

Feeding success of clupeoid fish larvae and stochastic thinking

Jan E. Beyer

The Danish Institute for Fisheries and Marine Research, Charlottenlund Castle,
DK-2920 Charlottenlund, Denmark

Abstract

Feeding success is defined as the probability of capturing the prey organism assuming attack and is derived from basic principles as a function of the mouth size of the predator, the prey width and the precision of the feeding strike. The model is evaluated with reference to data from the literature on larval anchovy (*Engraulis mordax*) and larval herring (*Clupea harengus*) feeding on *Artemia* nauplii.

A theoretical attack-index of prey size preference is obtained from the model under the assumption that larvae attempt to achieve maximum food consumption. Optimum prey width appears to be linearly related to larval mouth size.

Introduction

The larval stage is probably the most dynamic life-history stage of marine fishes. Radical developmental changes, daily growth rates of the order of 5-30 % in weight and total mortality rates of high but virtually unknown magnitude characterize the species-dependent 2 weeks to 2 months period of time from hatching to metamorphosis. The hypothesis that this period of early life holds the key to understanding stock and recruitment relations has not yet been rejected (Hunter, 1976).

Feeding success is just one of the many aspects of feeding behavior that is difficult to escape in the process of understanding growth and starvation-induced mortality of larval fishes.

This study is concerned with basic principles. We attempt to provide a first answer to the questions:

What are the major causal factors controlling feeding success, how do we integrate these factors into a quantitative and testable theory and, in which way may such a model be utilized from a feeding ecological point of view?

Focus is placed on clupeoid fish for two reasons the first of which is that the attack behavior has been studied in detail for clupeoids. Secondly, feeding success or conditional capturing probability is the result of a well-defined attack event.

Clupeoid larvae feed on small zooplankton in particular the young stages of copepods (Blaxter, 1979). Northern anchovy, *Engraulis mordax*, however, are able to subsist for up to 20 days at a depressed growth rate on a diet of the (50 μ m diameter) dinoflagellate *Gymnodinium splendens* (Lasker *et al.*, 1970, Theilacker & McMaster, 1971). As other marine fish larvae clupeoids are visual feeders

(Hunter, 1977b) and they appear to select individual prey (Blaxter, 1979). Characteristics of the clupeoidal attack process are given in the next section. The important thing, however, is that a feeding attack consists of only one strike. This is not a fixed rule of marine fish larvae. Hunter (op. cit.) provides examples on other attack strategies and this seems to be the best way of indicating the limitations of the present study.

Persistent attacks characterizes the feeding behavior of larval mackerel, *Scomber japonicus*. If the first strike fails the larva often reposition for a second strike by moving backward and so on. They feed on larger zooplankton right from the onset of feeding. However, Hunter observed that Pacific mackerel became piscivorous at 10 mm length under rearing conditions. They carry prey larvae crosswise in the mouth, periodically release and grasp prey until it dies and then swallow it. Northern sennet, *Sphyræna borealis*, also exhibit piscivorous habits and they prefer newly hatched fish larvae as food from age 10 days (Houde, 1972). Sennets seize other larvae from the side, move the grasp to either head or tail and then without losing grip swallow the prey (Houde, 1972). The same feeding behavior was observed by Hunter in a rearing tank in Pacific barracuda, *Sphyræna argentea*. They became sibling cannibalistic at age 5 days when the larvae were 4.4 mm long.

We return to the more peaceful feeding behavior of clupeoid larvae. These larvae do not possess the ability to swim backward and their overall maneuverability appears to be low compared to larvae of mackerel and plaice, *Pleuronectes platessa*. This may explain the low feeding success of clupeoid larvae at the onset of feeding (Blaxter & Staines, 1971). Feeding or strike success at initial feeding is 10 % for northern anchovy (Hunter, 1972) and 2-6 % for herring, *Clupea harengus* (Rosenthal & Hempel, 1969, Blaxter & Staines, 1971). Feeding success then gradually increases (Hunter, 1977b), reaching 90 % in about 3 weeks in anchovy (Hunter, 1972) and 90-100 % in about 7 weeks in herring (Blaxter & Staines, 1971).

For some reason it has become standard to report feeding success in relation to age. However, live larvae of the same age may deviate greatly in size. I have observed 1 month old live and apparently healthy larvae of herring (and various other species) that deviate up to a factor of 2 in length. Do such larvae operate with the same strike probability of capturing identical prey? Prey size characteristics are also factors which need to be specified in relation to feeding success. Other prey characteristics than size such as spines and other protective structures, color and avoidance behavior are also believed to play a certain role for selection patterns in larval fishes (Hunter, 1977b). In this study, however, we do not deal with the dynamics of the entire feeding sequence. Interest is focused on the last part of the feeding sequence: the attack.

Fundamentals of the attack process

Prior to an attack the larva slowly approaches the sighted prey, adjusting its body to compensate for movements by the prey and, at the same time, forms the characteristic S-shape striking posture (Hunter, 1972; Rosenthal & Hempel, 1969; Blaxter, 1965). The attack begins when the larva opens its mouth and straightens its

body. The larva darts forward and captures or misses the prey organism within 10 ms (Hunter, 1972). Clupeoid larvae do not follow a prey if the first strike fails (Rosenthal & Hempel, 1969) and there is no handling time involved if the strike is successful. The prey is engulfed by the mouth instantaneously and passes rapidly to the posterior end of the gut where digestion takes place (Blaxter, 1965; Hunter, 1972).

During larval life the strike gradually becomes integrated with swimming movements (Hunter, 1977b) but, in principle the attack behavior remains the same. Quantitatively, however, certain changes occur as the larva grows. The distance between the larval snout and the prey organism at the start of the attack increases roughly in direct proportion with larval length (Hunter, 1972). Larval darting speed, however, also increases with length (Hunter, 1972) implying that the attack-time remains almost constant at the 10 ms independent of the length of the larva. It seems as though the probability of the prey organism moving during the attack is very small and independent of larval length. However, the probability of the prey organism escaping during the initial stages of the feeding sequence is not negligible. We know from Hunter's (1972) anchovy study that the principal cause of failure in continuing a feeding sequence is an inability of the larva to closely approach the prey while forming the S-shape posture.

Development of fins, improved swimming abilities, maturation of sensory systems and increasing mouth size of the growing larva are believed to play a role for feeding success (Blaxter, 1965; Rosenthal & Hempel, 1969; Hunter, 1972, 1977b).

Problem statement

Interest is focused on the microscale events: clupeoid larvae attacking prey organisms. We are not here directly concerned with the feedback mechanisms that determine perception, reaction and successful approach to various prey organisms by the fish larva. Assuming the fish larva has managed to achieve the attack posture we simply ask what is the probability of capturing the prey organism. This probability of a successful strike is referred to as feeding success and we are in particular interested in obtaining a relationship that adequately describes the feeding success $\delta(l, d_p)$ as a function of predator length, l , and prey dimension, d_p .

Idealization of a feeding strike

A feeding strike may be considered as a simple biological experiment. Some idealization is needed from the outset since we must reach a decision about what constitutes the possible outcomes of the (idealized) experiment before the event of a successful feeding strike can be properly defined.

Fish larvae of length l are identical and the attack-distance is independent of prey size. The prey organisms do not move during strikes and they are taken end on.

The larva operates with a certain precision in a feeding strike. Or, alternatively, looking at the situation from the mouth of the larva, the prey organism approaches this target area with the same precision. Thus, a series of feeding strikes by the

larva of length l on identical prey organisms parallels the distribution of shots fired at a target; the bull's-eye being the centre of the mouth. Let (x, y) be the coordinates representing the errors of a shot with respect to two orthogonal axes through the mouth mid-point. This defines the possible outcomes of the idealized feeding strike experiment as being all points in the xy -plane.

There is apparently no good reason to expect successive errors or outcomes to be interrelated or, for example, to occur more often in one direction than in any other direction. In addition, the mouth or the target area may be described as a circular area in a first approximation. Thus, there is no need to operate with a two-dimensional stochastic variable (X, Y) in describing the outcome of the experiment because the relevant information lies in the distance $Z = (X^2 + Y^2)^{\frac{1}{2}}$ from the origin,

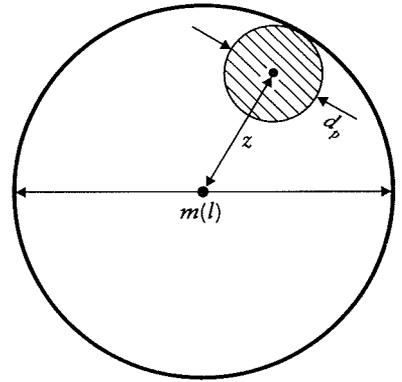


Fig. 1. Requirement for a successful attack in the model. The entire prey particle of cross-diameter d_p , the bullet in the firing-of-gun-analogy, must hit the target, the mouth of the larva with diameter $m(l)$.

$$\text{Feeding success: } \{Z \leq \frac{1}{2}[m(l) - d_p]\}$$

i.e. the mouth midpoint. The situation of this idealized experiment is depicted in Fig. 1. A circular cross-sectional area of the prey organism is assumed. An outcome is described by the distance z and the event 'a successful feeding strike' occurs if Z is less or equal to

$$z_c(l, d_p) = \frac{1}{2}[m(l) - d_p] \quad ; m(l) \geq d_p \quad (1)$$

where $m(l)$ is the mouth diameter of the larva of length l and d_p is the width or cross-diameter of the prey organism. Fig. 1 shows a situation of the occurrence of this critical distance i.e. the entire particle is just inside the target area. Each possible outcome may thus be classified as 'success' or 'failure' and the stochastic variable of interest becomes a simple Bernoulli variable:

$$S = \begin{cases} 1 \text{ (success) if } Z \leq z_c(l, d_p) \\ 0 \text{ (failure) if } Z > z_c(l, d_p) \end{cases} \quad (2)$$

We wish to obtain the probability of success

$$\delta(l, d_p) = \text{Prob}\{S = 1\} = \text{Prob}\{Z \leq z_c(l, d_p)\} \quad (3)$$

The probability of a successful feeding strike

We may formalize the simplifications considered in the firing-of-gun-analogy as follows. The errors in x and y directions are independent, the corresponding marginal density functions are continuous and the probability density at (x,y) shows radial symmetry. From this it follows directly that the error in any direction is normally distributed with mean zero and some variance σ^2 (Rao, 1965). Thus the distribution of shots is given by a bivariate normal density which by an integration within a circle of radius z from origin transforms into the probability density of Z , i.e. the distance between the centers of the mouth and the prey organism immediately after the attack, cf. Fig. 1. The result is the Rayleigh distribution,

$$f(z) = \frac{z}{\sigma^2} \exp\left\{-\frac{z^2}{2\sigma^2}\right\} \quad ; z \geq 0 \quad (4)$$

Hence the cumulative distribution function,

$$F(z) = \text{Prob}\{Z \leq z\} = \int_0^z f(r) dr = 1 - \exp\left\{-\frac{z^2}{2\sigma^2}\right\} \quad (5)$$

from which we obtain the feeding success, Eq. (3), by replacing z by the critical distance $z_c(l, d_p)$, i.e. from Eq. (1),

$$\delta(l, d_p) = 1 - \exp\left\{-\frac{1}{8\sigma^2} [m(l) - d_p]^2\right\} \quad (6)$$

where the larval mouth-diameter, $m(l)$, usually is expressed as a linear function of length,

$$m(l) = b_1 l + b_0 \quad (7)$$

The parameter of precision in the feeding strike, σ , is considered constant for all larval sizes.

Estimation procedure

From Blaxter & Staines' (1971) data on the percentage of feeding movements classified as 'successful', minimum and maximum values of success probabilities were obtained for herring larvae of different lengths. This measure of feeding success, however, is not the same as the δ defined in Eqs (3) and (6). Blaxter & Staines feeding success equals

$$\text{Prob}\{\text{Success}|\text{Reaction}\} = \text{Prob}\{\text{Success}|\text{Attack}\} \cdot \text{Prob}\{\text{Attack}|\text{Reaction}\} = \delta \cdot p_0$$

A reaction denotes the start of a feeding sequence and may be defined as an orientation of the head toward the prey sighted (Hunter, 1972). In Blaxter & Staines' notation the feeding success gives the joint probability of a feeding sequence resulting in an attack that is successful. The δ gives only the success probability assuming attack. Thus, in order to utilize Blaxter & Staines data it is necessary first

to obtain the probability of attack (i.e. a complete feeding sequence) assuming reaction,

$$p_0 = \text{Prob}\{\text{Attack}|\text{Reaction}\} \quad (8)$$

A continuous curve was eye-fitted to the graph presented by Blaxter & Staines (1971) on percentage of feeding movements classified as 'unfinished' from their 1967 experiments using *Artemia* nauplii as prey. A couple of functional relationships were tried and $0.1 + 0.8 \exp(-0.05 t)$ was found to give a reasonable fit. After transformation into length according to Blaxter (1968); $l = 0.1786 t + 7.5$ (mm), t in days (eye-fitted model), we then obtain $1 - p_0$ and, hence

$$p_0 = 0.9 - 6.531 \exp\{-0.28l\} \quad (9)$$

where l is in mm. The graph is shown in Fig. 2.

Using Eq. (9) the minimum and maximum values of success probabilities from the Blaxter & Staines study were divided by p_0 in order to obtain interval-estimates of δ .

From Eqs (6) and (7) we get, with

$$\alpha = \frac{b_1}{\sigma\sqrt{8}} \quad (10)$$

$$\beta = \frac{b_0 - d_p}{\sigma\sqrt{8}}$$

that

$$\delta = 1 - \exp\{-(\alpha l + \beta)^2\} \quad (11)$$

or

$$[-\ln(1 - \delta)]^{\frac{1}{2}} = \alpha l + \beta \quad (12)$$

Making this square-root-negative-log transformation of the $(1 - \delta)$ -intervals, it was possible to draw a straight line through all the transformed intervals ($\alpha = 0.2157 \text{ mm}^{-1}$ and $\beta = -1.586$). The resulting feeding success, δ , is depicted against larval length in Fig. 3. Note the S-shaped form. The diameter of a prey organism, d_p , and the precision of the strike, σ , can now be obtained from Eq. (10):

$$\sigma = \frac{b_1}{\alpha\sqrt{8}} \quad (13)$$

$$d_p = b_0 - \frac{\beta b_1}{\alpha}$$

Hunter (1977a) obtained the values $b_1 = 0.0366$ and $b_0 = 0.0431$ mm for the coefficients of mouth width of larval anchovy which implies

$$\sigma = 0.060 \text{ mm} \quad (14)$$

$$d_p = 0.313 \text{ mm}$$

It has been necessary to apply this ad hoc procedure in estimating σ and d_p because

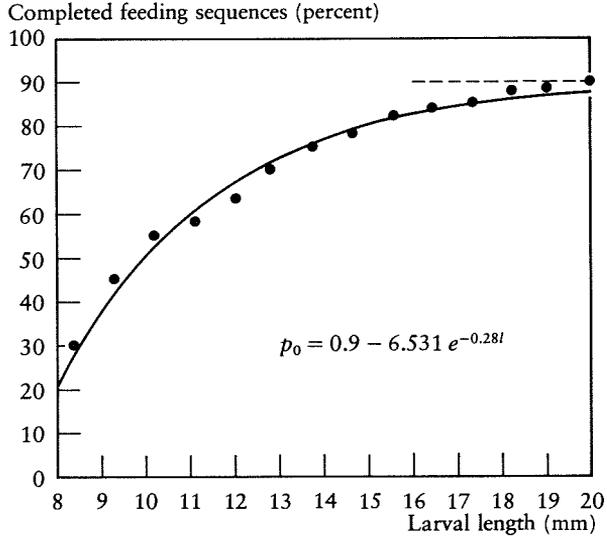


Fig. 2. The probability of a reaction to prey leading to a complete feeding sequence (i.e. attack) in the model. Points represent smoothed-out data from Blaxter & Staines (1971).

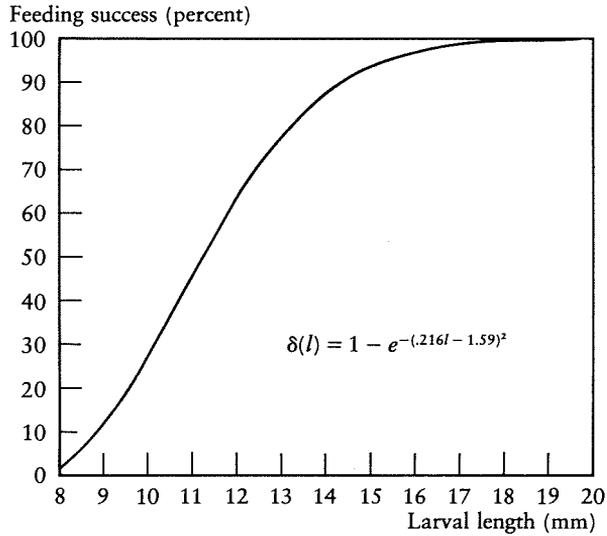


Fig. 3. The probability of an attack resulting in ingestion of prey. Model estimated from data in Blaxter & Staines (1971) on feeding success of larval herring attacking freshly hatched *Artemia* nauplii.

of lack of appropriate data. There seems to be no point in trying to obtain estimates of the variance of the estimators in this situation. Simultaneous data on length, mouth width and feeding success of individual larvae are needed in order to apply sound statistical principles. The work here merely suggests a testable theory which may be used as a guidance for future design of microscale feeding studies in the laboratory.

Results and discussion

The probability of an attack

Attacks occur only in complete feeding sequences. The important thing is that the event, 'a reaction to prey results in attack,' is stochastically independent of the past feeding behavior during that particular day. The probability of this attack event, p_0 , however, is not independent of the past feeding history starting right from the commencement of initial feeding. p_0 expresses the ability of the larva to approach a sighted prey, adjust its body to compensate for movements by the prey and, at the same time, forming the S-shape striking posture. In the model p_0 increases by length according to

$$p_0(l) = p_m - c_0 e^{-c_1 l} \quad (15)$$

This is, unfortunately, a good example of bad modelling. The functional relationship in Eq. (15) is chosen more or less at random because it provides a reasonable good fit to the data available. Hence, the parameter specification in Eq. (9) and the graphical representation in Fig. 2. In the present context Eq. (15) or any other empirical curve fitting model suffices because we only need $p_0(l)$ in order to transform Blaxter & Staines' (1971) data into feeding success. But from a feeding-ecological point of view Eq. (15) is useless. It is necessary to consider the fundamentals of the feeding sequence dynamics in order to develop an adequate p_0 -model. This will not be an easy task because the crux of the matter lies in an interaction between larval mobility, prey visibility, prey avoidance behavior and other biological factors. A first step could be to develop an appropriate random walk model for copepod movements and then obtain the probability of the copepod jumping out of the predators visual field etc. We shall not go into that here.

In addition to the reservations with respect to the ecological applicability of the functional form of Eq. (15), the final form given in Fig. 2 should be interpreted with care. The disagreement concerns in particular the level of the asymptotic value, p_m .

Rosenthal & Hempel (1969) reported that the frequency of attacking in percent of S-shaped positions for Downs herring larvae were 13 % at the end of the yolk-sac stage ($l \approx 9$ mm), 25 % 4-5 weeks post-hatching ($l \approx 15$ mm) and approximately 50 % about 7 weeks post-hatching ($l \approx 20$ mm). Since a feeding sequence may end at every stage up to and including the final strike posture (Hunter, 1972), Rosenthal & Hempel's frequencies must be deduced with a factor that gives the probability of a reaction resulting in a S-shaped position before we can compare with p_0 :

$$p_0 = \text{Prob}\{\text{Attack}|\text{Reaction}\} = \text{Prob}\{\text{Attack}|\text{S-shape}\} \cdot \text{Prob}\{\text{S-shape}|\text{Reaction}\}$$

In any circumstance Rosenthal & Hempel's values are considerably less than the values of p_0 obtained from Blaxter & Staines (1971). Hunter (1972) reports that about 40 % of all feeding sequences were completed for larval anchovy independent of age. However, events may occur faster for a species growing at 18 °C so Hunter's 40 % could be compared with the asymptotic p_0 -value of 90 % in the

case of Blaxter & Staines (1971) and 50% or less in the case of Rosenthal & Hempel (1969). Part of the discrepancy in p_0 -values may be caused by differences in the size of prey. Rosenthal & Hempel used *Artemia* nauplii and wild plankton but after 3 weeks metanauplii of *Artemia* were also used.

The Rayleigh distribution

The Rayleigh distribution is mathematically convenient to work with because of the analytically tractable form of the cumulative distribution function, Eq. (5). This is not the case for more wellknown probability distributions that have a certain resemblance in shape with the Rayleigh distribution such as the log-normal, the Gamma or Erlang and the Maxwell distribution in speed. The Rayleigh density, Eq. (4), starts in zero and reaches a maximum at σ , the mode, after which it levels off almost like the tail of the normal distribution, $N(0, \sigma^2)$.

The mean and standard deviation of the Rayleigh distribution are

$$\begin{aligned} E\{Z\} &= \sigma(\pi/2)^{\frac{1}{2}} = 1.253 \sigma \\ S.D.\{Z\} &= \sigma(2 - \pi/2)^{\frac{1}{2}} = 0.6551 \sigma \end{aligned} \quad (16)$$

Thus, as σ decreases, simulating increased precision of the attack, the probability mass moves towards zero, the bull's-eye, but the coefficient of variation remains constant at $0.6551/1.253$ or 0.5227 .

Percentiles of the Rayleigh distribution are easily obtained from Eq. (5). The requirement

$$p = F(z_p) = 1 - \exp\left\{-\frac{z_p^2}{2\sigma^2}\right\} \quad ; z_p \geq 0$$

gives

$$z_p = \sigma[-2 \ln(1-p)]^{\frac{1}{2}} \quad (17)$$

In particular we obtain

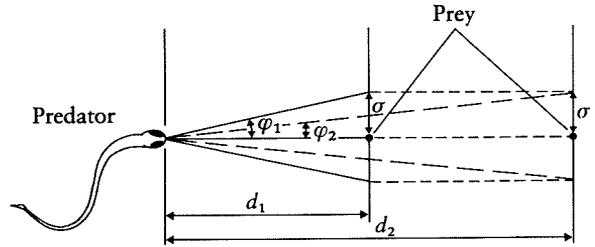
$$z_p = \sigma \cdot \begin{cases} 1.177 & p = .50 \text{ (50 \%)} \\ 2.448 & p = .95 \text{ (95 \%)} \\ 3.717 & p = .999 \text{ (99.9 \%)} \end{cases} \quad (18)$$

Basic characteristics of the Rayleigh distribution are thus directly proportional to the parameter of precision, σ .

The parameter of precision

The assumption of σ being constant is not in conflict with the hypothesis of increasing precision in the feeding strikes of larger larvae due to a maturation of sensory and locomotor systems. This is illustrated in Fig. 4. The figure is not drawn to scale since anchovy larvae attack prey organisms at a distance of only 7% of their body-length (Hunter, 1972). An 18 mm larva, for example, thus starts the

Fig. 4. Two dimensional representation of the precision of the larva's strike in the model. A larva of length l_1 strikes at the prey particle at a distance d_1 with angular precision φ_1 . A larva of length $l_2 = 2l_1$ strikes at a prey particle at a distance $d_2 = 2d_1$ with improved angular precision $\varphi_2 \approx \varphi_1/2$. Thus, the strike precision at the distance of prey, σ , remains constant.



attack at a snout-prey distance of 1.3 mm. This matches with Rosenthal & Hempel's (1969) picture of an 18 mm herring larva in attack posture but, otherwise, attack distances for herring larvae are apparently not reported in the literature. The essential point in relation to Fig. 4, however, is that the attack distance doubles as the larva grows twice as long but the parameter of precision, σ , remains constant implying almost a doubling in the angular precision of the strike.

We are at present not able to reject this very simple way of modelling an increasing precision of the strike with increasing length because Blaxter & Staines' (1971) data reveal a straight line in the plot of transformed feeding success against length according to Eq. (12). This somewhat supports the testable hypothesis of σ being constant but, clearly, a new and complete data set is needed in order to investigate statistically the validity of the entire theory.

Feeding success and larval length

The top picture of Fig. 5 depicts the Rayleigh density for the estimated precision of $\sigma = 0.060$ mm. The median (50%) and the 95% and 99.9% percentiles, computed from Eq. (18), are shown and indrawn as dashed circles on the target area at the bottom picture. However, only half of the target area is shown. Note that the Rayleigh distribution is not defined on the negative axis since the distribution only refers to the numerical strike-error measured from the mouth mid-point. Prey particles with the estimated diameter of 0.313 mm are shown as small circles at a position of the percentiles. The large half-circles represent the mouth area of anchovy larvae. The mouth diameters are:

$$m(l) = 0.0366l + 0.0431 = \begin{cases} 0.409 \text{ mm if } l = 10 \text{ mm} \\ 0.592 \text{ mm if } l = 15 \text{ mm} \\ 0.775 \text{ mm if } l = 20 \text{ mm} \end{cases} \quad (19)$$

The probability distribution at the top picture governs the strike-error for all larval sizes. The most likely error to occur in any single strike is $60 \mu\text{m}$, i.e. the mode. 50% of a great number of strikes are within the distance $71 \mu\text{m}$ (i.e. the median) but the mean error is $75 \mu\text{m}$.

The critical error-distance for a 10 mm larva is only $(409-313)/2$ or $48 \mu\text{m}$, so less than 50% of the strikes by 10 mm larvae are successful. The critical distance

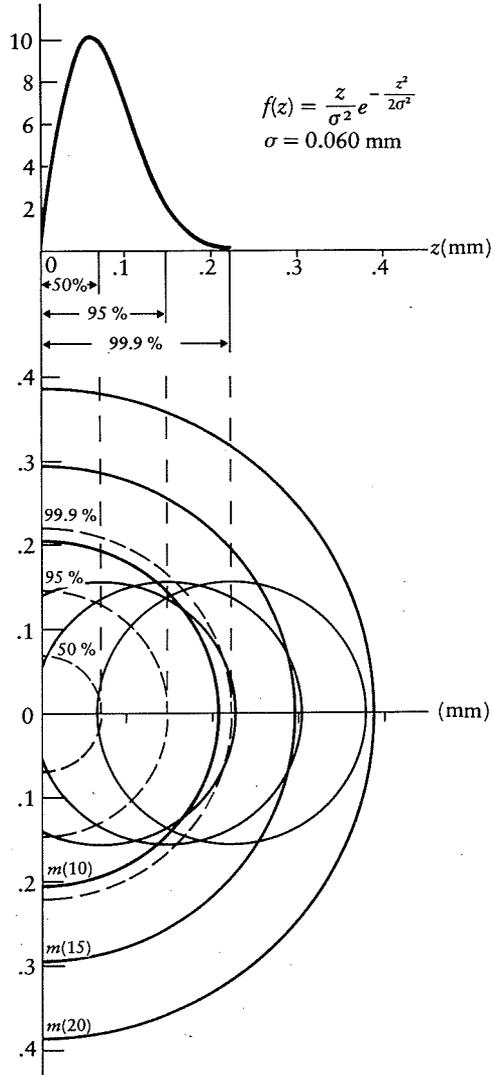


Fig. 5. *Top:* Probability density function of the strike-error Z , the distance between the centres of the mouth and the prey in the feeding strike. *Bottom:* The diameter of the mouth $m(l)$, for a 10, 15 and 20 mm long larva (i.e. heavy outlined half-circles) and the 50 %, 95 % and 99.9 % percentiles of Z (i.e. dashed half-circles). Heavy outlined circles represent prey particles at the position of the percentiles. A 15 mm long larva, for example, will capture the prey in almost 95 attacks out of 100 attacks because its mouth almost encircles the 95 %-percentile prey particle. Mouth data for larval anchovy, *Engraulis mordax* (Hunter, 1977 a).

for a larva twice as big, however, is $(775-313)/2$ or $231 \mu\text{m}$ which is more than the 99.9 % percentile of $3.717 \cdot 60$ or $223 \mu\text{m}$. Thus the probability of an unsuccessful feeding strike is virtually zero when the larva has reached a size of about 20 mm.

The complete quantification of the feeding success, δ , is depicted in Fig. 3, i.e. Eq. (11) or

$$\delta(l) = 1 - \exp\{-(0.216l - 1.59)^2\} \quad ; l \geq 7.37 \text{ mm} \quad (20)$$

This expression is mainly derived analytically from basic principles but its final form is based on three assumptions the first of which is the constant σ as discussed previously. The second assumption is a linear relationship between mouth size and

length of the larva. This assumption is not based on any biological hypotheses but simply belongs to the category of empirical work or bad modelling. In case of juvenile fish we may expect that the mouth width is directly proportional to the length because metamorphosed fish grow approximately as similar bodies. But this is not believed to be the case for larval fish as indicated by a power in weight-length relationships that exceeds 3 (Laurence, 1978). In addition, mouth data are usually reported over a narrow range of length preventing us from distinguishing between various relationships from a rough curve-fitting point of view. Thus the length-power of 1 in Eq. (20) should be interpreted with care. The third assumption is that only one size prey, d_p , was available for the herring larvae in Blaxter & Staines' (1971) feeding success experiment. This is probably a reasonable assumption since food consisted of freshly hatched *Artemia* nauplii. However, just a slight domain of variation in the prey size available may bias the feeding success results because it is a well established fact that larger larvae prefer to eat larger prey. The importance of specifying prey size for testing any refutable hypothesis on feeding success has already been indicated in the previous discussion.

Assuming Eq. (20), σ and d_p were estimated from Hunter's (1977) anchovy mouth-length Eq. (19). Alternatively, Blaxter (1965), using data from Blaxter & Hempel (1963), showed a length-regression line for the vertical gape of the jaws of young herring larvae living on their yolk supply. This line appears to be

$$m(l) = 0.0382l - 0.0147 \text{ (mm)} \quad (21)$$

Hence, from Eq. (13),

$$\begin{aligned} \sigma &= 0.063 \text{ mm} \\ d_p &= 0.267 \text{ mm} \end{aligned} \quad (22)$$

This only changes things slightly in Fig. 5. The mode, the median, the mean etc. of the Rayleigh distribution will increase slightly and the mouth sizes and the prey width will decrease. But the strike success, δ , of course, remains the same.

Two factors somewhat support this feeding success model. The estimates obtained for prey-dimension (0.313 mm and 0.267 mm) match with dimension data for *Artemia* nauplii. Copepods are usually taken end on with the antennae folded back along the body (Blaxter, 1965, Hunter, 1977a). Mean dimensions of *Artemia* in the tank of Hunter's (1977a) 4 hours feeding experiment were 0.260 mm width and 0.525 mm length whereas the mean size of the *Artemia* actually selected by 6-10 mm anchovy larvae was less (0.236 mm \times 0.433 mm). Secondly, Hunter (op. cit.) obtained the percent of anchovy larvae with one or more *Artemia* nauplii in stomachs after the 4 hours of feeding and he concluded 'for ingestion of prey to be independent of mouth width, the width of the mouth must exceed that of the prey by about 1.5 times'. If 'independent' is defined as a feeding success of at least 95 % then it follows from Fig. 5 that this criterion corresponds to about '2 times'.

Feeding success in a series of strikes

In this and the subsequent section we go more closely into Hunter's experiment in terms of the present model. Let N_t denote the total number of strikes a larva executes during t hours. The outcome of the i 'th strike is defined by a Bernoulli variable given in Eq. (2) and the total number of 'successes' or prey ingestions during the t hours feeding period becomes

$$S_t = S_1 + S_2 + \dots + S_{N_t} \quad (23)$$

The outcome of each strike is stochastically independent of the outcome of all other strikes and it thus follows that

$$\text{Prob}\{S_t = x | N_t = n\} = \binom{n}{x} \delta^x (1 - \delta)^{n-x} \quad ; x = 0, 1, 2, \dots, n \quad (24)$$

i.e. $S_t | N_t$ is binomially distributed. The mean and variance are

$$\begin{aligned} E\{S_t | N_t = n\} &= n\delta \\ \text{Var}\{S_t | N_t = n\} &= n\delta(1 - \delta) \end{aligned} \quad (25)$$

where the feeding success, δ , is given by Eq. (6).

We are now able to obtain the probability that a larva ingests one or more nauplii in executing n feeding strikes.

$$\begin{aligned} \delta_n(l, d_p) &= \text{Prob}\{S_t \geq 1 | n\} = 1 - \text{Prob}\{S_t = 0 | n\} \\ &= 1 - (1 - \delta)^n \\ &= 1 - \exp\left\{-\frac{n}{8\sigma^2} [m(l) - d_p]^2\right\} \quad ; m(l) \geq d_p \end{aligned} \quad (26)$$

That is, the probability of at least one successful strike in executing n strikes with precision σ equals the probability of a successful strike executed with precision

$$\sigma_n = \sigma / \sqrt{n} \quad (27)$$

As an example we put $d_p = 0.236$ mm which is the actual mean prey width obtained from stomach analyses in Hunter's experiment. The mouth size is given by Eq. (19) and the strike precision of $\sigma = 0.060$ mm presumably applies to larval anchovy. This brings Eq. (26) on the form

$$\delta_n(l) = 1 - \exp\{-n(0.2157l - 1.137)^2\} \quad ; l \geq 5.27 \text{ mm} \quad (28)$$

In case of only one attack, $n = 1$, we simply obtain the feeding success, i.e. $\delta_1 = \delta$. An 8.5 mm larva, for example, operates with a feeding success of 38 % according to this model. Hunter (1972) reported a feeding success of 37 % for anchovy larvae fed *Artemia* for the first time at length 8.5 mm (age 17 days). This supports the assumption of a 60 μm strike precision.

Table 1 indicates the sensitivity of $\delta_n(l)$ to changes in larval length and number of feeding strikes. The feeding success is most sensitive to changes in length at the point of inflexion which always occurs at a feeding success of 39.35 % (see the

Table 1. The probability in percent that larval anchovy of the given length ingests one or more *Artemia* nauplii of width $236 \mu\text{m}$ in executing the stated number of feeding strikes with precision $60 \mu\text{m}$. Derived from the feeding success model, Eq. (28).

Larval length (mm)	Percentage chance of capturing at least one prey in executing				
	1	5	10	50	100
5.5	0.24	1.2	2.4	12	22
6.0	2.4	12	22	71	92
6.5	6.8	30	50	97	100
7.0	13	50	75	100	100
7.5	21	69	90	100	100
8.0	29	82	97	100	100
8.5	38	91	99	100	100
9.0	48	96	100	100	100

section on feeding success and prey width). This happens at $l = 8.55 \text{ mm}$ when $\sigma = 60 \mu\text{m}$ and it appears from the column for 1 feeding strike that the feeding success increases from 38 % to 48 % when larval length increases from 8.5 mm to 9.0 mm. The other columns represent feeding success with the improved strike precision $\sigma_n = 60 \cdot n^{-\frac{1}{2}} \mu\text{m}$. In case of $n = 100$ we get a strike precision of $\sigma_{100} = 6 \mu\text{m}$ and the point of inflexion occurs already at length 5.60 mm. A 0.5 mm increase in larval length implies an increase of $18 \mu\text{m}$ in the mouth width, cf. Eq. (19). Thus, it is not surprising that the feeding success increases from 22 % to 92 % when larval length increases from 5.5 mm to 6.0 mm.

Feeding success in a period of time

The feeding success $\delta_n(l, d_p)$ as given by Eqs (26) and (28) relates to 'percent of anchovy larvae of length l with one or more *Artemia* in stomachs after executing n feeding strikes'. A stochastic description has been applied only because the outcome of each feeding strike is uncertain. The total number of feeding strikes, N_t , executed by individual larvae represents an additional source of stochasticity in Hunter's (1977a) calculations for 0.5 mm length classes of 'percent of anchovy larvae with one or more *Artemia* in stomachs after 4 hours feeding'.

In the absence of data on the number of feeding strikes executed by individual larvae over prolonged periods of time and under known food conditions we encounter problems in judging the validity of any statement concerning the probability distribution of N_t . Based on the reasoning given below we shall, however, take the liberty of assuming that a Poisson distribution in a first approximation governs N_t ,

$$\text{Prob}\{N_t = n\} = \frac{(\mu_t)^n}{n!} \exp(-\mu_t) \quad ; n = 0, 1, 2, \dots \quad (29)$$

$$E\{N_t\} = \text{Var}\{N_t\} = \mu_t \quad (30)$$

We then interpret Hunter's calculations as estimates of the unconditional feeding success

$$\begin{aligned} \delta_{\mu}^*(l, d_p) &= \text{Prob}\{S_t \geq 1\} \\ &= \sum_{n=0}^{\infty} \text{Prob}\{S_t \geq 1 | N_t = n\} \cdot \text{Prob}\{N_t = n\} \\ &= \sum_{n=0}^{\infty} \delta_n(l, d_p) \cdot \text{Prob}\{N_t = n\} \\ &= 1 - \exp\{-\mu_t \delta(l, d_p)\} \end{aligned} \tag{31}$$

Thus δ_{μ}^* equals a weighted sum of the δ_n 's, the weights being the probabilities of executing n attacks. The last expression in Eq. (31) follows by inserting Eqs (26) and (29) and utilizing $e^x = \sum x^n/n!$ but it may also be obtained directly as we shall see presently.

The reasoning underlying Eq. (29) is as follows. Let $s(l)$ denote the volume of water searched per unit time by the larva and assume that the nauplii are distributed at random with density γ . This implies that the larva perceives nauplii in a Poisson process with intensity $\gamma s(l)$. The total number of prey perceptions in a searching period of duration t is thus Poisson distributed with mean $\gamma s(l)t$. Assuming that the larva reacts to a prey visually perceived with probability $r(l)$ then the total number of reactions in the time period t follows a compound binomial distribution, i.e. a Poisson distribution with mean $r(l)\gamma s(l)t$. In other words the intensity of the reactive process is simply given by reducing the intensity of the perceptual process by the factor $r(l)$. We may say that the point process is being 'diluted'. The probability of a reaction to prey resulting in an attack has previously been denoted $p_0(l)$. The attack process represents again a thinning and the total number of attacks in the interval of time $(0, t)$ thus follows the Poisson distribution in Eq. (29) with the reduced mean:

$$\mu_t = p_0(l) \cdot r(l) \cdot \gamma \cdot s(l) \cdot t \tag{32}$$

The last thinning occurs at the transition from the attack process to the ingestion process. The probability of ingestion assuming attack is $\delta(l, d_p)$ and the total number of ingestions thus follows a Poisson distribution with mean $\delta(l, d_p)\mu_t$,

$$\text{Prob}\{S_t = x\} = \frac{[\delta(l, d_p)\mu_t]^x}{x!} \exp\{-\delta(l, d_p)\mu_t\} \quad ; x = 0, 1, 2, \dots \tag{33}$$

and Eq. (31) is directly obtained as $1 - \text{Prob}\{S_t = 0\}$.

We rewrite Eq. (31) with the purpose of estimating μ from Hunter's observations,

$$-\ln(1 - \delta_{\mu}^*) = \mu \delta$$

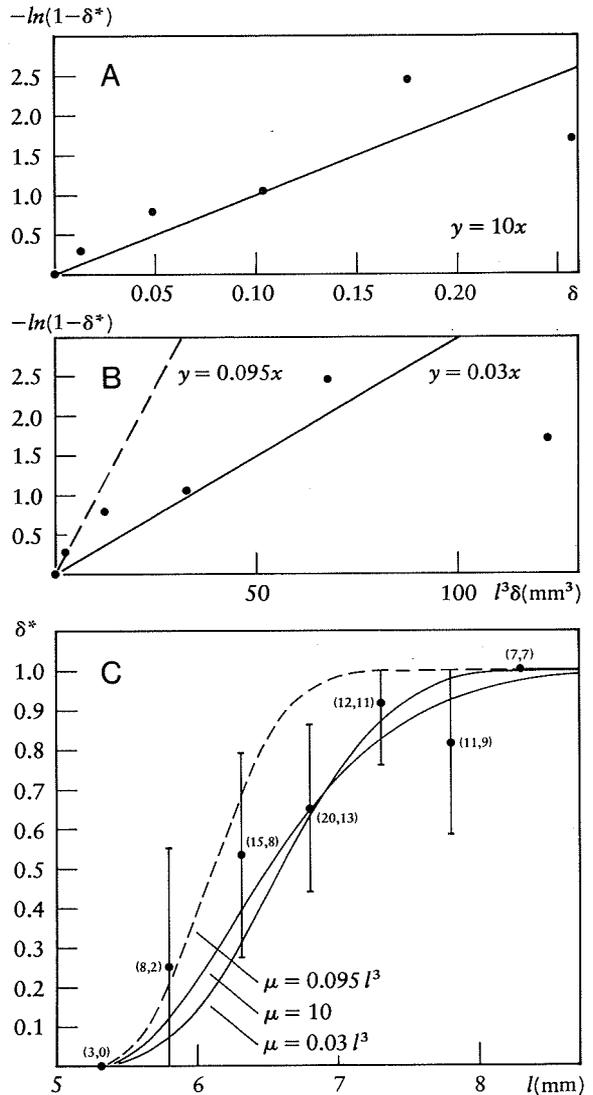
where δ is given by δ_1 in Eq. (28). Assuming for the moment that the mean number of attacks, μ , is constant (independent of larval length) then transformed δ^* -data plotted against δ ought to reveal a straight line through origin. Fig. 6A depicts the situation. We obtain a fair fit with $\mu \approx 10$ attacks the inconsistency in the last two data taken into consideration. Larger larvae operate with a higher strike success

Fig. 6. Plots of δ^* data (Hunter, 1977a), the proportion of anchovy larvae with one or more *Artemia* nauplii in stomachs after 4 hours feeding against larval characteristics.

A. The logarithm of the reciprocal of feeding failure (i.e. $1/(1 - \delta^*)$) plotted against computed strike success. Prey width equals $236 \mu\text{m}$ and a strike precision of $60 \mu\text{m}$ is assumed. Under the assumption that the number of feeding strikes executed by individual larvae is Poisson distributed, the indrawn line gives the situation of a mean attack rate of 10 per 4 hours independent of larval size.

B. Transformed feeding failure as in A but plotted against the cube of larval length times the strike success. The solid line represents the situation of a mean attack rate of $\mu = 0.03l^3$ per 4 hours. A slope three times larger (i.e. the dashed line) is necessary in order to account for Hunter's observation of a mean ingestion rate of 19 nauplii per 4 hours for 8.3 mm larvae.

C. Hunter's point estimates of δ^* for the various 0.5 mm length classes. The total number of larvae in each class (first number) and the number of feeding larvae (second number) are given. Bars represent computed '95 % confidence' limits of δ^* . The theoretical δ^* -graph for each of the three attack models (in A and B) is shown.



but Hunter estimated δ^* to 92 % for the 7.3 mm length class and only 82 % for the 7.8 mm length class. Presumably this only reflects statistical variation as will appear later. The length group 8.3 mm has not been utilized in the plot because Hunter (1977a) reported that all 7 larvae from this class had one or more nauplii in stomachs after the 4 hours feeding. This event is also likely to occur according to the model because the associated probability is $[\delta_{10}^*(8.3 \text{ mm}, 0.236 \text{ mm})]^7$ or 0.97⁷, i.e. 80 %. But Hunter also reported that the mean number of nauplii eaten by the 7 larvae was 19 which thus seems to invalidate this computation of a mean 4 hours attack rate of 10.

We may alternatively proceed according to Eq. (32) and attempt to express μ as an explicit function of larval length. Hunter (1972) reported that $p_0(l) = 0.40$ (see previous section on the probability of an attack). The next factor, $r(l)$, is more difficult to handle. We know virtually nothing about the interplay between perception and reaction to prey. We do know that only a fraction of the prey organisms perceived actually causes reaction in particular when the prey density is high. The larva, for example, does not react to other prey while engaged in a feeding sequence. Thus the assumption that the larva of length l operates with a constant probability of reacting to a perceived prey is questionable and this constitutes the main reason for the cautional remark that the Poisson distribution only is a first approximation. In order to proceed, however, we simply assume $r(l)$ to be constant. The third factor in Eq. (32) is the prey density which was high and approximately constant at 10 *Artemia*/ml in Hunter's experiment. The fifth factor is the constant time period of 4 hours. Thus, we assume that the major length dependency of μ , is due to the searching rate, $s(l)$. Hunter (1972) observed that the mean distance at which larval anchovy reacts to prey (at a high prey density) is $0.4l$. Searching takes place with a speed of approximately 1.0l/sec and prey reactions are believed to occur on a cross-sectional area at the reactive distance. This implies that searching rate (speed \times area) increases in proportion to length in a power of 3 and Eq. (32) thus takes the form:

$$\mu = \mu_0 l^3$$

Fig. 6B replots Hunter's transformed δ^* -data against $l^3\delta$ and, plainly speaking, a straight line gives a lousy fit. But let us again consider the stomach content of 8.3 mm larvae. With the model $\mu_0 = 0.03$ we obtain a mean of 17 attacks and $\delta_{17}^*(8.3 \text{ mm}, 0.236 \text{ mm}) = 0.997$. The event that Hunter's 7 larvae were feeding consequently occurs with probability $(0.997)^7$ or 98 %. The strike success, however, is only 35 % implying a mean stomach content of $17 \cdot 0.35$ or about 6 nauplii which still is very low compared to Hunter's observation of 19 nauplii. A stomach content of 19 nauplii would be expected if the 8.3 mm larva had executed about $19/0.35$ or 54 feeding strikes. This requires $\mu_0 = 0.095$ cf. dashed line on Fig. 6B.

We are, however, not able to reject the strike success model based on Hunter's data. This is shown in Fig. 6C. Let us use the 6.3 mm length class as an example. This class comprises 15 larvae and a Bernoulli approach is applicable because the larvae are considered as identical and non-interacting fish, i.e. the larvae do not interfere with each other in their feeding behavior. We proceed according to Eqs (23)-(25) with N_i replaced by the number of larvae and δ replaced by δ^* . The maximum likelihood estimator of δ^* is

$$\hat{\delta}^* = \frac{X}{15}$$

where X is the number of 'successes', i.e. larvae with one or more nauplii in stomachs. The variance of the estimator is

$$\text{Var}(\hat{\delta}^*) = \frac{\text{Var}(X)}{15^2} = \frac{\delta^*(1 - \delta^*)}{15} \approx \frac{\hat{\delta}^*(1 - \hat{\delta}^*)}{15}$$

Hunter obtained $X = 8$ and hence, $\hat{\delta}^* = 0.53$ and $\text{Var}(\hat{\delta}^*) \approx (0.13)^2$. Thus, δ^* may take a value anywhere from about $0.53 - 2 \cdot 0.13$ to $0.53 + 2 \cdot 0.13$ or from 27% to 79%. We see from Fig. 6C that the δ_μ^* -graph computed from Eq. (31) for each of the three models considered ($\mu = 10$, $\mu = 0.03l^3$ and $\mu = 0.095l^3$) falls within these '95% confidence limits' with only one exception at the 6.8 mm length class. None of the three models can be rejected based on Hunter's δ^* -data.

Feeding success and prey width

The feeding success is a function of the critical distance, Eq. (1), i.e. the quantity of importance is the difference between mouth size and prey width:

$$m(l) - d_p$$

Thus, larvae of mouth size 1.0 mm feeding on 0.9 mm prey, say, operate with the same feeding success as smaller larvae of mouth size 0.5 mm, say, feeding on 0.5-0.1 or 0.4 mm prey.

Except for a constant factor, a graph of feeding success against mouth size for a fixed prey width, d_p , (e.g. Fig. 3) equals the right half-part of the normal bell, $N(d_p, 2\sigma)$ upside down. The left-part of the bell $N(m(l), 2\sigma)$ upside down is similar to a graph of feeding success against prey width for a fixed mouth size, $m(l)$:

$$\begin{aligned} \delta &= 1 - \exp \left\{ -\frac{1}{2} \left[\frac{m(l) - d_p}{2\sigma} \right]^2 \right\} && ; m(l) \geq d_p \\ &= 1 - \exp \left\{ -\frac{1}{2} \left[\frac{d_p - m(l)}{2\sigma} \right]^2 \right\} && ; 0 \leq d_p \leq m(l) \end{aligned} \quad (34)$$

In the normal distribution the points of inflexion occur at mean \pm standard deviation, i.e. the most dynamic range of feeding success occurs at

$$m(l) - d_p = 2\sigma \quad (35)$$

when the feeding success is $1 - \exp(-\frac{1}{2})$ or 39.35%.

The domain of variation for all practical purposes occurs within 3 standard deviations, i.e. 6σ :

$$0 \leq \delta(l, d_p) \leq 0.99 \quad \text{if} \quad 0 \leq m(l) - d_p \leq 6\sigma$$

This explains the range of variation shown in each of the columns in table 1. The mouth size of a 5.27 mm anchovy larva is equal to $d_p = 0.236$ mm. Thus, feeding success is zero. Assuming $\sigma = 0.060$ mm the mouth size must grow to $0.236 + 0.360$ or 0.596 mm before feeding success reaches 99%. This occurs at length 15.1 mm and explains the relatively small variation of the 1-strike column. The 100-strike column may be interpreted as feeding success achieved with precision 0.006 mm. Thus, feeding success reaches 99% already at length 6.25 mm when the mouth size is 0.272 mm.

In continuation of the anchovy considerations we turn to an investigation of Hunter's (1972) food transition study:

'Feeding success of anchovy larvae dropped from 80 % to 40 % at age 17 days when the prey was changed from *Brachionus* to *Artemia* nauplii, but in 2 days their success increased to the former level (Hunter, 1972). Changes in mouth size or other developmental changes could not occur so rapidly, thus, the difference appears to be attributable to experience.' (Hunter, 1977b)

Kramer & Zweifel (1970) give the growth equation $l_t = 3.32 \exp(0.0555 t)$ mm (t in days) for larval anchovy under standard rearing conditions. Assuming that this equation also applies to Hunter's study we get a mean length of 8.53 mm at age 17 days implying a mouth width of 0.355 mm, Eq. (19). The width of the *Brachionus* is 0.133 mm (Hunter, 1977b) and with a strike precision of 0.060 mm we then obtain a feeding success of 82 % according to the model. The transition to 0.236 mm *Artemia* represents an increase in prey width of 0.103 mm and this brings the feeding success down to 39 %. The model is thus so far able to account for Hunter's observations. The drop to 39 % brings the feeding situation right down in the centre of the most dynamic range, cf. Eq. (35), and for this reason alone we expect a rapid increase in feeding success when the larvae start to grow on the new diet of *Artemia*. A feeding success of 80 % on *Artemia* nauplii requires a mouth width of 0.451 mm or an 11.1 mm long anchovy larva. This length is first achieved on day 22 according to the daily increase of 6 % in the length-age key given above. An 8.5 mm larva must in fact grow 14 % per day in order to reach a length of 11.1 mm in 2 days. This, perhaps, is unrealistic but we really need, for example, length/mouth data before a definite conclusion can be reached.

In elucidating the graphs of feeding success against prey width we turn to larval herring. From Eq. (21) we find mouth sizes of 0.367 mm and 0.749 mm for a 10 mm, respectively a 20 mm long larva. The strike precision, Eq. (22), is 0.063 mm and we get the feeding success

$$\delta = \begin{cases} 1 - \exp[-31.5(d_p - 0.367)^2] & ; l = 10 \text{ mm}, 0 \leq d_p \leq 0.367 \text{ mm} \\ 1 - \exp[-31.5(d_p - 0.749)^2] & ; l = 20 \text{ mm}, 0 \leq d_p \leq 0.749 \text{ mm} \end{cases} \quad (36)$$

Fig. 7 depicts the two graphs which are identical in principle except for a parallel displacement of 0.749 - 0.367 or 0.382 mm at the prey axis.

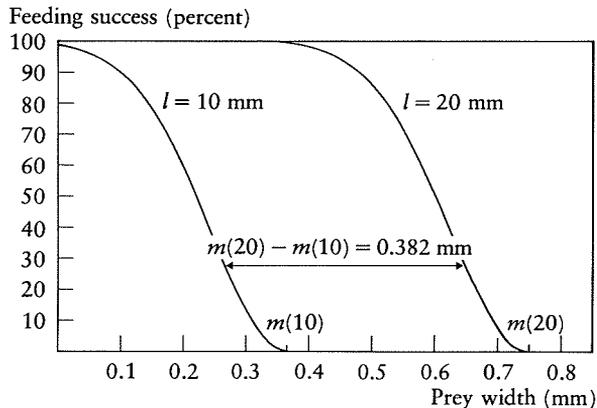


Fig. 7. Feeding success of larval herring against prey width according to the model. The graphs of 10 mm and 20 mm long larvae are shown and the respective mouth sizes indicated. If length 10 mm, say, is taken as standard then the feeding-success-graph of any other fish length is given by displacing the standard parallel to the prey axis according to the difference in mouth size.

An attack-index of prey size preference

We assume that the larval predator of length l attempts to maximize food consumption when it has the choice of attacking various sizes of prey, x . If F denotes the food consumed after one attack then, with reference to the feeding success considerations in Eq. (2),

$$F = \begin{cases} \omega(x) & \text{with probability } \delta(l,x) \\ 0 & \text{with probability } 1 - \delta(l,x) \end{cases} \quad (37)$$

where ω is the dry-weight of the attacked prey of width x and δ the feeding success given by Eq. (34). Assuming

$$\omega(x) = \omega_0 x^q \quad (38)$$

we obtain for the expected food consumption resulting from one attack

$$P(l,x) = \omega(x)\delta(l,x) = \omega_0 x^q \left\{ 1 - \exp \left[- \frac{1}{8\sigma^2} (x - m(l))^2 \right] \right\} ; 0 \leq x \leq m(l) \quad (39)$$

Clearly, it has not very much meaning to consider mean food consumption in relation to one attack only. But the mean of total food consumed after n attacks executed on the same prey size is $n \cdot P(l,x)$ and it is in this respect Eq. (39) should be interpreted.

The mean food consumption as a function of prey size x starts in zero because ingestion is zero although the fish larva operates with a high strike-probability of 'capturing a point'. Mean consumption then increases dominated by the ω -factor, reaches a maximum at some prey size after which it decreases due to the δ -factor. When the prey size equals larval mouth size the mean food consumption is again zero.

Differentiating $P(l,x)$ with respect to prey width, x , equalling zero and applying the inequality $\ln(1 + y) \leq y$ show that maximum food consumption occurs at a prey width x_0 that exceeds $m(l)/2$ if $q \geq 2$. This indicates a skewness to the left in expected food consumption as a function of prey width.

It is tempting to interpret $P(l,x)$ as an attack-index of prey size preference. More precisely let $X(l)$ denote the prey size larvae of length l will attack assuming that they have the choice of attacking all sizes of prey, i.e. the larvae are distributed in a body of water which comprises prey organisms of 'all possible sizes' in equal numbers. Then $P(l,x)$, normalized to unit area, represents the probability density function of the stochastic variable $X(l)$.

Clearly, each part of the process of feeding behavior needs to be quantified in order to form a complete and testable theory of size preference. At present we do not even know whether such a preference curve is characterized by a tail to the left (i.e. the predator prefers prey organisms almost as large as possible) or by, say, a long tail to the right. The length preference curves obtained in this study do show a skewness to the left but once again, they are obtained from a premature theory and they only refer to the last part of the feeding sequence for one type of particular feeders eating one type of food.

Larval herring as an example

We take $q = 3$ as a first guess of the power in the weight-width relationship, Eq. (38), of nauplii and copepodites. Assuming that the nauplii body-weight of $0.8 \mu\text{g-dry-wt}$ used by Beyer & Laurence (1980) applies to the *Artemia* nauplii of estimated width 0.267 mm , Eq. (22), we get with prey width x in mm,

$$\omega(x) = 42.0x^3 \quad \mu\text{g-dry-wt} \tag{40}$$

Using Blaxter's (1965) mouth-length relationship for larval herring, Eq. (21), and the strike precision of $\sigma = 0.063 \text{ mm}$ we obtain the attack-index of prey size preference, Eq. (39), on the form

$$P(l,x) = 42.0x^3 \{1 - \exp[-31.5(x - 0.0382l + 0.0147)^2]\} \quad \mu\text{g-dry-wt} \tag{41}$$

where x and l are in mm. The feeding success factor equals the expressions in Eq. (36) when larval lengths equal 10 mm and 20 mm .

A 10 mm herring larva achieves maximum food consumption at 0.242 mm prey (Fig. 8) which is slightly less than the estimated width, $d_p = 0.267 \text{ mm}$, of the prey available in Blaxter & Staines' (1971) feeding study. A 20 mm larva, however, achieves maximum food consumption at 0.555 mm prey (Fig. 9) which is more than twice d_p .

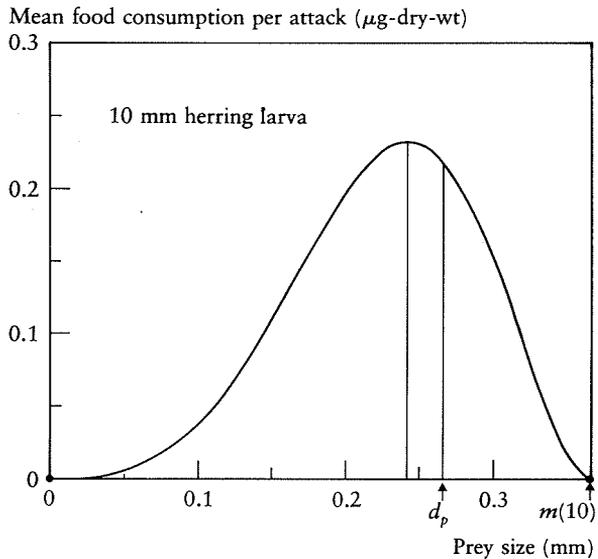


Fig. 8. Mean food consumption per attack against prey width for a 10 mm herring larva. Based on the feeding success model and the assumption that dry-body-weight of *Artemia* is proportional to size (width) in a power of 3.

A herring larva feeding on nauplii of $267 \mu\text{m}$ width would have to capture 9 times the number of prey to obtain the same ration as a larva feeding on copepodites $555 \mu\text{m}$ wide. The probability of a 20 mm herring larva ingesting a $267 \mu\text{m}$ wide prey in a feeding strike, however, is 1.00 (Fig. 7) whereas the probability is only 0.694 in case of $555 \mu\text{m}$ wide prey (Table 2). Thus, a 20 mm herring larva

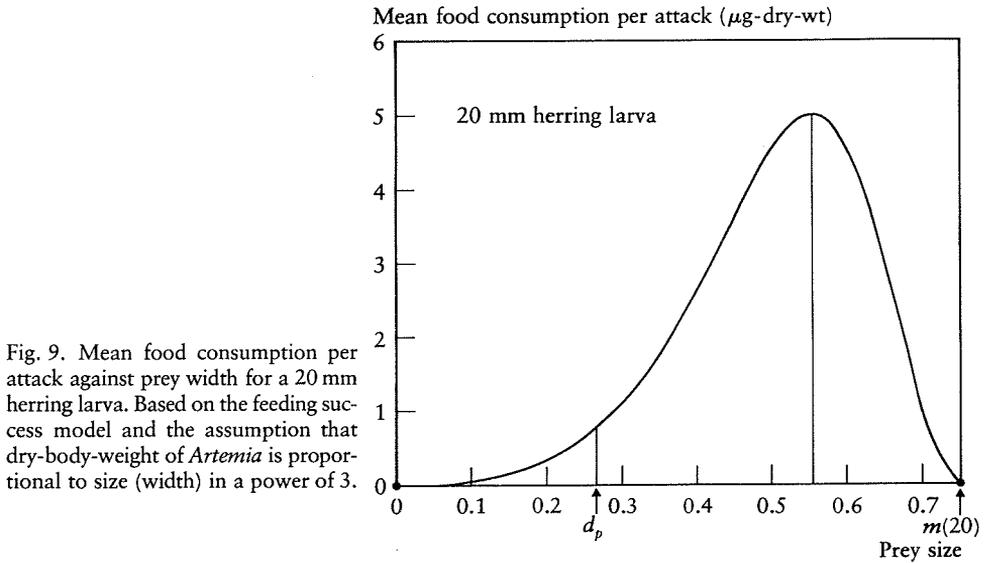


Fig. 9. Mean food consumption per attack against prey width for a 20 mm herring larva. Based on the feeding success model and the assumption that dry-body-weight of *Artemia* is proportional to size (width) in a power of 3.

Table 2: Optimum prey characteristics for various lengths of larval herring. Optimum implies that the larva of length l on the average ingests more food by executing feeding strikes on prey of width $x_0(l)$ than on any other prey size. The computation is based on the feeding success model and the assumption that the dry-weight of prey is proportional to its width in a power of 3.

Larval length l (mm)	Mouth width $m(l)$ (mm)	Prey width $x_0(l)$ (mm)	Prey weight $\omega(x_0)$ $\mu\text{g-dry-wt}$	Feeding success $\delta(l, x_0)$ (%)	Food ingestion per attack* $P(l, x_0)$ $\mu\text{g-dry-wt}$	Preference ratios		
						$\frac{x_0(l)}{m(l)} \cdot 100$ (%)	$\frac{2x_0(l)}{l} \cdot 100$ (%)	$\frac{\omega(x_0)}{\omega(l)} \cdot 100$ (%)
5	0.176	0.109	0.0544	13.2	0.00718	61.8	4.36	1.07
10	0.367	0.242	0.595	38.9	0.231	65.9	4.84	0.60
15	0.558	0.393	2.55	57.6	1.47	70.4	5.24	0.45
20	0.749	0.555	7.18	69.4	4.98	74.1	5.56	0.37
25	0.940	0.726	16.1	76.4	12.3	77.2	5.81	0.31
30	1.13	0.900	30.6	81.1	24.8	79.6	6.01	0.27

* Actual food ingestion resulting from any attack is either $\omega(x_0)$ (success) or 0 (failure).

The column gives expected food ingestion: $\omega(x_0) \cdot \delta(l, x_0)$

feeding on nauplii 267 μm wide would have to execute on an average $9 \cdot 0.694$ or 6.25 times the number of attacks to obtain the same ration as a 20 mm larva feeding on copepodites 555 μm wide. On the other hand, a herring larva feeding on copepodites 700 μm wide would only have to capture half the number of prey to obtain the same ration as a larva feeding on copepodites 555 μm wide, i.e. $(700/555)^3 = 2.0$. But the success probability of 20 mm herring larvae feeding on 700 μm prey is only 0.073. On the average, a 20 mm herring larva feeding on

700 μm copepodites would thus have to execute $\frac{1}{2} \cdot (0.694/0.073)$ or 4.7 times the number of attacks to obtain the same ration as a 20 mm herring larva feeding on 555 μm copepodites. It is in this way (stopping at the attack process) that we intend to interpret Fig. 9 for a herring larva of 20 mm length. The optimum prey width of 555 μm is 6.25 times more attractive than prey 267 μm wide and 4.7 times more attractive than prey 700 μm wide.

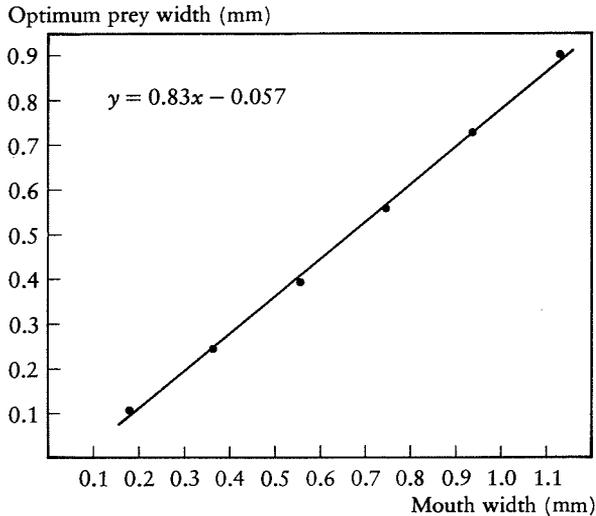


Fig. 10. Optimum prey width against mouth width of larval herring. Regression line is shown. Each point represents the prey width that optimizes the mean food consumption per attack for larvae with the associated mouth width. Derived from the feeding success model and the assumption that the dry-weight of *Artemia* is proportional to body-width in a power of 3.

Table 2 gives optimum prey characteristics for 5-30 mm long herring larvae. The ratio of optimum prey width to mouth size is 0.62 for 5 mm larvae and increases gradually to 0.80 for 30 mm larvae. A straight line seems to give a reasonable fit (Fig. 10) to optimum prey width, $x_0(l)$, against mouth size, $m(l)$:

$$x_0(l) = 0.83 m(l) - 0.057 \quad (\text{mm}), \quad 5 \text{ mm} \leq l \leq 30 \text{ mm} \quad (42)$$

This indicates incorrectly that the maximum value of x_0/m is 0.83 if the model for some reason is applied to metamorphosed fish.

We know from previous considerations (see for example Fig. 7) that the feeding success virtually is 100 % if the prey width is less than the mouth size minus 0.378 mm (i.e. 6σ). Hence

$$x_0(l) > m(l) - 0.378 \quad (\text{mm}) \quad (43)$$

It will thus be seen that $x_0(l)/m(l)$ approaches one when l continues to increase beyond 3 cm. As an example we may assume that the mouth-length relationship in Eq. (21) also applies to metamorphosed fish. The inequality (43) then implies x_0/m ratios for 5 cm, 10 cm, 20 cm and 30 cm fish that exceed respectively 0.802, 0.901, 0.951 and 0.967. The exact x_0 values obtained as in Table 2 by maximizing $P(l,x)$ result in x_0/m ratios of 0.856, 0.917, 0.953 and 0.967 for the respective fish sizes given above. The mouth size minus 6 times the strike precision thus represents a

good indication of the optimum prey width in case of juvenile and adult fish exhibiting feeding strikes according to the strike success model. However, piscivorous feeding in which the fish seizes relatively long prey from the side is probably more common for the juvenile and adult stages. The strike success model may perhaps apply to this grasping part of the attack but the subsequent manipulation of prey involves handling time. Kislalioglu & Gibson (1976) found an optimum prey size by minimizing the ratio of handling time to prey weight, i.e. a cost/benefit ratio. The optimum prey width was approximately half the mouth size of the predator and this result was found to agree closely with mean prey sizes of wild fish.

Apart from the strike success model the value of $q = 3$ is the only assumption underlying the computation of optimum prey width in Table 2. Optimum prey width, however, is not very sensitive to changes in this exponent of width in the width to dry-weight conversion of nauplii and copepodites (Table 3). The most sensitive range appears to occur at the nauplius stage where optimum prey width changes by 5-10% when q is reduced to 2 or increased to 4. Hunter (1977b) arrived at an exponent of about 2.5 for copepods. Size to dry-weight conversions of nauplii are apparently not yet available.

Table 3. Optimum prey width and its ratio to mouth size for various lengths of larval herring and three different exponents of the width of prey in the power function describing prey body-weight.

Larval length l (mm)	Optimum prey width in μm			Ratio of optimum prey width to mouth size		
	Exponent in the width to dry-weight relationship of prey					
	2	3	4	2	3	4
5	92.9	109	119	0.528	0.618	0.676
10	217	242	259	0.591	0.659	0.706
15	365	393	413	0.654	0.704	0.740
20	528	555	576	0.705	0.741	0.769
25	698	726	746	0.743	0.772	0.794
30	872	900	919	0.772	0.796	0.813

Assuming a length to width ratio of about 2 for nauplii and copepodites, the second last column in Table 2 gives optimum prey length in percent of predator length. A 5 mm larva prefers to attack prey of 4.4% of its own length (or, alternatively, the larva is 23 times larger than the preferred prey). The figure for 30 mm larvae is 6.0% (17 times).

The last column in Table 2 gives the optimum prey dry-weight in percent of predator dry-weight. The dry-weight of larval herring is obtained from the conversion formula reported by Laurence (1978):

$$w(l) = 0.005l^{4.3} \mu\text{g-dry-wt} \quad ; l \text{ in mm.} \quad (44)$$

A 10 mm herring larva, for example, weighs 100 μg (dry weight). The optimum

prey size is about $0.6 \mu\text{g}$ -dry-wt (cf. Table 2) and the 10 mm larva thus prefers to attack prey of 0.6 % of its own body-weight. A larva twice as long weighs 2.0 mg and prefers a $7.2 \mu\text{g}$ prey. Thus a 20 mm larva prefers prey of about 0.4 % of its own body-weight. In case of a 30 mm larva the preference ratio drops to about 0.3 %.

The optimum weight preference ratio is sensitive to changes in the width to weight relationship of prey, Eqs (38) and (40). This is shown in Table 4. The assumption that a $267 \mu\text{m}$ wide prey weighs $0.8 \mu\text{g}$ (dry-weight) is maintained when the exponent q is changed. This means, of course, that the coefficient in the relationship, ω_0 , must be changed accordingly. Let us first consider a 10 mm herring larva. The optimum prey width, x_0 , increases approximately from $220 \mu\text{m}$ to $260 \mu\text{m}$ when q increases from 2 to 4 (Table 3). Although smaller these x_0 values do not differ very much from the $267 \mu\text{m}$ and the optimum prey weights, $\omega(x_0, q)$, will thus be smaller than $0.8 \mu\text{g}$ but show a relatively small variation when q changes. It is to be seen from Table 4 that the optimum prey size or the preference ratio changes with about 15 % when q is reduced to 2 or increased to 4 in case of a 10 mm herring. The situation for 30 mm herring is quite different. The optimum prey width has increased to about $900 \mu\text{m}$ but is almost constant when q changes (Table 3). A $900 \mu\text{m}$ wide prey weighs only $8.5 \mu\text{g}$ according to the $q = 2$ relationship. But the weight increases by a factor of about 3.6 when q is raised by one. The weight reaches $112 \mu\text{g}$ in the $q = 4$ relationship.

Table 4. Optimum prey weight in percent of the weight of larval herring (predator) for three different width (x) to weight (ω) relationships of prey. The dry-weight of a 0.267 mm wide prey is $0.8 \mu\text{g}$ in all cases.

Larval length l (mm)	Larval weight $\omega(l)$ (μg -dry-wt)	Preference ratio $\frac{\omega(x_0)}{\omega(l)} \cdot 100 \%$ for $\omega(x(\text{mm}))$ equal to:		
		$11.2 x^2$ (μg -dry-wt)	$42.0 x^2$ (μg -dry-wt)	$157 x^4$ (μg -dry-wt)
5	5.06	1.9	1.1	0.62
10	99.8	0.53	0.60	0.71
15	570	0.26	0.45	0.80
20	1970	0.16	0.37	0.88
25	5130	0.11	0.31	0.95
30	11200	0.076	0.27	1.0

The ratio of optimum prey weight to herring weight is put to $\exp(-8)$ or 0.034 % in the Andersen & Ursin (1977) study. This value is low compared to the preference ratios obtained in Table 4 for larval herring. Two factors may cause this discrepancy the first of which is that although the preference ratios obtained in Table 4 represent virtually all geometrical shapes of prey (i.e. $2 \leq q \leq 4$) they still only relate to the attack process for one type of particular feeding. Secondly, Andersen & Ursin (op. cit.) do not distinguish between different life-history stages in relation to prey size preference. The weight preference of 0.034 % is adopted as a sort

of average value for the juvenile and adult stages and then applied to the early life-history stages as well.

The work of Andersen & Ursin (1977) shows the important role a theory of prey size preference occupies in providing a consistent description of predatory species interaction in the marine ecosystem. At any point of time the food available for a size class of predators is obtained by Andersen & Ursin (1977) as a weighted product-sum of preference index and abundance of all suitable prey categories occupying the same habitat as the predators. The ecosystem predation pattern thus changes as time elapses because the abundance of animals changes due to predation and other causes of mortality. But the rules of 'who wants to eat whom' is determined by the index of prey size preference of the predator. Andersen & Ursin (op. cit.) assume a symmetrical preference curve on a logarithmic weight scale, e.g. a prey of half the optimum weight and a prey of twice the optimum weight are considered equally attractive by the predator. This model of prey size preference appears to provide a fair description of available field data (Ursin, 1973, Andersen & Ursin, op. cit.).

In the field, however, it is difficult or expensive to provide data on prey size characteristics both for the food available and the resulting stomach content of the predators. Theories of prey preferences are probably more likely to be developed and tested under controlled laboratory conditions because each characteristic of prey may be isolated as a variable. The present study of feeding success represents a step in this direction.

References

- Andersen, K. P. & E. Ursin, 1977. A multispecies extension to the Beverton and Holt Theory of Fishing, with accounts of phosphorus circulation and primary production. – Meddr Danm. Fiskeri- og Havunders. N.S., 7: 319-435.
- Beyer, J. E. & G. C. Laurence, 1980. A stochastic model of larval fish growth. – Ecol. Modelling 8: 109-132.
- Blaxter, J. H. S., 1965. The feeding of herring larvae and their ecology in relation to feeding. – Calif. Coop. Oceanic Fish. Invest. Rep. 10: 79-88.
- Blaxter, J. H. S., 1968. Rearing herring larvae to metamorphosis and beyond. – J. mar. biol. Ass. U.K. 48: 17-28.
- Blaxter, J. H. S., 1979. Food habits and diets (natural and synthetic) for herrings and related species. To be published in CRC Handbook of Animal Nutrition.
- Blaxter, J. H. S. & G. Hempel, 1963. The influence of egg size on herring larvae. – J. Cons. Int. Explor. Mer 28: 211-240.
- Blaxter, J. H. S. & M. Staines, 1971. Food searching potential in marine fish larvae. – Four. Europe. Mar. Biol. Symp. (D. J. Crisp, ed.). Cambridge University Press, 467-485 pp.
- Houde, E. D., 1972. Development and early life history of the northern sennet, *Sphyræna borealis* DeKay (Pisces: Sphyrænidæ) reared in the laboratory. – Fish. Bull. U.S. 70: 185-195.
- Hunter, J. R., 1972. Swimming and feeding behavior of larval anchovy (*Engraulis mordax*). – U.S. Fish. Bull. 70(3): 821-838.
- Hunter, J. R. (editor), 1976. Report of a colloquium on larval fish mortality studies and their relation to fishery research, January 1975. NOAA Tech. Rep. NMFS CIRC. 395, 5 pp.
- Hunter, J. R., 1977a. Behavior and survival of northern anchovy *Engraulis mordax* larvae. – Calif. Coop. Fish. Invest. Reports 19.

- Hunter, J.R., 1977b. The feeding behavior and ecology of marine fish larvae. – National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, California 92038. To be published by the 'International Center for Living Aquatic Resources Management' (ICLARM), Manila.
- Kislalioglu, M. & R.N. Gibson, 1976. Prey 'Handling time' and its Importance in Food Selection by the 15-Spined Stickleback, *Spinachia spinachia* (L.). – J. exp. mar. Biol. Ecol., 25: 151-158.
- Kramer, D. & J.R. Zweifel, 1970. Growth of anchovy larvae (*Engraulis mordax* Girard) in the laboratory as influenced by temperature. – Calif. Coop. Oceanic Fish. Invest. Rep. 14: 84-87.
- Lasker, R., H.M. Feeder, G.H. Theilacker & R. C. May, 1970. Feeding, growth and survival of *Engraulis mordax* larvae reared in the laboratory. – Mar. Biol. 5: 345-353.
- Laurence, G.C., 1978. Larval length-weight relations for seven species of northwest Atlantic fishes reared in the laboratory. – U.S. Fish. Bull. 76: 890-895.
- Rao, C. Radhakrishna, 1965. Linear statistical interference and its applications. Wiley.
- Rosenthal, H. & G. Hempel, 1969. Experimental studies in feeding and food requirements of herring larvae (*Clupea harengus* L.). In: J.H. Steele (editor): Symp. Marine Food Chains, Univ. of Aarhus, Denmark 1968. pp. 344-364. Edinburg: Oliver and Boyd.
- Theilacker, G.H. & M.F. McMaster, 1971. Mass culture of the rotifer *Brachionus plicatilis* and its evaluation as a food for larval anchovies. – Mar. Biol. 10: 183-188.
- Ursin, E., 1973. On the Prey Size Preferences of Cod and Dab. – Meddr Danm. Fiskeri- og Havunders, N.S., 7: 85-98.