

A mathematical model of the relationship between larval anchovy (*Engraulis mordax*) growth, prey microdistribution, and larval behavior

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Synopsis

A prey concentration dependent random walk model of feeding behavior in larval anchovy based on behavioral experiments was used in conjunction with an experimentally verified Markov chain prey attack rate model to evaluate the relationship between anchovy larval growth from 0.4 to 2.0 cm at various levels of contagion and temperature in the food prey environment. Contagion was regarded as being described by the negative binomial distribution while the actual prey particle size distribution was taken from actual prey particle surveys in areas where anchovy larvae are found. Other important physiological parameters necessary for the construction of the model are taken from existing literature and a description of the complete computer integration of the various submodels presented. Results demonstrate the extreme importance of food microstructure geometry and behavior in the growth rates and growth curves of the anchovy larvae. In particular extremely nonlinear growth rates as functions of contagion are observed in the model with the highest growth rates not occurring at the highest level of prey contagion. The implications these results have in explaining current paradoxes between laboratory-grown larval anchovy prey concentration requirements and those found in the ocean are discussed. Also, the relationship between physical oceanography and larval survival is discussed in light of the results in addition to the need for a more detailed understanding of food prey microstructure in larval ecology.

Introduction

The survival of fish larvae in the open ocean has long been a question of great interest to biological oceanographers for both practical and theoretical reasons.

From a practical standpoint this interest stems primarily from the rather inconsistent relationship observed between the size of spawning populations of fish and the size of subsequent year classes. This relationship is believed to exist because of large scale fluctuations in larval mortality due to unassessable changes in predation, food availability, and other important environmental variables affecting larval survival and the effect larval survival ultimately has on recruitment. Thus, the practical importance of larval survival is its relationship to recruitment and how recruitment is variously used in fisheries management. Gulland (1973), however, states that at present, despite the vast amount of laboratory and field work on food chain analysis and its relationship to fish production, no promising and practical method exists to predict adequately recruitment short of vast and costly enterprises extended over long periods of time.

The theoretical interest in larval fish survival primarily centers on the relationship the young fish have to the whole ecological structure in which they find themselves. In the case of the larval anchovy, an intriguing aspect of such studies has been the apparent discrepancy between the density of appropriate food in the laboratory required for moderate growth and the density of analogous food types in the ocean where anchovy larvae are distributed (Kramer & Zweifel 1970, Lasker et al. 1970, Hunter 1972, 1976, 1977). This discrepancy has led most observers to conclude that rich feeding grounds must exist in the areas where anchovy larvae live which are not adequately detected by current sampling schemes. That is, although the mean densities of food particles ob-

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served would not support larval anchovy growth, isolated areas must exist in the sea, despite the mean density estimates, which can very adequately support such growth.

It was this reasoning which led Lasker (1975) to the successful search for such advantageous feeding grounds in the habitats of the larval anchovy and to study the relationship of such habitats to successful first feeding. This work pointed up the importance of more focused analysis on environmental food aggregations and how possible alterations of these aggregations could have important implications for larval survival. Lasker is no doubt correct that such habitats are truly advantageous to first feeding larvae as evidenced by the ability of his laboratory-reared larvae to fill their guts rapidly when placed in water drawn from these regions. However, these rich food areas probably cannot alone completely account for the immense success of the anchovy larvae which support the size of the population believed to exist off the California coast. That is, the blooms of *Gymnodinium* and other phytoplankters found by Lasker (1975), although excellent for first feeding larvae, will not support the young fish to a length exceeding 5.0 mm (Hunter 1977). Therefore, either other appropriate food types are aggregated in the blooms which allow the larvae to continue to grow or young fish can and do survive in other areas where such appropriate food types can exist in sufficient density.

These considerations naturally give rise to the question of the relationship between the amount and geometric distribution of food in the environment of larval anchovies and the animal's growth rate and ultimate survival. However, such questions require for their solution relatively detailed understanding of both the structure of the important environmental parameters on small scales and the behavioral and physiological modifications of the larvae induced by such parameters. Unfortunately, too little is known at the necessary scale about the food structure of the larval anchovy to permit a completely realistic formulation of these relationships. A sufficient amount of information, however, is now available about the changes induced in the behavior and physiology of anchovy larvae 0.4 to 2.0 cm in length by different environmental factors to allow an attempt at such an understanding dependent on building a realistic model of the food microstructure from available data. Such an approach has the advantage of being species specific and of being able to test environmental structures at scales not detected with current sampling schemes. The results obtained can be compared with

known laboratory growth studies and provide an insight into the small-scale relationships in the ocean which may have significant consequences for the survival of these organisms and which cannot be assessed with present methods.

It is the purpose of this paper to construct and analyze a model that will simulate dynamically the interrelationship between the anchovy's larval physiology and behavior and its food microdistribution, particularly as they affect larval growth. The model will simulate the growth of the larvae at the beginning of exogenous nutrition from 0.4 cm to the onset of schooling at 2.0 cm for various levels of contagion of food organisms. This range was selected because our knowledge of behavioral and physiological modulations by the environment have only been determined quantitatively for these size ranges. The model will be presented in five sections each dealing with the major components required to construct the complete system. The assumptions underlying each submodel will be discussed and data presented to verify the predictions of the submodels when such data exists. The complete system of submodels and the flow diagram of their interactions will be presented in a final section, and the growth simulations created using the complete system analyzed and discussed. The implications these studies have for larval growth requirements in the ocean and the need for possible alternative investigative methods or approaches to the study of the larval food microenvironment will then be re-evaluated in light of the model obtained.

A random walk model of larval anchovy feeding behavior

The foraging behavior of the larval anchovy has been well documented and analyzed (Hunter 1972, Hunter & Thomas 1973) and, in general, is well suited to mathematical modeling. This is primarily because larval anchovy forage behavior can be easily separated into discrete excursion elements in three dimensions (Hunter 1972, Vlymen 1974). Foraging behavior by the larval anchovy is not a purely random three dimensional motion but rather one that within distances comparable to the larval length exhibits only small excursions perpendicular to the previous direction of motion. This allows for the application of a behaviorally-modified three dimensional random walk which models the significant elements of the animal's foraging behavior as observed in the laboratory.

The classical random walk problem in three di-

mensions effectively seeks to calculate the mean distance traveled after N steps or excursions of fixed length when each subsequent excursion is taken at a random orientation or heading from the preceding (Debye 1946). Casual observation of foraging anchovy larvae may suggest this to be an appropriate description but if such a description was correct it would imply that at each motion the probability of relatively 'behind' excursions i.e., in the opposite direction to the previous excursion, was approximately the same as relatively 'forward' excursions i.e., in the same direction as the previous excursion. For a fish larva which has forward binocular vision and which morphologically is designed for basically forward motions, this seems to be a too unrestricted and unrealistic description. The more likely description of the situation is that forward excursion probabilities are weighted or preferred by the larva with the degree of preference being determined by environmental factors.

This type of behavior was quantitatively elucidated by Hunter & Thomas (1973) who utilized a four direction, two dimensional bounded random walk analysis to investigate the effect of prey distribution and density on the searching and feeding behavior of larval anchovy. They found a distinct preference for 'ahead' motions that were continuously modulated by prey density and which ultimately affected the amount of area searched as calculated by their analysis. That is, high food density tended to equalize the value of each of the four directional probabilities they measured and to decrease the area covered by the anchovy, while low food densities tended to increase the ahead probabilities compared to the other three and to increase the amount of area covered. Hunter & Thomas (1973) felt this behavioral modulation had significant survival implications because it allowed anchovy larvae to remain in areas of high food density longer and thus increase their food ration and ultimate survival.

The data obtained by Hunter & Thomas (1973) suggests that an adequate continuous mathematical description of this behavior could be attained by use of the circular normal distribution. This distribution has had wide application in the study of biological phenomena and a thorough discussion of its use in the biological sciences can be found with relevant bibliography in Batschelet (1965). Using the notations of Batschelet (1965), the density function, $f(\alpha)$, for the circular normal distribution is given by

$$f(\alpha) = \frac{1}{2\pi I_0(k)} e^{k \cos(\alpha - \psi)} \quad (1)$$

where ψ is the angle where $f(\alpha)$ takes its maximum value, k is a coefficient of concentration or, as I call it here, the dispersion coefficient (to prevent confusion with particle concentrations later on) and $I_0(k)$ is the modified Bessel function of the first kind. This density function says in effect that the probability of an angle heading by the feeding larval anchovy in the range α to $\alpha + d\alpha$ is given by $f(\alpha)d\alpha$ and is greatest for headings or angle directions in the vicinity of ψ . That is, the circular normal distribution has an inherent central tendency, the degree of which is determined by k , the dispersion coefficient. The analogy to the results of Hunter & Thomas (1973) is now clear and the foraging pattern can be described by a circular normal distribution with a food concentration dependent dispersion coefficient $k(c)$, where c is the food concentration in particles-cm⁻³. For simplicity and without loss of generality, ψ can be assumed to be zero, as the choice of the coordinate system is arbitrary. Thus, the 'forward' direction will be regarded as having the heading 0, 'left' $\pi/2$, 'behind' π , and 'right' $3\pi/2$ where the directions are in the sense of Hunter & Thomas (1973). Now the description of the foraging behavior as I have reformulated it is as follows. Let an anchovy larva be allowed to execute foraging excursions starting at an arbitrary angle heading θ in a concentration of food particles c . The probability that the i th excursion has a heading between θ_i and $\theta_i + d\theta_i$ is then given by

$$\frac{e^{k(c) \cos \theta_i}}{2\pi I_0(k(c))} d\theta_i \quad (2)$$

and constitutes the formulation for the heading probabilities that will be used in the subsequent random walk derivation.

The functional relationship $k(c)$ can be found by computing k using the directional probabilities for each concentration of food type as given in Hunter & Thomas (1973). The method used is outlined in Batschelet (1965) and consists of first finding the empirical mean vector which points toward the center of mass of the food concentration data. If we designate the directional probabilities at each concentration of food type by $p_i(c)$ then the components of the mean vector are given by

$$\rho_x(c) = \sum_i p_i(c) \cos \theta_i \quad (3)$$

$$\rho_y(c) = \sum_i p_i(c) \sin \theta_i \quad (4)$$

where the θ_i , refer to the four directions given above.

The magnitude of ρ is given by

$$\rho(c) = \sqrt{\rho_x^2 + \rho_y^2}$$

and for the circular normal distribution this turns out to be related to k in the following manner

$$\rho(c) = \frac{I_1(k(c))}{I_0(k(c))}, \quad (5)$$

where $I_1(k(c))$ is the modified Bessel function of the second kind. The results of the above analysis using the data in Hunter & Thomas (1973) are shown in Figure 1 and the least squares fit to the data yields the relation

$$k(c) = 1.47 c^{-0.247} \quad (6)$$

This relation has the desired characteristic of a decreasing dispersion coefficient i.e., reducing the tendency to go straight ahead as the food concentration increases.

The anchovy larva's movements may now be regarded as a random walk in three dimensions with a circular normal heading probability distribution which in turn incorporates a food density dependent dispersion coefficient. What is needed is an estimate of the mean square distance traveled, $\langle r^2 \rangle$, where brackets refer to an average over all geometric configurations of the system, after N excursions or steps of length 1. Since the larva's foraging activity has a constrained or restricted heading probability in three dimensions, recourse can be made to a large body of literature dealing with such systems namely, the statistical mechanics of chain molecules and in particular their growth by sequential covalent linkage. The definitive exposition of such systems is the treatise by Flory (1969) and his development of an expression for the characteristic ratio, $C_N \equiv \frac{\langle r^2 \rangle}{Nl^2}$ of a polymer chain with N angle restricted covalent bonds of length 1. Following the notation of Flory (1969), the identical development can be done making appropriate changes consistent with the different heading probability distribution being used.

The configurational average of the projection of the $i + k$ -th excursion vector on the i -th is

$$\left\langle \tilde{l}_i \cdot \tilde{l}_{i+k} \right\rangle = l^2 \prod_{j=i}^{i+k} \cos \theta_j, \quad (7)$$

where $|\tilde{l}_i| = 1$ for all i and θ_i is the angle heading regarding the $i - 1$ -th as zero. This expression can then

be used in the expression for $\langle r^2 \rangle$ which is

$$\left\langle r^2 \right\rangle = Nl^2 + 2 \sum_{i < j}^N \left\langle \tilde{l}_i \cdot \tilde{l}_j \right\rangle,$$

where $0 < i < j \leq N$. Thus from the above

$$\begin{aligned} \langle r^2 \rangle &= Nl^2 + 2l^2 \sum_{i < j}^N \prod_{m=i}^j \cos \theta_m \\ &= Nl^2 + 2l^2 \sum_{k=1}^{N-1} (N-k) \prod_{m=1}^k \cos \theta_m, \quad (8) \end{aligned}$$

where in the last step we have combined terms where $j - i = k$. In this case the last step is not totally justified because the set $\{\theta_i\}$ does not have the property that for $j - i = j' - i' = k$

$$\prod_{m=i'}^{j'} \cos \theta_m = \prod_{m=i}^j \cos \theta_m$$

as in the analogous development for the polymer chain where $\theta_i = \theta_j$ for $i, j \leq N$. However, in our development the θ_i are normally distributed about the initial heading, and since the ensemble average is desired, the average over θ , $\langle C_N \rangle_\theta$, where such an identity is correct is computed and the derivation follows

accordingly. To show this replacing $\prod_{m=i}^j \cos \theta_m$ by

$$\begin{aligned} \left\langle \prod_{m=i}^j \cos \theta_m \right\rangle_\theta &\text{ we must show that } \left\langle \prod_{m=i}^j \cos \theta_m \right\rangle_\theta \\ &= \left\langle \prod_{m=i'}^{j'} \cos \theta_m \right\rangle_\theta \text{ when } j' - i' = j - i = k. \text{ Because of} \end{aligned}$$

the probability distribution of the θ_m we get,

$$\begin{aligned} \left\langle \prod_{m=i}^j \cos \theta_m \right\rangle_\theta &= \frac{1}{[2\pi I_0(k(c))]^N} \int_{-\pi}^{\pi} \cdots \int_{-\pi}^{\pi} \\ &\quad \left[\prod_{m=i}^j \cos \theta_m \right] e^{k(c)(\cos \theta_1 + \cdots + \cos \theta_N)} d\theta_1 \cdots d\theta_N \\ &= \left[\frac{I_1(k(c))}{I_0(k(c))} \right]^{j-i} = \rho^{j-i}(c). \end{aligned}$$

Thus for $j - i = j' - i' = k$

$$\left\langle \prod_{m=i'}^{j'} \cos \theta_m \right\rangle_\theta = \left\langle \prod_{m=i}^j \cos \theta_m \right\rangle_\theta = \rho^k(c).$$

Thus

$$C_N = \frac{\langle r^2 \rangle}{Nl^2} = 1 + 2 \sum_{k=1}^{N-1} N \rho^k(c) - \frac{2}{N} \sum_{k=1}^{N-1} k \rho^k(c)$$

from the above expression for $\langle r^2 \rangle$ and using the relation for $\left\langle \prod_{m=1}^j \cos \theta_m \right\rangle_\theta$ just derived. Now since $\rho^k(c) \leq 1$ for all c , we have via the geometric series the relationship

$$C_N(c) = \frac{1 + \rho(c)}{1 - \rho(c)} - \frac{2}{N} \rho(c) \frac{[1 - \rho^N(c)]}{[1 - \rho(c)]^2} \quad (9)$$

Thus our estimate of the distance traveled after N excursions, R_N , by an anchovy larva of length L in a concentration of food particles c is given by

$$R_N = (Nl^2 (L) C_N(c))^{1/2} \quad (10)$$

where $C_N(c)$ is given above. The excursion length or step size l is shown as a function of L , an explicit relationship of which will be given later.

Model of attack rate in various concentrations of food prey

The random walk model derived above constitutes the quantitative relationship between the behavior of the larval anchovy and of food prey concentration. Since this relationship is expressed in terms of a distance which is a function of a given prey concentration, it constitutes a geometric connection between behavior and prey environment. Also, since the number of excursions and larval length are known for any distance traversed in a given prey environment, one can easily calculate the energy debt incurred by these excursions from the relationship derived by Vlymen (1974). However, an element of crucial importance to any growth simulation is an assessment or estimate of the amount of energy or food taken in by the larva in the course of these foraging excursions.

A widely held concept in fish growth simulations used in estimating energy input or ration size is that of search volume. That is, one assumes or determines experimentally a given visual perceptible area, which when multiplied by swimming speed and prey concentration during foraging gives an estimate of the amount of food consumed by the fish. Such models,

however, severely underestimate the minimum environmental food content necessary to meet basic metabolic and activity caloric requirements, primarily because they assume the fish react and successfully capture every available prey organism that enters their perceptible field. Even the most cursory observation of laboratory reared anchovy larvae will reveal this to be false and demonstrates the necessity for a more sophisticated and realistic approach to the problem. Because of the absence of adequate empirical data to formulate a well grounded relationship between feeding rate and food consumption, an alternate theoretical solution to this problem will be presented and the results of the proposed theory compared with the data gathered in the laboratory.

Observations of feeding anchovy larvae reveal that feeding during foraging can be basically regarded as a two event system. The anchovy larva swims in discrete steps or units mentioned earlier and referred to as excursions. At the end of each excursion the larva either sights an appropriate prey particle and commences an attack or does not attack. During the episodes where attacks take place only one appropriate prey is perceived and attacked even though many identical acceptable prey may be in the same area. Because of the nature of the subsequent attack sequence (Hunter 1972), the anchovy larva ends up many perceptible distances away from the region where the attack was commenced and hence must initiate the whole forage procedure again -- in a new area. There is also an extremely low incidence of attacks occurring immediately one after another, i.e. attacks separated by nonattack excursions. These observations lead to two important assumptions which will be used in the theoretical development to follow:

- (i) Each excursion is associated with a new random sample of the environment by the larva via the perceptible volume, and
- (ii) attacks on prey occurring immediately one after another, occur with a non-zero but infinitesimally small probability.

We cannot proceed, however, with only these two assumptions to a development of the attack rate of a larval anchovy in various concentrations of food prey until we make the one additional assumption that

- (iii) the three dimensional distribution of prey particles is locally random.

It is important to understand that this last assumption does not mean that the prey particle distribution is random, an assumption made by most growth models. In fact, a crucial feature of this work will be the importance of exactly the opposite condition,

i.e., nonrandomness, or global contagion on the growth of the anchovy larvae. Assumption (iii) implies only that within the scale of the anchovy larva the prey distribution is spatially random or manifests extremely low degrees of contagion. Large scale contagion, however, is extremely important and will be considered quantitatively later in the section on prey distributions and environmental geometries.

From assumption (i) we know that each excursion presents the anchovy larva with a new sample of the prey field, the volume of the sample being determined by the size specific reactive perceptive volume of the larva. From Hunter's (1972) measurements of the 95% confidence limits of the reactive perceptive field for anchovy larvae feeding on dense concentrations of similar sized prey organisms, we can regard the reactive perceptive volume as a segment of a specific solid of revolution. Hunter's (1972) figures 7 and 8 provide that this volume be equivalent to a circle of radius $0.37L$ lying in the plane of motion with one point on the circumference coincident with the larval snout and a diameter parallel to the direction of motion rotated approximately 53° about an axis passing through the snout and perpendicular to the direction of motion. This volume corresponds to a portion of a torus formed by the corresponding circle but with the distance to the rotation axis taken as one circle radius. The volume for a complete rotation is then $2\pi^2 r^3$ and for a 53° rotation the volume is

$$V_p = .294 \pi^2 r^3.$$

Using the numbers given above we get

$$V_p = .147 L^3, \quad (11)$$

where L is the length of the larva.

Before using the relation above let us examine the consequences and underlying assumptions in the use of the perceptive volume concept and the possible modifications of that concept for more generality. The perceptive volume concept is an attractive and simple one but suffers from the fact that it is not prey size dependent nor is there one simple method generally agreed upon to delimit the boundary of such a volume. The limits used here are 95% confidence intervals and the geometry of the field chosen by eye fit to the data. No detailed visual field studies were done to determine 95% confidence limits in three dimensional space nor is prey size varied over a wide enough range in the data available to elucidate

the functional relationship between these two variables even with a priori fixed perceptive field boundaries or geometries. However, for the purposes of this model the visual field concept gives a reasonable estimate of the perceptive field. Thus, assume that the volume calculated above is proportional to the real visual field for any size prey and, in general for any larval size, the field being larger for large prey and smaller for small prey,

$$V_{pr} = k_v(\bar{d}_p) V_p,$$

where $k_v(\bar{d}_p)$ is a monotonically increasing function of mean prey diameter \bar{d}_p . Since data are insufficient to evaluate the function $k_v(\bar{d}_p)$ but data on smaller larvae exist to test the theory to be developed on attack rates, the k_v appropriate for this set of data can be determined and retained throughout the model. The net effect is to underestimate the visual sample size for larger larvae which feed on larger, but scarcer prey but is appropriate to first feeding larvae which feed on smaller, more abundant prey. Since the attack rate is derived from probabilities of occurrence of prey in the visual sample, this choice of k_v will not have as large an effect on the model were one to determine k_v for larger larvae.

Thus the true or corrected visual field V_{pr} is calculated as $k_v V_p$ where k_v is now not a function but a constant and V_p is as given previously. The attack model can now be developed by determining the k_v that yields the best fit to the data or, alternately, corrects V_p to a functional visual field. This is different than comparing observed with expected values of attack rates obtained by an adjustable constant since the model is nonlinear and k_v occurs within the model as an independent variable and not a constant. Thus, good correlation between observed and expected values of attack rates can be regarded as support for the general model hypothesis and not an artifact of variable manipulation. The constant k_v is introduced only to obviate some of the inaccuracies and simplicities of the perceptive volume concept as they have been discussed.

From assumption (i) at each excursion the larva is confronted by a perceptive field of volume $k_v V_p$ or a visually evaluated sample of the prey field of the same volume. Then with assumption (iii) and an acceptable* volumetric prey concentration of λ the

* It will be shown later that as anchovy larvae grow older their food size preferences change so that even in the face of

probability of k particles in the perceptive field is Poisson distributed and is given by

$$P(k) = e^{-\lambda k_V V_p} \frac{(\lambda k_V V_p)^k}{k!}$$

In a prey size compensated visual field, we can assume that the minimum number of prey particles in the perceptive volume necessary for awareness by the larva is one. The probability of one or more acceptable particles in the visual field is given by

$$P(k \geq 1) = 1 - \exp(-\lambda k_V V_p)$$

This is termed the probability of 'awareness' of prey in the visual field.

Now the probability of attack on a food prey must be less than or equal to the probability of awareness because the larva makes decisions about the appropriateness of the prey of which it is aware. Although as shown, the animal is sampling visually from a concentration of λ , the probability of awareness must be multiplied by the probability of occurrence of the acceptable size range in the population as a whole to obtain the probability of attack

$$P(\text{Attack}) = P(k \geq 1) P(\text{Acceptable Size Range}).$$

The acceptable prey size range is determined as the difference between a length dependent lower bound which is known from observations of larvae collected from the ocean and an upper bound chosen as the maximum mouth diameter. Calling these two limits d_L and d_u respectively, and E_1 the event 'attack' we can rewrite the equation above as,

$$P(E_1) = P(k \geq 1) P(d_L \rightarrow d_u) \quad (12)$$

where $P(d_L \rightarrow d_u)$ represents the probability of prey sizes in the mean diameter range of d_L to d_u . If E_2 is defined as the event 'not-attack' we have together with E_1 a two-event Markov chain from which can be constructed the stochastic matrix using the above

abundant smaller prey a certain size range is selected. Thus λ above can be more appropriately regarded as a function of length. However, this is not accomplished in the final model by using a specific length dependent function for λ but is determined separately each time because of its multifactorial nature and reinserted iteratively into the model as needed. Thus the length dependence of λ will not be shown explicitly in the equations to follow, but will become manifest as the whole model is described.

probabilities, assumption (ii), and hence allowing calculation of the mean recurrence time, μ_1 , for the attack event. If the excursion frequency is given by f_E the attack rate, \dot{A} , can be identified simply as

$$\dot{A} = f_E (\mu_1)^{-1} \quad (13)$$

A two event Markov chain stochastic matrix contains four elements or transition probabilities, p_{ij} , where p_{ij} refers to the probability of the event E_j given that the event E_i has occurred at the previous trial or excursion or alternatively the probability of the transition $E_i \rightarrow E_j$. I choose to identify p_{11} as $\delta \ll 1$ according to assumption (ii) and because of the requirement that any stochastic matrix satisfies the relation $\sum_k p_{jk} = 1$, p_{12} is automatically determined as $1 - \delta$; I also identify $P(E_1)$ above with p_{21} and hence p_{22} with $1 - P(E_1)$. The resulting stochastic matrix is then

$$P = \begin{pmatrix} \delta & 1-\delta \\ P(E_1) & 1-P(E_1) \end{pmatrix}$$

The event E_1 is persistent and aperiodic and hence in this case

$$p_{11}^{(n)} \xrightarrow{n \rightarrow \infty} \mu_1^{-1}$$

where $p_{11}^{(n)}$ is the probability of finding the system at time $r + n$ in state E_1 given that at time r it was also at E_1 (Feller 1957). For this two event system it can be shown, taking $\delta \approx 0$ (Feller 1957), that the $p_{jk}^{(n)}$ matrix is given by

$$p^{(n)} = \frac{1}{P(E_1) + 1} \left[\begin{pmatrix} P(E_1) & 1 \\ P(E_1) & 1 \end{pmatrix} + \begin{pmatrix} (-P(E_1))^n & -(-P(E_1))^n \\ (-P(E_1))^{n+1} & (-1)^n (P(E_1))^{n+1} \end{pmatrix} \right]$$

whence

$$p_{11}^{(n)} \xrightarrow{n \rightarrow \infty} \frac{P(E_1)}{P(E_1) + 1} \text{ yielding } \mu_1 = \frac{P(E_1) + 1}{P(E_1)}$$

To test this theory and also to determine k_v , we have recourse to a single block of data collected, using very young larvae at a variety of temperatures and feeding on a laboratory-grown stock of the dinoflagellate *Gymnodinium splendens* (Hunter 1977). The exact size distribution of this stock is known from multichannel Coulter Counter* analysis and the variable temperatures allows for testing the theory on animals with basically the same visual apparatus but at different excursion frequencies. Before testing the theory, however, the relationship between excursion frequency and temperature must be determined.

Hunter (pers. comm.) has collected data on swimming speed for anchovy larvae of different lengths and at various temperatures from 13° to 19° C. By averaging the swimming speed in body lengths (B.L.) - sec⁻¹ for each temperature, the sets of data corresponding to larval lengths of 0.6, 0.8, 1.0, and 1.2 cm yield a straight line with least squares equation (B.L.) - sec⁻¹ = 0.110T - 0.941, where T is in degrees Celsius.

From Hunter (1972) we know that at 17° to 18° C the mean excursion frequency for feeding larvae of all sizes is 1.57 excursions-sec⁻¹. From this swimming speed data it is seen that at temperatures higher than 16° C there appears to be no further increase in swimming speed with temperature. Part of this trend is artifactual because of the random walk character of the motion. That is swimming speed is determined as distance per time but distance increases as the square root of the number of excursions which is temperature dependent. Thus, at high temperatures or excursion frequencies the slope of the swimming speed versus temperature curve should decrease as indeed it does, even though the excursion frequency per se is not exhibiting this behavior. Hence, given the inflexion point at T = 16° C of the swimming speed versus temperature curve which corresponds to an excursion frequency of 1.57 excursions-sec⁻¹ the body length per second curve may be converted into an excursion frequency curve by simply multiplying by

$$\frac{1.57}{0.110(16) - 0.941} = 1.916 \text{ or excursion frequency} \\ = 0.211T - 1.80. \text{ That is, the two curves are isomorphic.}$$

In addition to the excursion frequency relation for various temperatures, the distributional characteristics of the prey population used in Hunter (1977) are needed. It is generally agreed (Lasker 1975) that a

* Use of trade names does not imply endorsement by the National Marine Fisheries Service.

minimum critical sized particle is necessary before even the smallest first feeding anchovy larvae will attack prey. Although no well defined lower limit to prey size exists, larvae of approximately 5.0 mm in length, as occur in the data we are considering, will require prey particles at least 40 μm in mean diameter before any significant feeding takes place. Thus, for purposes of calculation we will take

$$P(E_1) = P(k \geq 1) P(\bar{d}_p \geq 40 \mu\text{m}).$$

Now the concentration of *G. splendens* in the data of Hunter (1977) is ~ 200 cells-cm⁻³ and multi-channel Coulter Counter analysis of this culture reveals that

$$P(\bar{d}_p \geq 40 \mu\text{m}) = 0.168.$$

Thus all data are available to test the theory except for the determination of k_v . The theoretical attack rate in attacks-min⁻¹ for these data is then given by

$$\dot{A} = \left[\frac{P(k \geq 1) P(\bar{d}_p \geq 40 \mu\text{m}) + 1}{P(k \geq 1) P(d_p \geq 40 \mu\text{m})} \right]^{-1} \\ [0.211T - 1.80] 60 \text{ sec-min}^{-1},$$

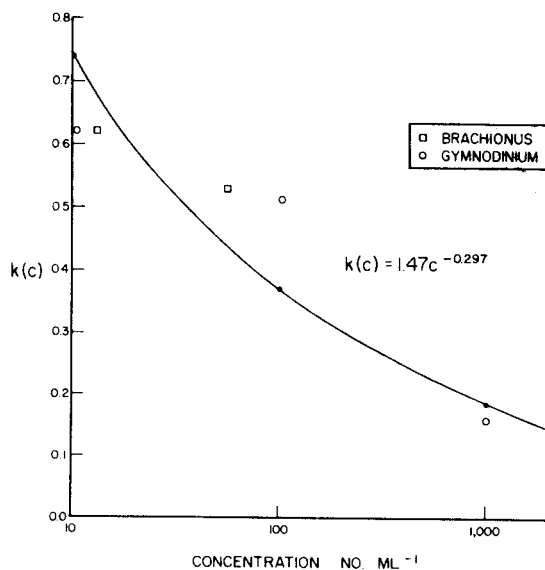


Fig. 1. The food prey concentration dependent dispersion coefficient of the circular normal distribution, $k(c)$, computed from the heading probabilities in Hunter and Thomas (1973) for anchovy larvae feeding on the dinoflagellate *Gymnodinium* and the rotifer *Brachionus*.

where $P(k \geq 1) = 1 - \exp(-29.4 k_v L^3)$ and the values in parentheses are derived from the appropriate constants already given to these data.

Calculation of \dot{A} with the previous equation for larval lengths of 0.45–0.50 cm and temperatures of 13.1° to 18.9° C as given in Hunter (1977) yields an extremely good correlation with measured attack rates as shown in Figure 2, with $k_v = 0.108$. As predicted for small sized prey $k_v \leq 1$, and although k_v as alluded to earlier is prey-size dependent, we will retain the k_v determined here for all size prey and regard the length dependent volume visual field as given by

$$V_{pr} = 0.0159 L^3.$$

A brief discussion of this attack rate model is in order, together with some modifications to make it correspond specifically to the larval anchovy. As is obvious, this model is not species specific save for the inclusion of a perceptive volume indigenous to the larval anchovy. Of great interest is the observation that at any specific excursion frequency the attack rate increases asymptotically with prey concentration. This is a feature found in numerous studies on plankton grazing rates in marine animals (Steele 1974a) and is a gratifying and a priori unexpected result of the Markov model. However, because

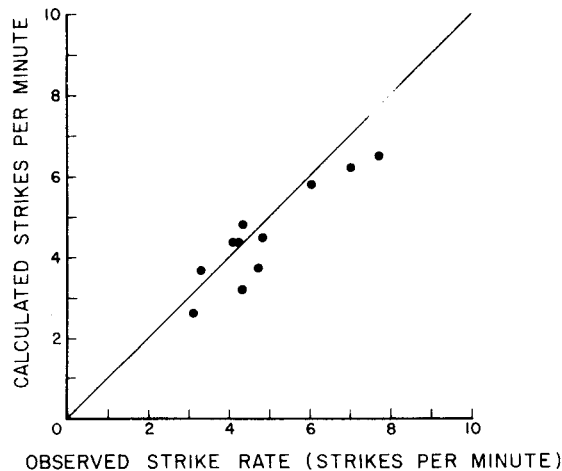


Fig. 2. Observed prey strike rate for 0.5 cm anchovy larvae feeding on laboratory grown stock of *Gymnodinium* with known size distribution from Hunter (1976a) plotted against strike rate calculated from Markov chain attack rate model (see text).

of this character the attack rate exhibits a maximum asymptotic value that obviously occurs as $P(k \geq 1)P(d_L \rightarrow d_U) \rightarrow 1$. Since $\mu_1 \rightarrow 2$ in this case the model predicts at any excursion frequency a maximum asymptotic attack rate of $\dot{A}_{max} = f_E \mu_1^{-1} = f_E/2$ or an attack sequence every other excursion. Obviously such high attack rates cannot be maintained for physiological reasons and to use this model effectively it is necessary to limit the maximum attack rates to those observed in the laboratory. Hunter (personal communication) has data which reveal a maximum attack rate of ~ 10 strikes-min⁻¹ under all circumstances. If we take the mean excursion frequency to be 1.57 excursions-sec⁻¹, this requires the recurrence time for the attack event to be no less than 9.46 excursions-attack⁻¹ to yield a maximum attack rate of 10 attacks-min⁻¹. Thus, the attack recurrence time will be taken as the calculated value above for $\mu_1 > 9.46$ and equal to 9.46 when the calculated μ_1 is less than 9.46.

With the inclusion of this asymptotic attack recurrence time we now have an attack rate model that yields results similar to those found by experiment and is completely consistent a posteriori with the laboratory determined criteria for successful larval anchovy feeding as outlined in Lasker (1975) and the qualitative and quantitative description of anchovy larval feeding behavior as contained in Hunter (1977).

However, an adequately descriptive attack rate model cannot be used to determine energy input primarily because not all attacks on prey are successful. This characteristic of the anchovy larval feeding behavior has been well documented and quantitatively described by Hunter (1972). The relationship elucidated by Hunter suggested that success of capture of various appropriate food types displayed the form of a learning curve and the data obtained was adequately represented by the equation

$$\text{percent success} = 93.2 \log_{10} t - 33.30.$$

where t is the larval age in days. It should be pointed out that success in capture of prey is only important for determining energy input. Each attack has an associated energetic cost to the larva whether or not the attack is successful and constitutes one of the energy debts incurred by the organism in the course of foraging.

Thus the rate of successful attacks on prey is given by the Markov attack rate given above times the success percentage associated with the age of the larva.

Prey size distribution and environmental geometries

The attack event probabilities $P(E_1)$ given in the preceding section depend quantitatively on the characteristics of the prey size distribution. The size of the particle consumed, which will be regarded later as the mean in the acceptable range or segmental mean of the prey size distribution, is also dependent on the characteristics of the prey distribution. The only efficient means of integrating a prey size distribution into a dynamic model that has ecological significance is to use a size distribution that is representative of the actual particle spectrum in the region where anchovy larvae are found.

A particularly ubiquitous and simple size distribution found in nature and one which possibly could apply equally well to the size distribution of living organisms in the ocean is the hyperbolic size distribution. A thorough discussion of this distribution and its applicability to the description of various naturally occurring particulate systems can be found in Bader (1970). According to Bader (1970) this size distribution is characterized by an associated cumulative number distribution of the form

$$N_d = k_H d^{-m} \quad (14)$$

where N_d is the number of particles cm^{-3} greater than mean diameter d and m and k_H are characteristic constants. The term hyperbolic is given to the distribution because on linear scales the function can be plotted as a hyperbola when $m = 1$.

The inshore region of the Los Angeles Bight is one of the major spawning grounds of the northern anchovy. To get an assessment of the mean particle size distribution anchovy larvae are confronted with in this region, data from multichannel Coulter Counter analysis of Niskin casts from approximately 1 to 20 m in depth (R. Eppley pers. comm.) were averaged over the water column and plotted as a cumulative distribution via equation (14). As can be seen from Figure 3, the hyperbolic distribution adequately describes the total particulate size distribution. Least squares evaluation of the constants k_H and m in equation (14) yield the values of 446,963 and 2.81, respectively. It must be stressed, however, that various environmental and biological conditions can affect the magnitude of these constants, but the effects are remarkably small. Recalculation of the constants k_H and m during blooms of dinoflagellates for instance, does not affect m and has only a limited tendency to

increase k_H . Thus we will regard the constants calculated here as representative of the particle size distribution in the major spawning ground of the northern anchovy and the distribution which will be used in modeling larval growth.

From the hyperbolic relation (14) two important quantities necessary for the model are derived, namely the segmental means $\bar{d}(d_L, d_u)$ and the range concentration $C(d_L, d_u)$.

If the number of particles- cm^{-3} with mean diameter $> d$ is $k_H d^{-m}$, then the probability of a particle having a mean diameter between d_L and d_u is given by

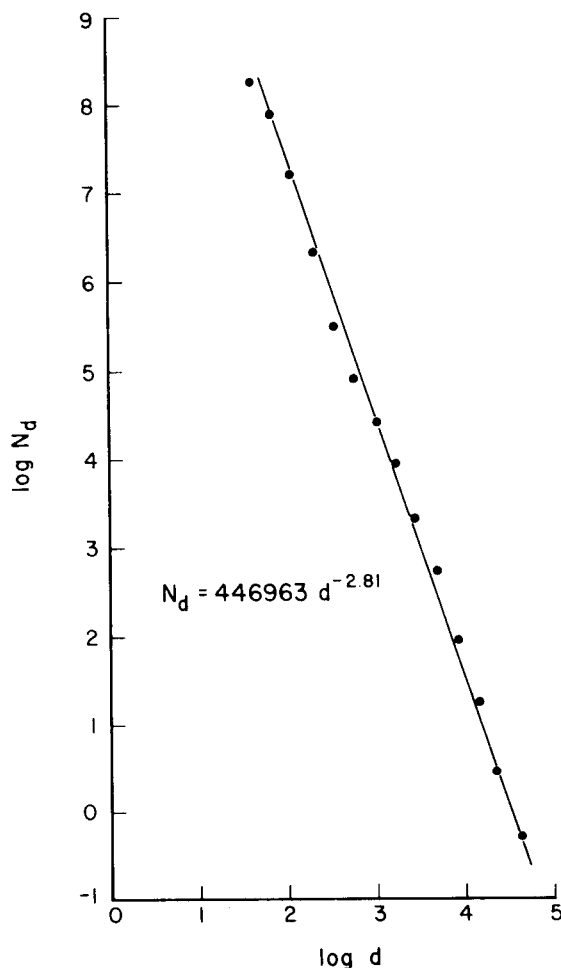


Fig. 3. Hyperbolic distribution of particle sizes in the Los Angeles Bight where N_d is the number of particles cm^{-3} greater in mean diameter than d , where d is in μm .

$$P(d_L \leq d \leq d_u) = \frac{k_H d_L^{-m} - k_H d_u^{-m}}{N_t},$$

where N_t is the total number of particles cm^{-3} greater than some extremely small reference size. Now for anchovy larvae only particles $> 20 \mu\text{m}$ in smallest dimension are found in the gut at even the earliest stages of the larval period (Berner 1959). Thus we

$$\text{take } N_t = k_H(20)^{-m} \text{ and } P(d_L \leq d \leq d_u) = \frac{d_L^{-m} - d_u^{-m}}{(20)^{-m}}.$$

Since the density function $f(r)$ for this range must satisfy

$$\int_{d_1}^{d_u} f(r) dr = P(d_1 \leq d \leq d_u),$$

$$\int_{20}^{\infty} f(r) dr = 1$$

and

$$f(r) \geq 0.$$

we get $f(r) = \frac{mk_H r^{-m-1}}{N_t}$. The segmental mean is then for $m > 1$

$$\begin{aligned} \bar{d}(d_1, d_u) &= \left[\frac{\int_{d_1}^{d_u} r f(r) dr}{\int_{d_1}^{d_u} f(r) dr} \right] \\ &= \frac{m}{m-1} \left[\frac{d_1^{(1-m)}}{d_1^{-m}} - \frac{d_u^{(1-m)}}{d_u^{-m}} \right]. \end{aligned} \quad (15)$$

The particle concentration in the range d_L to d_u is simply

$$C(d_L, d_u) = k_H(d_L^{-m} - d_u^{-m}). \quad (16)$$

In the above formulations it will be noted that particle concentration and particle mean size are only between an upper and lower limit referred to as d_u and d_L respectively, because, as discussed previously, anchovy larvae of given length demonstrate a specific particle size preference in their diets. To determine these limits the field observations on gut contents in larval anchovy by Arthur (1956) and Rojas de Mendiola (1974) may be used. Although Rojas de Men-

diola was concerned with a different species, namely *Engraulis ringens*, a comparison with Arthur's (1956) data for *Engraulis mordax* reveals no fundamental differences between the two species.

Certainly an upper bound, d_u , for the size preference range is the maximum width of the mouth. This does not indicate that the animal selects food prey as large as its mouth but rather the mouth size limits the maximum prey size it can eat. Data from Hunter (1977) reveals that the maximum mouth width for anchovy larvae can be adequately described by the relation,

$$d_u(L) = 54.302 + 345L, \quad (17)$$

where $d_u(L)$ is in μm and L is in cm .

The lower size range is determined directly from the observational data quoted above. From Rojas de Mendiola (1974) and Arthur (1956) we see that as anchovy larvae get larger, the smallest prey they are observed to take also get larger. Even in the face of abundant small prey they are observed to remain true to this preference. The data suggest that up to 2.0 cm in larval length the lower size limit of food prey taken rises linearly. Above 2.0 cm larval length, however, the lower limit remains relatively constant at least up to 3.0 cm larval length. Using a linear two point equation the lower size range is given by

$$d_L(L) = 100L \quad L \leq 2.0 \text{ cm} \quad (18)$$

where $d_L(L)$ is in μm and L is in cm .

It is interesting to plot $\bar{d}(d_L, d_u)$ from equation

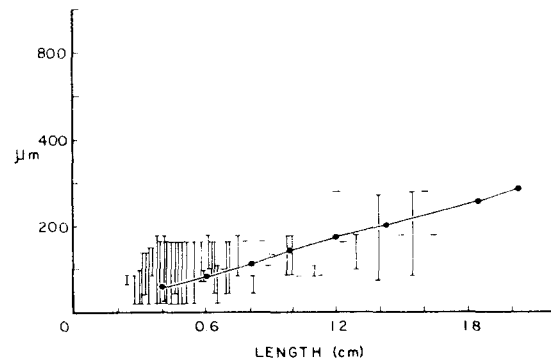


Fig. 4. Stomach content size ranges for particles found in guts of larval anchovies from Rojas de Mendiola (1974) plotted with segmental means calculated from hyperbolic particle size distribution (see text).

(15) using the $d_u(L)$ and $d_L(L)$ above and the particle distribution for the Los Angeles Bight. It is seen from Figure 4 that these means always lie within the bounds of the particle sizes actually found in anchovy larvae from Rojas de Mendiola (1974) and are almost equal to the observed means themselves. It also is observed that the mean size particle from the hyperbolic size distribution in a size range where the upper bound is increasing very rapidly is not much larger than the lower limit itself and corresponds well to what is observed in anchovy larvae feeding in a natural environment. With this quantitative concept of the particle size distribution fed on by anchovy larvae and the length dependent ranges of selection that the larvae feed upon, we can address the most complex of all environmental questions, namely prey particle microdistribution and patchiness.

Virtually no data exists on the three-dimensional distribution of prey particles of approximately 20 to 200 μm on a scale of 1 to 10 cm. It may well be asked if such a distributional scale even exists. To such questions there is no singular answer but it may be said, to quote J. H. Steele (1974b) on the structure of marine ecosystems: 'patchiness or spatial heterogeneity can occur on nearly every scale of measurement and must depend on the nature of the response of organisms to their aquatic environment.' Older descriptions of patchiness, particularly Bainbridge (1957) concentrated on discrete patches of phytoplankton a few meters wide to hundreds of square kilometers. More recently detailed distribution maps of certain species of zooplankton in a small bay (Anraku 1975) have shown the dramatic three dimensional diversity and character of plankton patchiness at scales of ~ 1 m. It, therefore, seems inevitable that when devices become available to investigate even smaller distributional scales patchiness will again be observed as a prominent feature.

Although no general model of the spatial distribution of all species in the ocean could exist, various attempts have been made to elucidate some of the relationships between the physical and biological parameters in the ocean at the mesoscale level, i.e., 10 m to 10 km, for phytoplankton. An excellent review of such studies may be found in Wroblewski et al. (1975). However, it is obvious from such studies that phytoplankton have certain advantages over zooplankton regarding modeling and that most such models elucidate only general characteristics even at the extremely large scales considered. Thus, if one is to consider the spatial characteristics of the larval anchovy food microenvironment at small scales, re-

course must be made to theoretical models based on reasonable assumptions. This is exactly the theoretical analog of the situation considered experimentally in Ivlev (1961) when he analyzed the variation of food ration in fishes as a function of the aggregation of food material. The results of his study will be discussed at the conclusion of this work.

Before presenting a spatial model of the food microstructure it is important to discuss a fine point in the reasoning of the dynamics of the structure to be presented. Since the spatial characteristics of the food microstructure are a result of the operation of both deterministic and random forces, any purely deterministic model of that structure is strictly not representative. Thus the geometric properties attributed to that environment are not representative of the true environment but rather to an 'environment-like' region with well defined spatial properties. Hence, the results of interactions of a behavioral submodel with the environmental submodel really pertain only to the specific characteristics of the environmental submodel used. By the exigencies discussed above this environmental submodel may differ significantly from reality. However, the behavioral submodel, because of its secure experimental foundation, does not. Hence significant correlations observed between larval growth and environment as a result of the submodel interactions does indeed address itself meaningfully to the question of environmental effects on larval growth. Only when detailed data on the exact character of the environmental geometry is elucidated will the magnitude and significance of the correlations demonstrated in the model become known.

The theoretical determination of the spatial relationships in the environment taking into account the contagiousness of the prey population will be done using the concept of mean crowding developed by Lloyd (1967). However, even with this concept some assumptions about the nature of the underlying patchy distribution must be made. The negative binomial distribution is the one chosen here as a global description of the underlying distribution because it has been shown to be ecologically sound and fits adequately many sets of empirical data (Feller 1943, Skellman 1952). Under these conditions Lloyd (1967) demonstrated that the ratio of mean crowding, c^* , to mean density c is given by

$$\frac{c^*}{c} = 1 + \frac{1}{k} \quad (19)$$

where k is the nondimensional contagion parameter

of the negative binomial distribution. Mean crowding as developed by Lloyd is a measure of the mean number per particle of other particles in the same patch. This, of course, implies that we have sampled the distribution with sample sizes approximately equal to the mean size of the patches which in our case is unknown. However, whatever range concentration we consider, the approximate relationship between the concentration of particles in the patch, c_p , will be regarded as related to the mean particle concentration by

$$c_p \cong c(1 + 1/k) \quad (20)$$

Given the patch concentration in the contagious distribution by equation (20) and assuming as before the particle distribution is locally random, we can calculate the distance to the nearest neighbor in the patch using Chandrasekhar's (1943) numerical solution of the Hertz distribution of the nearest neighbor in a random distribution of particles

$$R_{\text{nearest}} = 0.554 \left(\frac{g}{D} \right)^{1/3}, \quad (21)$$

where g is the mean mass of a patch particle and D is the particle mass density. From the above relations this is given by

$$R_{\text{nearest}} = 0.554 [c(1 + 1/k)]^{-1/3} \quad (22)$$

Once we have an estimate for the patch concentration we must provide some measure of the patch's geometric radius, r_{patch} . This is obviously a random variable whose value is a function of multifractional biological and physical forces. However, since we are interested in the response of a larva to a given environmental geometry we will provide a reasonable but deterministic estimate of the mean patch radius by assuming that the mean patch diameter is R_{nearest} weighted by a nondimensional factor proportional to the number of particles per patch or $c^* + 1$. That is, $r_{\text{patch}} = \frac{R}{2} \text{nearest} (c_p^* + 1)$ where $c_p^* = c_p/c'$ and c' is an arbitrary reference concentration. Taking c' as 1 cm^{-3} and using (22) we get the following estimate of patch radius:

$$r_{\text{patch}} = 0.277 \left([c(1 + 1/k)]^{2/3} + [c(1 + 1/k)]^{-1/3} \right) \quad (23)$$

This will constitute our estimate of patch radius for a degree of contagion k and range concentration c .

The relation is seen in Figure 5 plotted for c values of 5, 10, and 15 particles- cm^{-3} and where r_{patch} is in cm. It can be seen that this relation has certain heuristically desirable properties. Namely, the patch radius for any degree of contagion is greater for higher mean concentrations of particles, and patch radius increases with progressively higher degrees of contagion (i.e., lower k). It is of no consequence that there exists a specific value of r_{patch} as $k \rightarrow \infty$ for any given c because in this case the behavioral model makes no distinction between patches despite a finite r_{patch} because $c_p = c$.

Thus far, only one portion of the food microstructure geometry has been determined, namely the patch radius and concentrations for any given value of k and c . To complete the structure an estimate of the mean interpatch distance and interpatch concentration is needed. This can only be done if one considers a specific volume and a specific number of particle patches. Both of these quantities are random variables if we regard one or the other as fixed. To obviate this difference and make these estimates more deterministic the same formalism is applied so that the patch itself can be regarded as the elementary particle.

Since the patches are regarded as distributed randomly in space, we use equation (2) to calculate the R_{nearest} of the patches themselves. In this case

$$g = \frac{4}{3} \pi c_p r_{\text{patch}}^3 \bar{X}$$

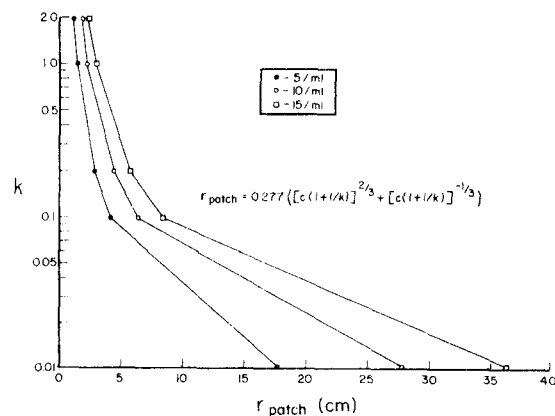


Fig. 5. Theoretical patch radius, r_{patch} , plotted as a function of prey contagion parameter, k , for three particle concentrations (see text).

where \bar{x} is mean mass per patch particle. D then is the mass density not of elementary particles but of patches. Obviously an upper bound for D is patch mass per patch volume or $c_p \bar{x}$. However, this would make the environment uniformly composed of patches which is not a realistic model. Thus we will set an upper bound for D of $c \bar{x}$ rather than $c_p \bar{x}$. This yields a patchy environment that retains the important feature of patch discreteness. Thus r_{inter} in this case becomes

$$\frac{R_{nearest}}{2} = 0.277 [4/3 \pi (1 + 1/k) r_{patch}^3]^{1/3}. \quad (24)$$

The interpatch concentration will then be approximated as the value of c or the mean concentration of the system. The relationship (24) is shown in Figure 6 and demonstrates the desirable properties of increasing interpatch distance with increasing patch diameter and with degree of contagion i.e., decreasing k .

The total environmental geometry as developed here, although not derived explicitly from particle mass conservation methods, does have properties of a mass conserved system. That is, high k or low contagion yields closely spaced small patches of particle concentrations not significantly higher than the mean, whereas low k or high contagion yields widely

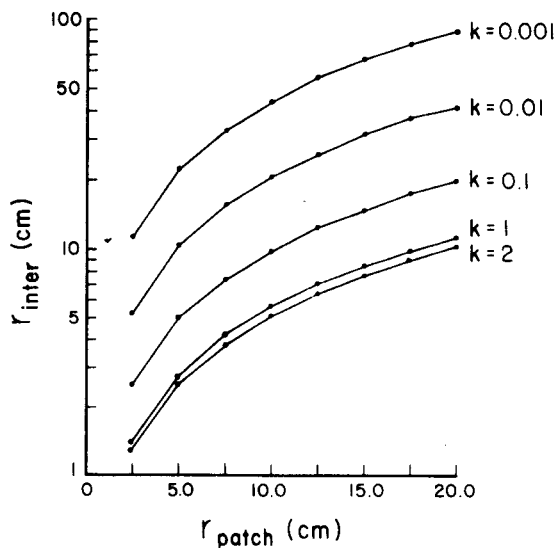


Fig. 6. Interpatch radius, r_{inter} , as a function of patch radius, r_{patch} , for five different values of prey contagion parameter k (see text).

spaced large patches of particle concentrations significantly greater than the mean. The only aberrant property of the system presented here from an ideal mass-conserved system is the assumption of the mean particle concentration for the interpatch regions. This implies that when this environmental structure is interfaced with the behavioral model larvae will grow more rapidly at high degrees of contagion than they would in an analogous mass conserved system for the same degree of contagion. However, the trends will be similar because of the basic similarities discussed.

In essence then we have an environment with explicit contagion dependent geometric and prey density parameters that can be interfaced with the behavioral submodel already developed. This interaction will yield various growth curves for larval anchovies from 0.4 to 2.0 cm in length that can be viewed as functions of these contagion dependent parameters and hence as functions of purely geometric and prey density elements and show how interactions between behavior and environmental substructure affect growth in the larval anchovy.

Additional physiological components

Certain quantitative relations for elements of the various submodels must be determined before any simulations can actually be performed. These components are not discussed in any great detail since their use has been described implicitly or explicitly in the preceding sections or will be described in the section on computer simulation.

Excursion length: The step length as a function of larval length $l(L)$ in equation (10) is an example of such an element that must be determined from experimental data. Hunter (1972) provides data demonstrating that at 17° C the relationship between larval anchovy swimming speed and larval length is given by $S = 1.038L - 0.215$, where S is in $\text{cm}\cdot\text{sec}^{-1}$ and L is in cm. The excursion frequency at this temperature is $1.57 \text{ excursions}\cdot\text{sec}^{-1}$ and dividing the speed equation above by the excursion frequency yields the desired relation

$$l(L) = 0.661L - 0.136 \quad (25)$$

Maximum gut volume: A length dependent function for maximum gut volumes of anchovy larvae is also needed in the following simulation. To determine this gut content data (Hunter pers. comm.) of newly fed larval anchovies of various lengths were examined

for those animals displaying the largest quantities of gut contents for any particular larval length. The food types varied from nauplii of the brine shrimp *Artemia* and the rotifer *Brachionus* for small larvae to numerous copepods of the genus *Tisbe* for larger larvae. The gut contents analysis data included the exact size and number of each prey type in the gut. The total volume of these prey in μ^3 was determined using analogies to appropriate geometric shapes. The results were analyzed by least squares and yielded the relation

$$G_{vol} = (1.30 \times 10^9) L^{1.63} \quad (26)$$

where G_{vol} is in μ^3 and L is in cm.

Caloric values of prey particles: A representative relationship between mean particle diameter and caloric value for a spectrum of food prey types acceptable to anchovy larvae is also needed for this model and was determined from data in Hunter (1977). Least squares analysis of the data yielded the relation

$$C_{particle} = (8.319 \times 10^{-11}) d_p^{3.39} \quad (27)$$

where $C_{particle}$ is in calories and d_p is in μm .

Digestive times: Digestive times in anchovy larvae which will become important in our studies have not been intensively studied. Arthur (1956) provides some inferential data concerning anchovy larvae digestive times in which he concludes that digestive time depending on temperature is between 1 and 3 hours. This is a very rapid rate compared with detailed studies by Blaxter (1965) on herring larvae, a related clupeoid, in which a rate of 4 to 8 hours was observed. More recently as a result of studies in progress on predation by young adults (Hunter pers. comm.) digestion rates of 2 hours or less were observed. Thus, the digestive time of an anchovy appears to be extremely rapid and not to vary greatly throughout life as evidenced by the studies above. Also, although digestive times are temperature dependent, insufficient data on anchovy larvae are available to elucidate such a relationship. We will thus assume that the mean digestive time for a full gut by anchovy larvae of all sizes is 2 hours which is the median of the times given by Arthur (1956) and partially supported by Hunter.

Basal metabolic rate: A basal metabolic rate as determined by controlled experiments where activity has been observed to be at a minimum is not available for the anchovy larvae. However, such studies are available for sardine larvae, a similar species. Lasker &

Theilacker (1962) found that the respiration rate of inactive sardine larvae was $1.33 \mu l O_2 \cdot mg \text{ dry wt}^{-1} \text{ hr}^{-1}$ at $14^\circ C$. From Lasker et al. (1970) we know the length weight relationship of the larval anchovy is given by

$$W = 0.3186 L^{3.3237} \quad ,$$

where W is in mg dry wt and L is in cm. Multiplying the basal respiration rate above by the length-weight relationship yields a basal metabolic rate (B.M.R.) of

$$(5.08 \times 10^{-2}) L^{3.3237} \quad (28)$$

B.M.R. in calories-day $^{-1}$, L in cm, and assuming a caloric equivalent of $5 \text{ Kcal} \cdot l O_2^{-1}$ and 24 hours-day $^{-1}$. This equation is very similar to the figure obtained by using Winberg's (1956) basal metabolic value for fish of 24 calories-gm wet wt $^{-1}$ day $^{-1}$ which yields an alternate basal metabolic rate relation of B.M.R. = $(5.10 \times 10^{-2}) L^{3.3237}$. Using equation (28) and assuming a Q_{10} of 2 we can then write the temperature and length dependent B.M.R. for larval anchovy as

$$\text{B.M.R.} = 5.08 \times 10^{-2} [1 + 0.1 (T - 14)] L^{3.3237} \quad (29)$$

T in degrees Celsius.

Excursion energies: The energy required for swimming during foraging is an extremely important energetic debt and is equivalent to the energy per excursion multiplied by the excursion frequency. The energy required per excursion is given by Vlymen (1974) as

$$E_S = 27.5 L^{4.48}$$

where E is in ergs and L in cm. According to Vlymen (1974) the efficiency of this motion is 24.6%. Converting to calories the energetic cost per excursion to the anchovy larvae is then given by

$$E_S = (2.671 \times 10^{-6}) L^{4.48} \quad (30)$$

Processing energy requirement: In all fish there is an energetic requirement for the mechanical processing of food, primarily for the manipulation of prey and intestinal propulsion of gut contents. Although this value has not been calculated for anchovy larvae it may be estimated from studies on other fish. Kerr (1971) has determined this value for trout and found that it is linearly related to the ration of the animal in the following manner

$$E_p = 0.29 R \quad , \quad (31)$$

where E_p is the processing energy and R is the total energetic equivalent of the ration. This value is probably smaller than the corresponding value for a larval fish because of the different amount of musculature devoted to these processes in the larval versus the adult fish. In this study I use the above relation as an estimate of this energetic debt in the anchovy larvae.

Digestive efficiency: It is generally observed that digestive efficiency is very high in most fish species, being 80% or greater in value (Winberg 1961). However, once digestion has taken place the absorbed food has to be converted into usable energetic substrates. The efficiency of this process varies with differing food categories and with what are regarded as the conversion end-points. It is doubtful, however, that this efficiency exceeds 60% (Sharp and Francis 1976). Thus, of the daily ration, approximately 48% (i.e., 0.6×0.8) is available energy and is taken as the estimate of available energy for use in the model.

Conversion of excess energy growth: Assuming a caloric equivalent of 5 Kcal-g dry wt⁻¹ and using the length-weight relation from Lasker et al. (1970) we have the energy difference between two lengths L_{n+1} and L_n as

$$\Delta E = 1.593 (L_{n+1}^{3.3237} - L_n^{3.3237}) \quad ,$$

$$L_{n+1} = \left[\frac{\Delta E}{1.593} + L_n^{3.3237} \right]^{0.301} \quad . \quad (32)$$

Thus given an energy excess of ΔE during a day when the larval length is L_n the larval length for the next day is L_{n+1} and is given by (32).

Computerized growth simulation

The flow sheet of computer operations for the growth simulation model (Figure 7) uses the actual Algol computer names for the various functions discussed. These names, their definitions, and the corresponding equation in the text where the function and its associated discussion may be found will be used in the description to follow. The description of the simulation will follow the direction of the arrows in Figure 7 from left to right, down, and then up.

The first part of the simulation involves the establishment of initial conditions for day and length at the time of complete yolk absorption, namely

$L = 0.4$ cm and $N = 0$. It is important to remember that the initial condition for the number of days does not represent time from hatching but time from complete yolk absorption. Once the initial conditions are set the iterative loop values are designated under which the simulation is to be performed. The rectangles represent these iterative loops and show that the simulation is to be performed for water temperatures of 14°, 15°, 16°, and 17° C and for each temperature the simulation executed for prey contagion or k values of 0.001, 0.005, 0.01, 0.05, 0.075, 0.085, 0.095, 0.1, and 0.15. Considering that $k = 8$ is virtually identical to a completely random distribution of prey it might appear that these k values represent unnaturally high a priori values of contagion. However, in many ocean investigations where the negative binomial has been fitted to collected data, low k values in this range have been routinely obtained (Zweifel & Smith MS*).

In the iterative loops the first two operations are the computation of the temperature dependent excursion frequency, BTFQ, and the age-dependent-success-of-capture-function, SUCL, derived in an earlier section. It is seen that the independent variable of SUCL is $N + 4$. This is so because the success of capture function was computed for days after hatching, not days post yolk absorption. A 0.4 cm larva is on the average 4 days old, hence the addition of four in the argument.

Next in order are the calculations of the length dependent upper, UPLM, and lower, LOLM, prey concentration limits as given by equations (17) and (18), respectively. These are used to calculate the interpatch concentration, CI, given by equation (16) using the hyperbolic distribution constants k_H and m determined for the Los Angeles Bight of 446,963 and 2.81 respectively. This value of CI is then used to calculate CP, the intrapatch concentration, using the loop contagion value k , which is then used to calculate the patch radius, DP, via equation (23), and the intrapatch distance, DI, via equation (24). All computed concentrations and distances are given in numbers of particles-cm⁻³ and cm, respectively.

These calculations have an important but implied geometric meaning, namely, that every ontogenic stage of the anchovy larvae, because of continuously changing food size preferences, is modulated concomitantly by continuously changing prey geo-

* Data from a manuscript by J. Zweifel & P. E. Smith tentatively titled 'Formal confidence interval estimates for survey estimates of fish egg and larval abundance.'

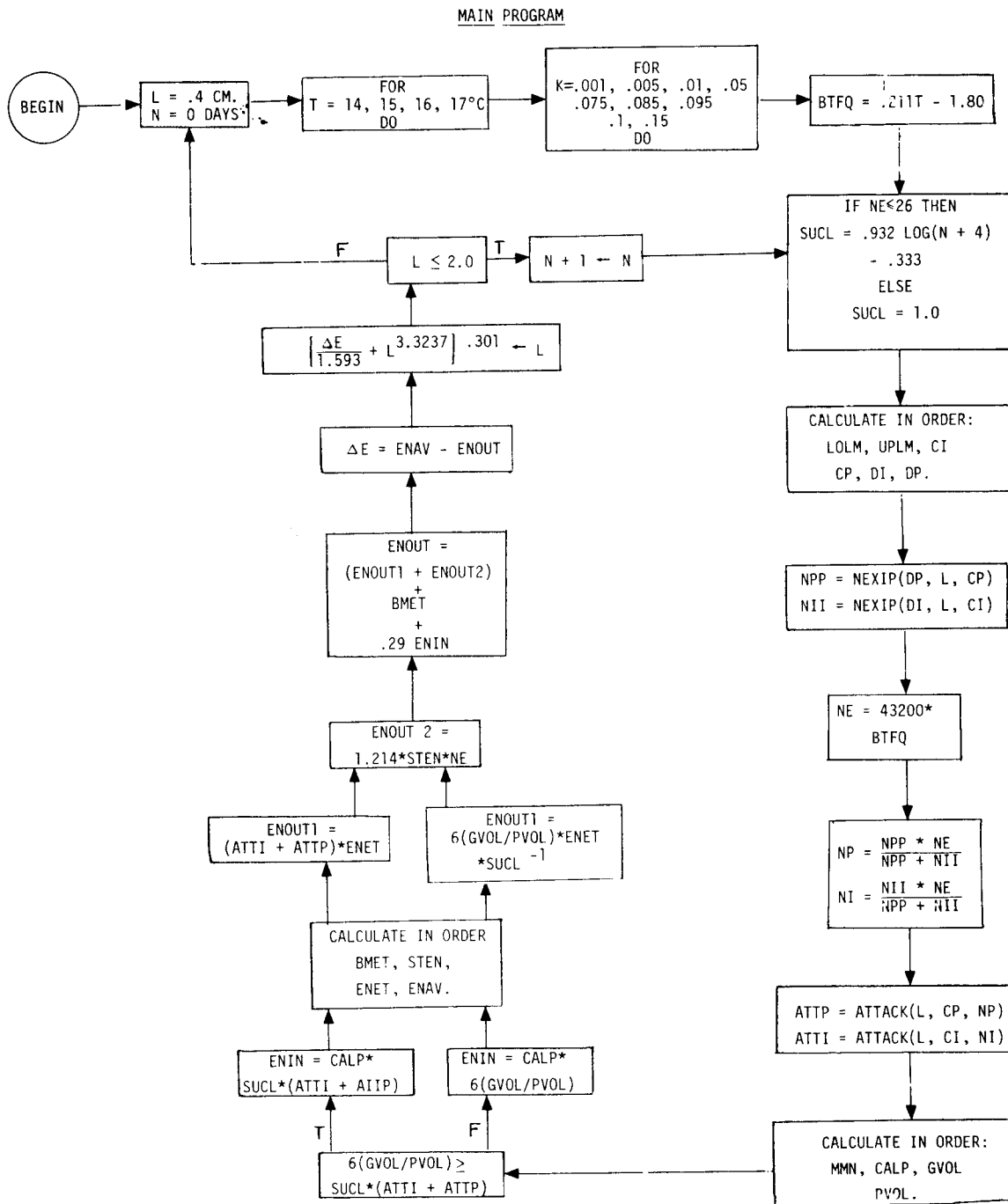


Fig. 7. Flow diagram of complete computer growth model. See text for explanation of symbols.

metries. Thus, any given value of k throughout the growth span of 0.4–2.0 cm gives rise to a continuous spectrum of spatial prey geometries.

The next sequence of calculations involves the invocation of the procedure NEXIP (D, L, C) using the parameters L and the previously calculated quantities CI , CP , DI , and DP . The procedure NEXIP (D, L, C) determines the number of steps of length given by equation (25) required to traverse a distance D in a concentration of food particles C as given by equation (10) and discussed in the first section. Thus $NPP = NEXIP(DP, L, CP)$ is the number of excursions a larva of length L will require to traverse a patch of radius DP and concentration CP , and $NII = NEXIP(DI, L, CI)$ is the number of excursions for a larva of the same length to traverse an interpatch distance of length DI and particle concentration CI . It will be noticed that according to equations (23) and (24) DP and DI represent respectively the mean patch radius and $1/2$ the mean intrapatch distance. These numbers are used rather than the total values of patch diameter and intrapatch distance because calculations are being made of the mean growth of a larva of length L swimming through a particular prey environment for 1 day. That is, the ensemble average of such motions requires the number of larval excursions to traverse the patch radius and $1/2$ the interpatch distance on the average since the patches are randomly distributed in space.

The following two calculations in the flow diagram are the number of excursions during the 12 hour foraging period, $NE = 43,200 * BTFQ$, and the proportion of the total daily foraging excursions spent in patches, NP , and in between patches, NI . Only a 12 hour foraging period is considered because it is well established that anchovy larvae feed only during the day (Arthur 1956).

The procedure ATTACK (L, C, N) calculates the number of attacks on prey made by an anchovy larva of length L executing N excursions in prey concentration C by the method outlined in the second section. This calculation is performed differently from the example in the second section in two details. First, the recurrence time is limited by the calculated minimum of 9.46 excursions and second, we no longer multiply $P(k \geq 1)$ by $P(d_L \rightarrow d_u)$ since $P(d_L \rightarrow d_u)$ is always 1 when $P(k \geq 1)$ is calculated from the range concentration. Thus $ATTP = ATTACK(L, CP, NP)$ is the total number of attacks on prey made by an anchovy larvae of length L in patches during the day and $ATTI = ATTACK(L, CP, NI)$ is the number of such attacks between patches.

Next calculated is the mean size, MMN , of the particles attacked and consumed given by equation (15), $CALP$, the caloric value of particles of size MMN given by equation (27), $GVOL$, the maximum gut volume of an anchovy of length L given by equation (26), and $PVOL$ the volume of the mean particle using standard mensuration formulae.

The calculation of the daily ration which follows is based on the following decision. If, assuming a digestion time of 2 hours, as discussed in under 'Additional physiological components', the maximum number of particles that could be processed in a day, $6(GVOL/PVOL)$, is greater than the number of particles successfully attacked, $SUCL * (ATTI + ATTP)$, then the number attacked successfully is regarded as the daily ration. If the inequality is false, then although conditions may have existed for consuming more food, the most that can be processed is taken as the maximum. Thus, in the first case the daily ration in calories is $ENIN = SUCL * (ATTI + ATTP) * CALP$ and in the second case $ENIN = 6(GVOL/PVOL) * CALP$.

Following this decision and selecting the appropriate value of $ENIN$ we calculate $BMET$, the temperature and length dependent basal metabolic debt for 24 hours given by equation (29), $STEN$, the energy per excursion given by equation (30), $ENAV$, the available energy of 0.48 $ENIN$ discussed above, and $ENET$, the attack energy of 3 $STEN$. This latter estimate is made from data in Vlymen (1974) and Hunter (1972).

Next, depending on the preceding decision $ENOUT1$, the first component of the energy debt, is calculated. This component, the energetic debt of the attacks made during the foraging period and depending on the truth or falsity of the previous decision is $ENOUT1 = (ATTI + ATTP) * ENET$ or $ENOUT1 = 6(GVOL/PVOL) * ENET * SUCL^{-1}$, respectively.

$ENOUT2$, the second component of the energy debt is the energetic debt of swimming for a 24 hour period. If the excursion frequency remained the same during the day and night, the number of excursions made during a 24 hour period would be $2 * NE$. However, anchovy larvae reduce their activity at night and although we do not know the exact magnitude of this reduction, experiments with other clupeoid larvae can give an estimate of this factor. Blaxter (1973) found an activity reduction of 78.6% in herring larvae experiencing maximally decreased light levels. Thus the number of larval anchovy excursions at night using this figure would be estimated as $0.214 * NE$ the total

for day and night being $ENOUT2 = 1.214 * NE * STEN$.

Following this calculation the total energetic debt, ENOUT, for a larvae of length L swimming for 24 hours at temperature T in a prey environment of global contagion k is estimated. This is simply $ENOUT = ENOUT1 + ENOUT2 + BMET + 0.29 ENIN$. The last summed debt is the cost of handling and processing the daily ration as discussed above.

The excess energy for the day, ΔE , is calculated as the difference between the available energy from the daily ration, ENAV, and the energetic debts incurred, ENOUT. This difference, if positive, is converted into a length via equation (32). If the difference is negative the process is terminated and a statement printed in the computer output that growth has ceased at day $N + 1$. If the new length is ≥ 2.0 cm the day is incremented by 1 and the new length used in the loop again. When the length reaches 2.0 cm the process is terminated, the loop control limits shifted and the process continued with new loop variables starting with $L = 0.4$ cm and $N = 0$.

Results and discussion

The computer simulation outlined in the previous section was converted into an Algol program and executed on a Burroughs 6700 computer. Although the results of that execution can be displayed in a variety of ways because of the multifactorial nature of the problem, two methods are selected here which visually yield the greatest amount of information. In Figure 8, for each temperature selected, the average

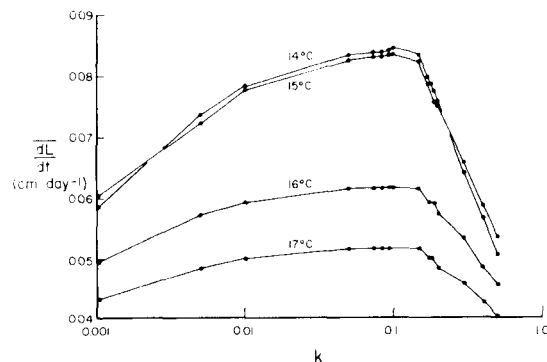


Fig. 8. Average growth rate in cm day^{-1} plotted as a function of prey contagion parameter k for temperatures of 14° to 17° C.

growth rate $\frac{dL}{dt}$ in cm-day^{-1} from 0.4 to 2.0 cm is plotted against global contagion k and in Figure 9, 17° growth curves are plotted against various degrees of contagion along with a representative 17° C growth curve obtained in the laboratory. The geometric parameters of the environment that the degrees of contagion represent can be determined only by calculating the patch radius and interpatch distance appropriate for the size larva being considered because of the length dependent preference range for the particle concentration used.

Neglecting the variation with temperature it can be seen from Figure 8 that the average growth rate is a nonsymmetric, nonlinear function of contagion k . For very high degrees of contagion, i.e. low k , one observes moderate growth rates that increase progressively as the degree of contagion decreases, i.e. higher k . This increase in growth rate is approximately 20% for the higher temperatures and 50% for the lower temperatures with a decrease in prey contagion of 100. A single peak maximum growth rate is obtained for all temperatures at the same degree of contagion of $k = 0.10$. Further decreases in contagion result in a precipitous decline in average growth rate and it may be seen from Figure 9 that the majority of this decrease is due to very slow growth in the early stages of ontogeny.

Several interesting interpretations related to fisheries can be inferred from these graphs. First, these results are in contrast to the experimental work of

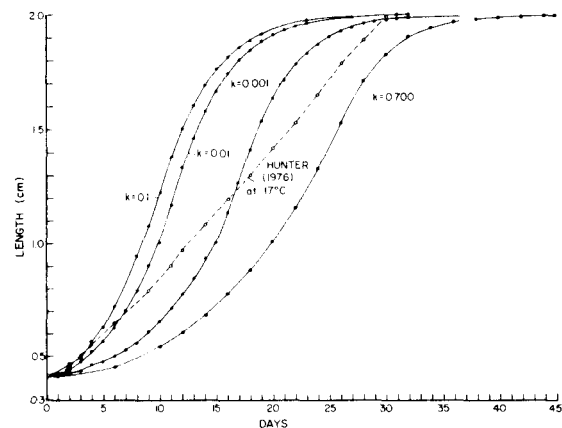


Fig. 9. Complete growth curves computed by the model for five representative levels of the prey contagion parameter, k , at 17° C along with a representative growth curve obtained in the laboratory at 17° C from Hunter (1977).

Ivlev (1961) which showed a monotonically increasing ration with increasing contagion. It seems that this is due to the different and more complete nature of the analysis done here as opposed to the two dimensional limited experimental work of Ivlev. However, although Ivlev understood the possible importance of prey geometry in fish growth studies and attempted to elucidate these relationships experimentally, he did not take into account the multifactorial nature of the problem and in particular the importance of behavior and its modification by prey contagion.

Second, one can formulate an optimal survival strategy for an anchovy larva based on these curves. It must be understood, however, that if the real ocean prey environment could be thoroughly analyzed, contagion would be anisotropic and also dependent on larval density. Thus the strategy deduced here applies strictly to the fixed geometries of the model and is simply that for long term survival prey areas yielding maximum growth rates are not advantageous because of their instability. Given that environmental forces are usually stronger in dissipating contagion at small scales than biological forces are in maintaining it, the probability is higher that contagion will decrease at any point then increase. Thus for areas yielding the maximum larval growth rate the high probability of decreases in contagion result in drastic reductions in growth rate. If we assume that total mortality of anchovy larvae for a given range of sizes from all factors is related to the time at risk in that size range, then slight reductions in contagion from the maximum growth point will greatly increase the total time at risk and hence the mortality from 0.4 to 2.0 cm. On the other hand, an optimal strategy would be to spend the majority of time in areas of higher contagion than those yielding the maximum growth rate. At these points a decrease in contagion slightly increases the growth rate while increases in contagion when they occur, slightly decrease the growth rate. Thus changes in contagion at these points do not drastically increase the total time at risk and hence the mortality from 0.4 to 2.0 cm.

This subjective explanation can be formulated in a more precise mathematical form. If the contagion varied in a simple sinusoidal manner the growth rate, as determined from Figure 8, would also vary sinusoidally.

Let the value of the contagion be that which yields the maximum growth rate, i.e., k_{max} and let the contagion vary sinusoidally over some fixed range, i.e., $k_{max} - \epsilon$ to $k_{max} + \epsilon$. With these conditions the growth rate

would vary sinusoidally between $\left(\frac{dL}{dt}\right)_{k_{max}}$ and $\left(\frac{dL}{dt}\right)_{k_{max} + \epsilon}$. The mean growth rate would then be

$$\left[\left(\frac{dL}{dt}\right)_{k_{max}} + \left(\frac{dL}{dt}\right)_{k_{max} + \epsilon} \right] / 2$$

and the total growth over any time period t_0 would be

$$L(t_0) = \frac{t_0}{4\pi} \left[\left(\frac{dL}{dt}\right)_{k_{max}} + \left(\frac{dL}{dt}\right)_{k_{max} + \epsilon} \right].$$

In a similar manner for the same degree of sinusoidal variation about $k < k_{max}$ the growth over a time period t_0 would be, where $k + \epsilon \leq k_{max}$,

$$L(t_0) = \frac{t_0}{4\pi} \left[\left(\frac{dL}{dt}\right)_{k + \epsilon} + \left(\frac{dL}{dt}\right)_{k - \epsilon} \right].$$

From Figure 8 there exists an ϵ such that $k + \epsilon \leq k_{max}$, $k < k_{max}$, and

$$\left[\left(\frac{dL}{dt}\right)_{k_{max}} + \left(\frac{dL}{dt}\right)_{k_{max} + \epsilon} \right] < \left[\left(\frac{dL}{dt}\right)_{k + \epsilon} + \left(\frac{dL}{dt}\right)_{k - \epsilon} \right].$$

Thus, the length achieved after time t_0 for oscillations about k_{max} is less than the length achieved for oscillations about $k \leq k_{max}$. The time at risk and hence mortality is thus greater for oscillations about k_{max} than $k < k_{max}$.

The temperature dependence of average growth rate in the model at any degree of contagion reveals a curious trend as observed in Figure 8. Except for the very high degrees of contagion one finds a reversal of the trend expected and normally observed in laboratory reared animals. That is, the lower temperatures exhibit strikingly higher average growth rates. This is most likely due to insufficient information in the model concerning substrate conversion efficiency and the fact that the total amount of food available in the model is limited, whereas in the laboratory it is not. In the model, substrate conversion efficiency is re-

garded as a temperature independent factor of 0.60. However, it is well known that at higher temperatures such efficiencies increase and since this factor determines the total energetically accessible ration the failure of this factor to increase appropriately with temperature and the fact that the amount of food remains fixed does not offset the increasing debts of metabolism, foraging, and feeding with higher temperature and hence one observes a lower average growth rate. Experimental information about the temperature dependence of this factor in larval fish is lacking and hence is not included. Since any model is a dynamic entity, physiological data on this relationship when available can be incorporated into the simulation.

It will also be noted in Figure 8 that the curves are not plotted beyond $k = 0.50$. Actually the curves extend beyond this point but do not extend past $k = 0.78$. That is, starting with a contagion value of $k = 0.78$, larvae of 0.4 cm after 1 day have a negative total energy balance. Thus, despite any time allowance between starvation and 'point of no return' (Lasker et al. 1970) these animals, as far as the simulation is concerned, will die. While larger animals will survive at these degrees of contagion, 0.4 cm first feeding larvae fail to survive at these lower levels of contagion.

What relationship does this value of $k = 0.78$ have to the recent studies on critical feeding in anchovy larvae? Lasker (1975) demonstrated in the laboratory that first feeding in anchovy larvae required particles $\geq 40 \mu\text{m}$ and between 20 to 40 particles- cm^{-3} . Because the model has integrated geometric properties we can only give the range of prey concentration for interpatch and patch concentrations of particles $>40 \mu\text{m}$ at $k = 0.78$, i.e., the contagion value just allowing for day 1 survival as determined by the computer. This particle concentration for first-feeding larvae is between 14.0 to 31.9 particles- cm^{-3} . This range of particles means that any one of the numbers could represent an environment which is structured. If only interpatch areas were sampled the value of 14.0 particles- cm^{-3} would be obtained. If, however, by some fortuitous series of events only patch regions were sampled, a value of 31.9 would be obtained. Thus, although laboratory experiments by Lasker (1975) reveal no first-feeding at average particle concentrations of 5 to 20 particles- cm^{-3} for any temperature, average concentrations without some concept of geometric structures are without meaning. This is, I believe, one of the reasons for the discrepancy between the high laboratory food requirements for minimal survival

and the concentrations observed in the ocean of analogous appropriate prey types. Certainly, large concentrations of food as in *Gymnodinium* blooms are greatly advantageous but the importance of microstructure in the remainder of the environment may be of equal or greater importance.

The natural extension of such concepts is to the associated sampling problem. Fisheries scientists have never really considered the relevance of environmental microscale in larval survival but as shown above these concepts can explain a number of inconsistencies. With large scale sampling the resultant concentrations of particles determined will always trend toward the mean or the interpatch concentration. As we have seen, this concentration is almost always below that determined in the laboratory for successful first feeding. Thus, what is needed is a way of assessing the microstructure of prey aggregations on a large scale.

The actual characteristics of the larval growth curves as determined by the simulation are worthy of discussion. It can be seen from Figure 9 that they are markedly sigmoidal in character compared to the curve for laboratory grown larvae. This, I believe, is due basically to two factors. First with this model we are actually seeing the manner in which fixed geometric properties of the microenvironment modulate the larval anchovy growth. When contagion was sinusoidally varied, depending on the phase and amplitude of the oscillation, the curves, although showing the effects of the oscillations, became more linear. Also, as the environment becomes more uniform, i.e., with high k , we see that the growth curves become more parallel to the laboratory curve and essentially represent a nonstructured prey environment. Second, the foraging costs used in the model slightly underestimate these values in the early stages of ontogeny and overestimate them in the latter stages of life. This accounts partially for the rather fast growth early in ontogeny and the slower growth later on.

The inhomogeneous nature of contagion in the ocean most likely gives rise to growth curves which are very similar to those observed in the laboratory. More precisely if the value of contagion is a function of time and place, i.e. $k = k(r, t)$ and $f(k, T)$ represents the relationship between growth rate and temperature from Figure 8 then the length of the anchovy larva after time t and distance travelled r is

$$L(t, r, T) = \int_0^r \int_0^t f(k(r', t'), T) dr' dt' .$$

In conclusion it should be said that from this preliminary model numerous concepts emerge which justify further investigation and elaboration. The model itself as a dynamic entity is subject to further refinement and restructuring consequent to new revelations in larval anchovy physiology and behavior. However, some things seem to be clear. These are that studies of physiology and behavior are of critical importance in the understanding of any fisheries problem related to larval fish, whether it is the growth or the relationship of growth to larval mortality. Also, environmental microstructure of food particles has an intimate relationship with the behavior and physiology of larvae and this whole model can in effect be regarded as a theoretical rationalization and justification for increasing our understanding of extremely small-scale relationships in the ocean. It might be argued that this model, suffers the same defects as many biological models in that it is too deterministic. However, this determinism should properly be regarded as elucidating a species specific biological relationship which is the result of the intermodulation of several other deterministic biological parameters. As such it can be reformulated in the language of stochastic variables just as other biological systems can be reformulated today. Such a reformulation constitutes the further extension into realism which is necessary for proper understanding of the complex biological systems with which we are concerned. This work is only one step in furthering that goal of a realistic understanding of the anchovy larvae and hopefully it will serve as a starting point for other similar investigations.

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