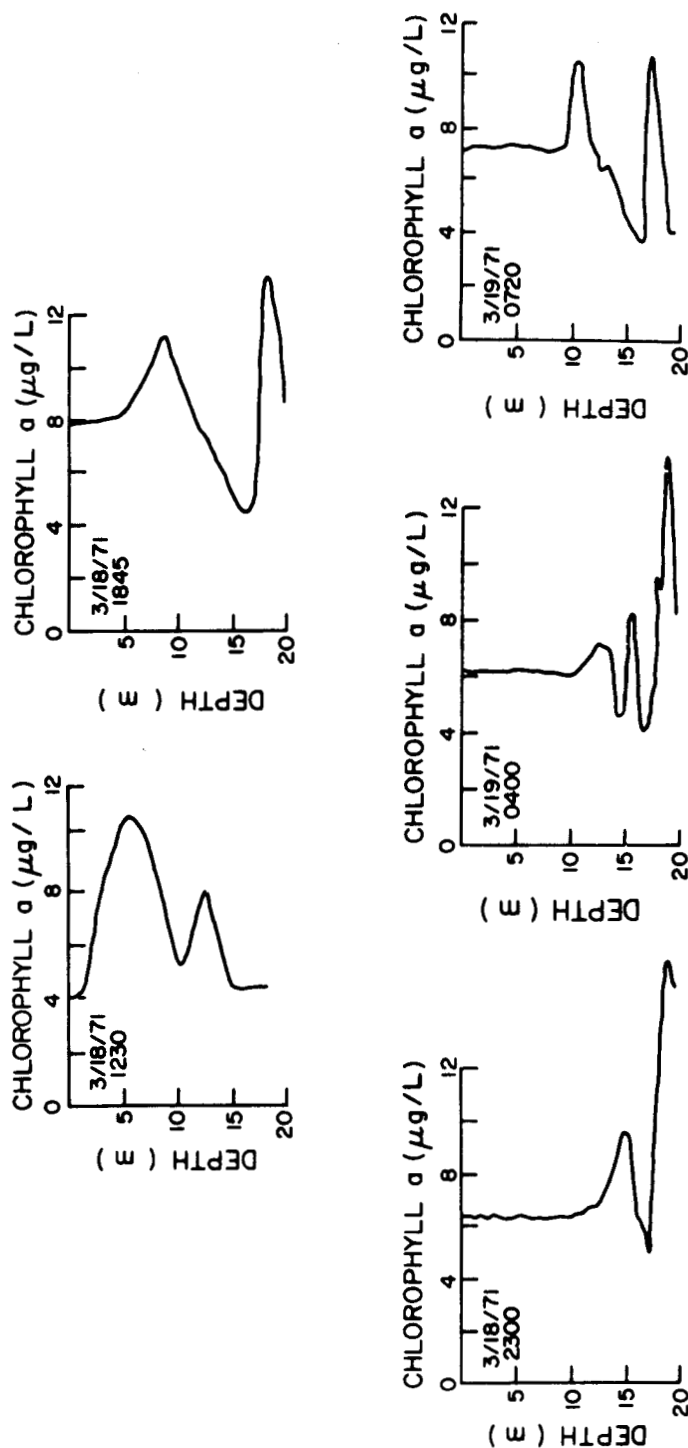


Figure 3. Profiles of the concentration of chlorophyll *a* based upon fluorescence profiles. The upper layer of *Gymnodinium splendens* at 1230 h was concentrated at 6 m; by 1845 it had moved to 8 m and reached 15 m by 2300. Movement upward commenced at 0200 reaching 10 m by 0720. The lower layer remained relatively close to the bottom during this time. Profiles were obtained in Coyote Bay, Bahia Concepcion, Mexico (lat. 26°43.0'N, long. 111°53.0'W) (from Kiefer and Lasker, 1975).

Zooplankton

When food is found in anchovy larvae intestines, it usually consists of copepod nauplii, copepod eggs and a variety of similarly small microzooplankters, regardless of where the anchovy population is found*. Yet, as we indicated before, the sampled densities of these potential food organisms have always seemed to be too low to maintain engraulids. This conflicting evidence leads one to believe that patches of microzooplankton may be prevalent in productive areas where anchovies are found, but present sampling gear underestimates the concentration factor. On occasion, when a sample of water is discovered to have a large number of nauplii or other microzooplankters, the sample, when retaken in the same place, does not duplicate the results. However, on one occasion, Lasker (1978) showed that in samples containing over 100 microzooplankters per liter taken 0.8 km apart, i.e., 2 and 2.8 km from the California shore, there was a remarkable coherence in the numbers and size distribution of copepod nauplii and post-naupliar copepods (Figure 4). This duplication indicated that a patch of at least 0.8 km in linear extent offshore was sampled despite a prevailing along-shore current. It should also be noted that motile phytoplankton food reproduce on an hourly or daily scale while nauplii are a stage in a copepod life cycle of several weeks. The predation on copepods by a major fish population like the Northern anchovy could cumulatively have a marked depressant effect on the local abundance of nauplii.

The point we wish to make is that temporal and spatial stability of the ocean is a prerequisite for successful feeding by clupeid larvae. Food organisms must have time to aggregate and, once patches are formed, they must have a sufficiently long life to permit larval fish feeding. However, it is much more likely that there will be aggregations of small particles than large ones and this in turn favors first day larval survival and growth.

The model described here to determine adequate feeding of various size particles for first-feeding anchovy larvae can be extended to older larvae as Vlymen (1977) has shown in his analysis of the effect of prey microdistribution to larval anchovy growth.

*Most of the anchovy larvae examined have no food in their intestines. Whether this is due to rough treatment in plankton nets, to the severity of the usual Formalin preservation, or is the normal situation in the sea is not known. Kjelson *et al.* (1975) have shown, however, that menhaden larvae lose much of their gut contents with rough laboratory handling equivalent to field capture.

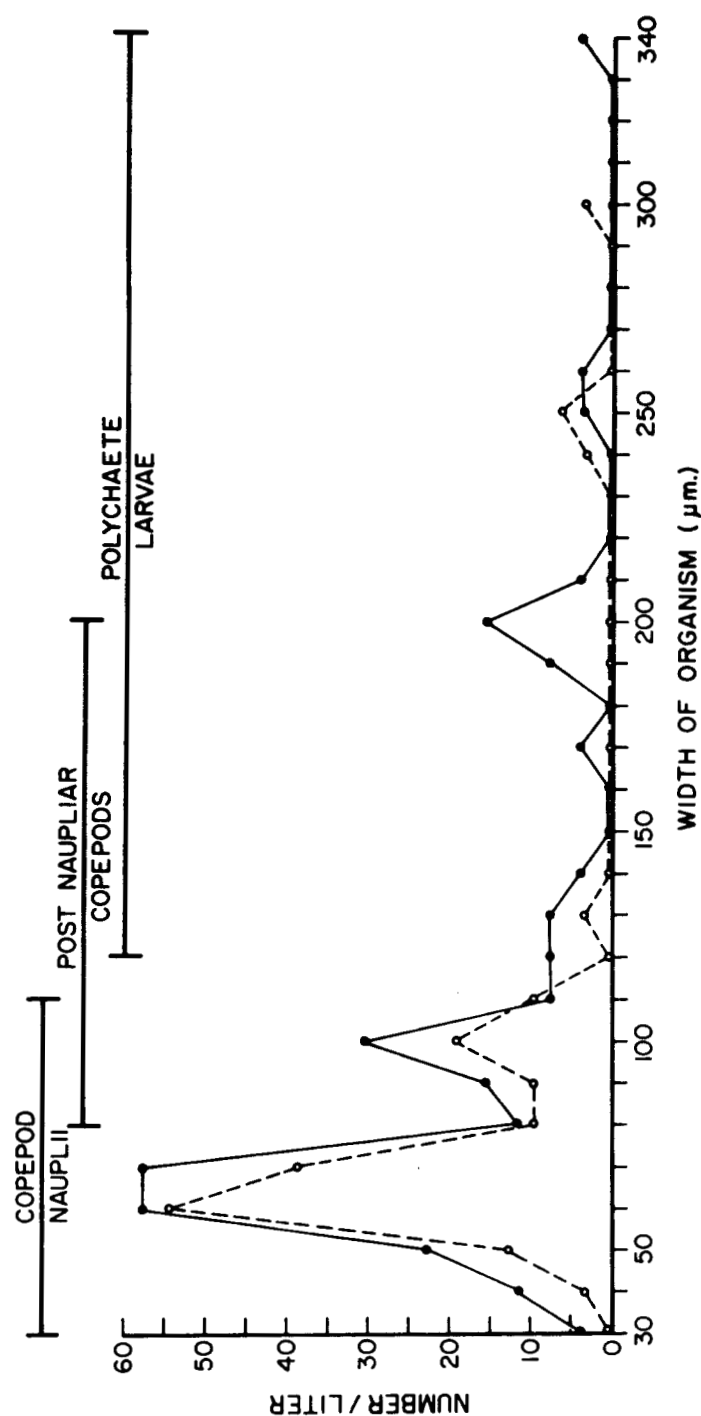


Figure 4. Width frequency distribution of two samples of microzooplankton taken from the chlorophyll maximum layer in March 1976, 0.8 km apart within 2 km of the shore off San Onofre, California. Closed circles indicate the sample taken nearest the shore which contained 280 microzooplankters per liter. The other sample contained 117 microzooplankters per liter. These were the only two of hundreds of pump samples taken in the Southern California Bight over a 3-year period which contained more than 100 microzooplankters per liter (from Lasker, 1978).

We know from the simulation presented in this paper that the enigma presented by the lack of reasonably large numbers of nauplii in the sea for larval anchovy food may be explained because the larvae don't need them, nor do the larvae encounter them with a sufficiently high frequency for these large particles to make more than a token contribution to survival and growth on the first day of feeding.

SUMMARY

Based on laboratory and field data, a simulation model of first-feeding anchovy larvae, *Engraulis mordax*, was constructed to investigate the effect of different prey size on survival and growth. First-feeding, naive anchovy larvae must depend almost entirely on small particles (ca. 45 μm diameter) for early survival, despite their ability to capture large particles. The absolute concentration of large particles (ca. 90 μm diameter) does not govern their capture by the larvae; rather, the more numerous small particles distract the larvae from capturing large particles. Simulation shows that a 10% prey capture efficiency will not suffice for survival or growth and that, at higher capture efficiencies (20-30%), there is a threshold of 30-50 small particles per milliliter needed for substantial survival and growth. Large particles, e.g., copepod nauplii, can enhance survival when they reach concentrations between 10 and 100 per liter in the same environment containing above-threshold numbers of small particles. An important distinction is made between survival and average growth; it is shown that larvae may survive in significant numbers in feeding regimes in which the average growth for the population is negative. These results are discussed in relation to actual field data from the spawning ground of the Northern anchovy.

ACKNOWLEDGEMENTS

We thank Dr. William J. Vlymen, radiologist-bioengineer, Stanford University Medical Center, for his generous help. Partial funding for this work was provided by the Oceanography Program of the Brookhaven National Laboratory, Energy Research and Development Administration (ERDA), Upton, Long Island, New York.

REFERENCES

- Arthur, D. K., 1976: Food and feeding of larvae of three fishes occurring in the California Current, Sardinops sagax, Engraulis mordax, and Trachurus symmetricus. Fish. Bull. U.S., 74, 517-530.
- Arthur, D. K., 1978: Differences in heart size between ocean-caught and laboratory-grown larvae of the northern anchovy, Engraulis mordax: implications for larval behavior and survival. J. Exp. Mar. Biol. Ecol., in press.
- Gallagher, B. S. and J. E. Burdick, 1970: Mean separation of organisms in three dimensions. Ecology, 51, 538-540.
- Gulland, J. A. and L. K. Boerema, 1973: Scientific advice on catch levels. Fish. Bull. U.S., 71, 325-335.
- Hjort, J., 1914: Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. P.-v. Reun. Cons. Perm. Int. Explor. Mer., 20, 1-228.
- Hunter, J. R., 1972: Swimming and feeding behavior of larval anchovy, Engraulis mordax. Fish. Bull. U.S., 70, 821-838.
- Hunter, J. R., 1976: Culture and growth of northern anchovy, Engraulis mordax, larvae. Fish. Bull. U.S., 74, 81-88.
- Hunter, J. R., 1977: Behavior and survival of northern anchovy, Engraulis mordax, larvae. Cal. Coop. Fish. Invest. Rep., 19, in press.
- Hunter, J. R. and C. Sanchez, 1976: Diel changes in swim bladder inflation of the larvae of the northern anchovy, Engraulis mordax. Fish. Bull. U.S., 74, 847-855.
- Hunter, J. R. and G. Thomas, 1974: Effect of prey distribution and density on the searching and feeding behavior of larval anchovy, Engraulis mordax Girard. In The Early Life History of Fish, J.H.S. Blaxter (ed.), pp. 559-574, Springer-Verlag, Berlin.
- Kiefer, D. A. and R. Lasker, 1975: Two blooms of Gymnodinium splendens, an unarmored dinoflagellate. Fish. Bull. U.S., 73, 675-678.
- Kjelson, M. A., D. S. Peters, G. W. Thayer and G. N. Johnson, 1975: The general feeding ecology of postlarval fishes in the Newport River estuary. Fish. Bull. U.S., 73, 137-144.
-

- Lasker, R., 1964: An experimental study of the effect of temperature on the incubation time, development and growth of Pacific sardine embryos and larvae. Copeia 1964, 399-405.
- Lasker, R., 1965: The physiology of Pacific sardine embryos and larvae. Calif. Coop. Ocean. Fish. Invest. Rep., 10, 96-101.
- Lasker, R., 1975: Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull. U.S., 73, 453-462.
- Lasker, R., 1978: The relation between oceanographic conditions and larval anchovy food in the California Current: identification of factors contributing to recruitment failure. Rapp. P.-v. Reun. Cons. Int. Explor. Mer., 173, 212-230.
- Lasker, R., H. M. Feder, G. H. Theilacker and R. C. May, 1970: Feeding, growth and survival of Engraulis mordax larvae reared in the laboratory. Mar. Biol., 5, 345-353.
- Murdie, G., 1971: Simulation of the effects of predator/parasite models on prey/host spatial distribution. In Statistical Ecology, G. P. Patil, E. G. Pielou and W. E. Waters (eds.), Vol. 1, pp. 215-233, The Pennsylvania State University Press.
- O'Connell, C. P. and L. P. Raymond, 1970: The effect of food density on survival and growth of early post-yolk-sac larvae of the northern anchovy (Engraulis mordax Girard) in the laboratory. J. exp. mar. Biol., 5, 187-197.
- R. de Mendiola, B., 1974: Food of the larval anchoveta Engraulis ringens J. In The Early Life History of Fish, J.H.S. Blaxter (ed.), pp. 277-285, Springer-Verlag, Berlin.
- Scura, E. D. and C. W. Jerde, 1977: Various species of phytoplankton as food for larval northern anchovy, Engraulis mordax, and relative nutritional value of the dinoflagellates Gymnodinium splendens and Gonyaulax polyedra. Fish. Bull. U.S., 75, 577-583.
- Vlymen, W. J., 1974: Swimming energetics of the larval anchovy, Engraulis mordax. Fish. Bull. U.S., 72, 885-899.
- Vlymen, W. J., 1977: A mathematical model of the relationship between larval anchovy (Engraulis mordax) growth, prey microdistribution, and larval behavior. Environ. Biol. Fishes, 2, 211-213.
-