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SIZE SELECTIVE PREDATION BY LARVAL FISH

by

Ellen Bang Christensen

Villy Christensen

Jan Erik Beyer

Danish Institute for Fisheries and Marine Research
Charlottenlund Slot
DK - 2920 Charlottenlund

SUMMARY

A quantitative appraisal of selective feeding by marine fish is given in terms of the Ivlev indices of electivity, the Andersen and Ursin index of suitability, their log-normal size preference model and the concept of optimal diet derived from optimal foraging theory.

The problem is exemplified by considering stomach contents of one type of predators which have been feeding in non-changing environments comprising known size groups of one prey species.

Data are limited to results obtained from short-termed feeding experiments with Atlanto-Scandian herring larvae of 10-20 mm standard length. The herring larvae were reared in the laboratory on a diet of one day old *Artemia* nauplii. In all feeding experiments the larvae were starved in the experimental systems for about 20 hrs before the larvae were offered a diet of *Artemia* in the length-range 0.4 to 1.2 mm. Three types of size-selection experiments differing in prefeeding food-size conditions of the larvae were performed. Simple models of feeding behaviour and digestion are used to compare the size of prey found in stomachs to the size of prey offered.

The testable hypothesis of an adaptative effect on size selection cannot be rejected on the present data.

It is emphasized that knowledge of the mechanisms of selective feeding by marine fish cannot be obtained from stomach analysis alone. The results indicate that the minimum requirement consists of data on the abundance and the accessibility of various prey types, as well as data on predatory feeding behaviour, stomach contents and digestion.

On the population level, forgetting about the selective feeding mechanisms of the individual fish larvae, the analysis presented here suggests that the log-normal model may give an adequate description of "prey size selection by the average predator".

1. INTRODUCTION

This paper attempts to deal with basic principles in studying and understanding some of the elements in size selective feeding by clupeoid fish larvae. The motivation for such studies originates in the stock and recruitment problem and in the more general concept of species interaction.

In the marine environment the fish larvae operates as a predator but at the same time serve as potential prey to other predators. It is usually believed that, if the fish larva is unsuccessful as a predator its vulnerability as prey to predators increases. We are not here concerned with the question of whether unsuccessful feeding by the larva ultimately results in death due to starvation, due to predation. The important thing is that the way the fish larva is able to operate as a predator is strongly related to its chance of surviving.

As the fish larva grows the spectra of its potential types of prey and of its predators gradually change. Size is one of the elements of major importance. We know that as a rule big predators eat larger prey than do small predators of the same species. In a quantitative selection analysis of this factor, Ivlev (1961) stresses that it is not the absolute sizes of predator and prey that is important, but the size ratio. He defines the degree of "rapacity" of a predator as

$$\xi = \text{"Optimum size of prey"}/\text{size of predator} \quad (1)$$

and uses this factor as a basis for distinguishing between "predatory" species (high ξ value) and "peaceful" species (low ξ value).

This type of approach has been used to model species interaction in the marine environment. Andersen and Ursin (1977) assume that prey size preference of the predator is exclusively a function of the ratio of prey size to predator size. According to Ursin (1973), a cod prefers to eat prey with a bodyweight that is 100 times less than its own, i.e. $\xi = 0.01$, whereas the factor is about 1000 for the more "peaceful" dab, i.e. $\xi = 0.001$.

We return to Ivlev's work at the individual predator level and Andersen and Ursin's work at the population level in the next section. The important thing here is to note that Eq. (1) more or less represents the state of the art in modelling species interaction. This is due to incomplete data on the effect of predation and, in particular, on the underlying mechanisms.

Stomach analysis of predators in most cases represent the only key available to studying the mechanisms of predation. Unfortunately this key is not a direct one to understanding selective feeding. The stomach content of an individual fish at time t represents the undigested part of the total amount of food the fish has ingested during a certain past: $(t-\Delta t, t)$. Thus in addition to the wellknown problems of avoiding spontaneous regurgitation or defaecation in the sampling procedure, difficulties are encountered in the very problem of estimating the frequencies of prey types (species, size) ingested based on stomach content data. Small prey, for example, are likely to be underrepresented in the stomachs because they are digested faster than larger prey. A second problem is that the distribution of prey types consumed by one type of predators

reflect the accumulated result of several factors operating simultaneously. One set of factors characterizes the feeding predator (e.g. properties inherent in the species, size, state of hunger). Another set of factors characterizes the food environment during (the often unknown) foraging period. These factors include density and distribution of potential prey types (i.e. degree of availability to predation) and their inherent protective structures and avoidance behaviour (i.e. degree of accessibility or vulnerability to predation).

Thus, an attempt to infer properties of the mechanisms governing food selection is likely to result in misleading conclusions if the data only represent stomach contents and vague ideas of the matching food environment. With this in mind we attempt to deal critically with the available theories on size selection in relation to one of the simplest possible situations: one type of predators feeding in a known environment comprising size groups of one type of prey.

2. PROBLEM SPECIFICATION AND HYPOTHETICAL MODELS

2.1 FEEDING BEHAVIOUR, STOMACH CONTENT AND DIGESTION

Fish larvae are visual feeders and they appear to select individual prey in a continuous mode of feeding behaviour. Continuous feeding should here be understood in contrast to discrete feeding, i.e. consecutive meals interrupted by relative long digestion periods.

Clupeoid fish larvae are not persistent in their attack behaviour. In an attack the larva forms the characteristic S-shape striking posture, darts forward and captures or misses the prey. An ingested prey passes rapidly to the hindgut where digestion probably starts at once. Satiation control seems to be one of digestion rather than one of ingestion, i.e. food passes faster through the hindgut at high prey densities (Werner and Blaxter, 1980).

The problem we here attempt to deal with in terms of simple models relates to the length distribution of prey found in larval stomachs compared to the length distribution of prey ingested. Let us restrict attention to the case in which a herring larva with empty gut starts feeding at time 0. When a food organism is eaten digestion is considered to begin immediately. In a first approximation the processes of digestion of the individual food organisms take place independently of each other because food organisms are more or less placed on a line in the gut. Let T denote the time of ingestion of a food organism of length L_e . We assume a linear model of the decrease in length of the food organism due to digestion, that is

$$L_d = L_e - \gamma(t_s - T) \quad (2)$$

where L_d is the length of the food organism in the gut at the time of sampling, t_s , i.e. at the end of the feeding experiment. The model is depicted in Fig. 1. Maximum shrinkage in length, s_{max} , occurs if the food organism considered is ingested at the very start of the feeding experiment, i.e. $T=0$.

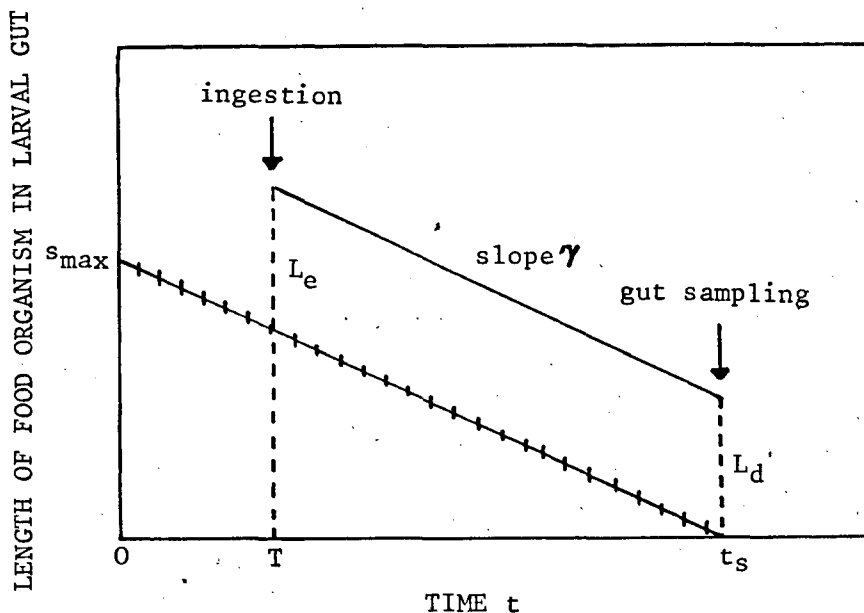


Fig. 1: Linear digestion model in length of individual prey. The food organism of length L_e is ingested at time T and has the reduced length L_d when the larval gut is sampled at time t_s .

Introducing

$$s_{\max} = \gamma t_s \quad (3)$$

in Eq. (2) gives

$$L_d = L_e - s_{\max} \left(1 - \frac{T}{t_s}\right) \quad (4)$$

The time of ingestion, T , and the length of the prey ingested, L_e , are usually unknown and should thus be considered as stochastic variables. This in turn makes prey length in gut at sampling, L_d , a stochastic variable which is given by Eq. (4) assuming the linear model.

It may be noted that we here not directly are concerned with "the state of the food organisms at complete digestion". The rapid gut passage of food in case of high prey densities (Werner and Blaxter, 1980) must take place at the cost of less efficient total digestion, i.e. the food organism is not broken completely down. This merely indicates difficulties in estimating rate of food consumption based on stomach content and we are not concerned with that here.

Let us first consider the case of a constant feeding environment comprising identical prey. Under such circumstances it is often assumed that the larva eats prey in a Poisson process at constant rate. Let the duration of the feeding period, t_s , be less than the complete digestion time of a food organism, i.e. the number of food organisms found in the gut at sampling represents total food consumption in the interval of time $(0, t_s)$. It then follows directly from the Poisson model that the times of ingestion are uniformly distributed over this interval, $(0, t_s)$. Thus, as depicted in Fig. 2 (left), T follows a $U(0, t_s)$ distribution, that is with mean and variance

$$\text{INGESTION MODEL I: } \begin{cases} E(T) = \frac{1}{2} t_s \\ V(T) = \frac{1}{12} t_s^2 \end{cases} \quad (5)$$

Note that it has been assumed that no information is available with respect to the relationship between a food organism position in the gut and the time of ingestion. T is the point in time at which a food organism, randomly chosen from the gut content of time t_s , was ingested.

The model represented by Eq. (5) does not take into account that hungry larvae often respond to food by eating comparative many prey in the first period of feeding. Such an effect is incorporated in the T -model by moving more probability mass towards time 0, i.e. start of feeding. As an example we use a triangular distribution of T , see Fig. 2 (right).

$$\text{INGESTION MODEL II: } \begin{cases} E(T) = \frac{1}{3} t_s \\ V(T) = \frac{1}{18} t_s^2 \end{cases} \quad (6)$$

Returning to the digestion model in Eq. (4), the next problem concerns the variability in the length of prey, L_e , ingested by the larva. We have only information on the length distribution of prey offered, L_0 , to the larva which differs from the distribution of L_e in case of size selection by the larva. However, assuming that effect of size selection is negligible if the coefficient of variation of L_0 is small we obtain from Eqs. (4)-(6) that

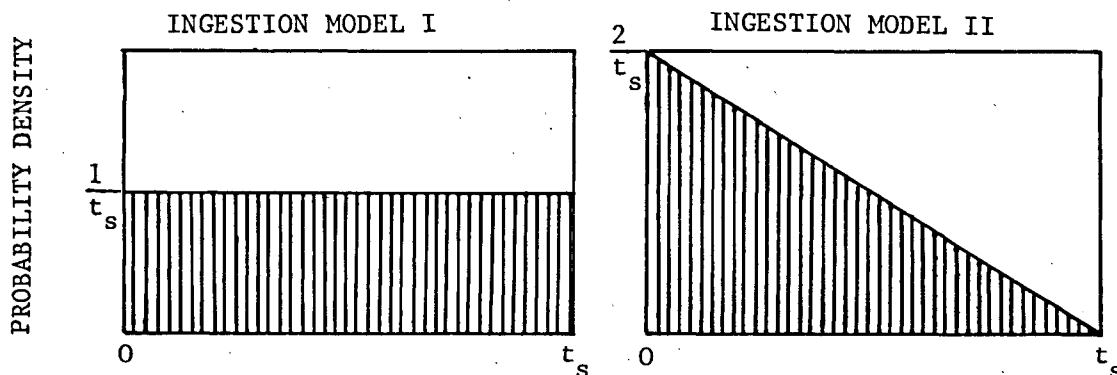


Fig. 2: Probability density functions of T , the point in time a food organism, chosen at random from the larval gut at time t_s , has been ingested. MODEL I exemplifies constant feeding behavior of the larva during the feeding period. MODEL II represents a situation of decreasing feeding activity in the constant environment.

$$\text{MODEL I: } \begin{cases} E(L_d) \approx E(L_0) - \frac{1}{2} s_{\max} \\ V(L_d) \approx V(L_0) + \frac{1}{12} (s_{\max})^2 \end{cases} \quad (7)$$

$$\text{MODEL II: } \begin{cases} E(L_d) \approx E(L_0) - \frac{2}{3} s_{\max} \\ V(L_d) \approx V(L_0) + \frac{1}{18} (s_{\max})^2 \end{cases} \quad (8)$$

Thus, in case of no size selection, the mean length of food organisms in the gut after a short feeding period is less than the mean length offered. The variance of prey lengths in the gut exceeds the variance of prey lengths offered. Note that size of prey ingested and time of ingestion here are considered stochastic independent (since we have just added the variances).

2.2 EMPIRICAL INDICES OF FOOD SUITABILITY

2.2.1 ON INDICES OF ELECTIVITY

Let V denote the volume of water considered which is assumed to hold k types of prey and one type of predator. Let A_i denote the number of prey of the i 'th type, i.e. the relative abundance of type i or the ratio of the number of type i prey to total number of prey is

$$P_i = \frac{A_i}{\sum A_i} \quad (9)$$

A \sum denotes a summation over all prey types (i.e. $i = 1, 2, \dots, k$) unless otherwise stated.

In the same way we define

$$r_i = \frac{N_i}{\sum N_i} \quad (10)$$

where N_i is the total number of prey of type i found in the stomachs of the predators.

Ivlev's (1961) first and second indices of electivity are

$$E'_i = \frac{r_i}{p_i} \quad (11)$$

$$E''_i = \frac{r_i - p_i}{r_i + p_i} = \frac{E'_i - 1}{E'_i + 1} \quad (12)$$

$E'_i = 1$ is interpreted as no selection at all on type i whereas greater values than 1 is interpreted as selection and values between 0 and 1 as avoidance. The second index is merely a scaling of the first index so that $-1 \leq E''_i < 0$ expresses avoidance and $0 < E''_i < 1$ expresses selection.

Each of these indices thus expresses selectivity on the same absolute scale for the different types of prey. The prey type which is associated with the greatest E' value is also the prey type of greatest E'' value because E'' is a monoton increasing function of E' . It is this prey type, representing the mode of the empirical distribution of electivity indices, that Ivlev refers to as "the optimum size of prey" in Eq. (1).

It is not clear to which degree it has meaning to express the relative availability of a prey type exclusively in terms of its relative abundance, Eq. (9). A visual predator is likely to be able to perceive larger prey in greater distance than smaller prey. This will bias the indices of selection. It is also necessary in some way to incorporate the degree of patchiness of the individual prey types into the computation of food availability. Ivlev (1961) gives examples on changes in the E indices due to different degree of patchiness but at fixed p_i -values. One of his experimentally based conclusions is that "a uniform increase in the degree of irregularity in the distribution of all component parts of the food complex leads to a much deeper divergence of electivity values while the general order of the distribution of indices is preserved".

2.2.2 THE ANDERSEN AND URSIN INDEX OF SUITABILITY

Andersen and Ursin (1977), Anon. (1980) and Sparre (1980) operate on the population level with the same index of food suitability. The biomass of food available to the predators is defines as

$$AVAI = \sum SUI T_i \cdot w_i \cdot A_i \quad (13)$$

where w_i is the body-weight of prey type i . That is, the sum of the biomasses weighted by the index of suitability of each prey type.

The suitability index is determined as a product of three factors:

$$\text{SUIT} = \text{HAB} \cdot \text{VULN} \cdot \text{SIZE} \quad (14)$$

where

$$\begin{aligned} 0 &\leq \text{HAB} \leq 1 \\ 0 &\leq \text{VULN} \leq 1 \\ 0 &\leq \text{SIZE} \leq 1 \end{aligned}$$

HAB is intended to express the fraction of the prey population that is likely to occupy the feeding habitats of the predators in the marine environment. HAB is not yet incorporated in the North Sea model of species interaction (Andersen and Ursin, 1977) but the work is in progress (Ursin and Gislason, personal communication). In the present case we put $\text{HAB} = 1$ for all types of prey. VULN is intended to describe differences between prey types of equal size in vulnerability to predation by the considered type of predator. Since focus in this paper is placed on juvenile prey of the same species we put tentatively $\text{VULN} = 1$ for all types of prey. Small differences in colour and swimming behaviour between different sized nauplii (the prey) may cause small differences in such an index of vulnerability. This is thus disregarded by putting $\text{VULN} = 1$. This leaves differences in suitability caused by differences in prey size. We return to SIZE in paragraph 2.3.1.

Interest is here focused on the empirical determination of SUIT and its relation to the Ivlev indices. We largely follow the notation by Sparre (1980). Andersen and Ursin (1977) assume that the fraction prey type i constitutes of total food consumption is proportional to the available biomass of type i . Effects of digestion are then neglected and the same argument used for the stomach content of the predators, i.e.

$$\text{FOOD}_i \propto \text{STOM}_i \propto \text{SUIT}_i \cdot w_i \cdot A_i$$

or

(15)

$$\text{SUIT}_i \propto \frac{1}{w_i A_i} \cdot \text{STOM}_i$$

where \propto designates proportionality and STOM_i is the fraction of the stomach content constituted by the biomass of type i prey. It follows directly from these proportionalities by normalizing that

$$\text{STOM}_i = \frac{\text{SUIT}_i \cdot w_i \cdot A_i}{\sum \text{SUIT}_i \cdot w_i \cdot A_i} \quad (16)$$

and

$$\text{SUIT}_i = \frac{\frac{1}{w_i A_i} \cdot \text{STOM}_i}{\sum \frac{1}{w_i A_i} \cdot \text{STOM}_i} \quad (17)$$

which are the equations given by Sparre (1980). SUIT_i has here been normalized to sum up to 1, i.e. $\sum \text{SUIT}_i = 1$. We return to this point in a moment.

From the stomach analysis we obtain

$$\text{STOM}_i = \frac{N_i w_i}{\sum N_i w_i} \quad (18)$$

Inserting this expression in Eq. (17) or simply by utilizing Eq. (15) that is

$$\text{SUIT}_i \propto \frac{1}{w_i A_i} \cdot N_i \cdot A_i = \frac{N_i}{A_i}$$

we get

$$\begin{aligned} \text{SUIT}_i &= \frac{N_i/A_i}{\sum N_i/A_i} & (19) \\ &= \frac{r_i/p_i}{\sum r_i/p_i} \\ &= \frac{E'_i}{\sum E'_i} \end{aligned}$$

That is SUIT equals Ivlev's first index of electivity (Eq. 11) relative to the total electivity index sum. SUIT is thus a relative measure of selectivity in the sense:

$$\frac{\text{SUIT}_i}{\text{SUIT}_j} = \frac{E'_i}{E'_j} \quad (20)$$

where i and j are two types of prey.

The adjusting of SUIT to $\sum \text{SUIT}_i = 1$ is questionable. SUIT_i is in Eq. (14) defined to take values between 0 and 1 so in the applications it is probably more reasonable to adjust so that $\max\{\text{SUIT}_i\} = 1$, cf. Andersen and Ursin (1977). These matters, however, need careful considerations in the future if the absolute value of the SUIT index is used in ecological considerations.

2.3. MODELLING SIZE SELECTION

2.3.1 THE ANDERSEN AND URSIN LOG-NORMAL SIZE SELECTION MODEL

Andersen and Ursin's (1977) size selection model was developed in 1971 based on the assumptions (1) that there exists a preferred prey size, (2) that the ratio of predator weight to preferred prey size remains the same through a predator's lifetime and, (3) that a prey twice the preferred size is equally attractive as a prey half the preferred size. These assumptions lead to a

log-normal size selection model. Adjusting the SIZE selection curve to a maximum value of one, we get

$$\text{SIZE}_i = \exp\left(-\frac{1}{2}\left(\frac{\log\frac{W}{w_i} - \eta}{\sigma}\right)^2\right) \quad (21)$$

where W is the weight of the predator and w_i the weight of the i 'th prey size group. Thus, in accordance with Eq. (1) the optimum size ratio becomes

$$\text{Preferred prey weight/Predator weight} = e^{-\eta} \quad (22)$$

If we apply the usual rule of thumb, that wet weight in gram = $0.01 \text{ gram/cm}^3 \times (\text{length in cm})^3$ to both predator and prey the equation reads

$$\text{Preferred prey length/predator length} = e^{-\eta/3} \quad (23)$$

As an example, Andersen and Ursin (1977) use $\eta = 8$ for herring. This implies that a herring always evaluates prey in relation to its own size and prefer prey 3000 times less in weight (or 14 times less in length).

2.3.2 OPTIMAL DIET THEORY

Models for optimal foraging are based on the assumption that prey are selected so that the cost of foraging (search time, handling time, etc.) per consumed unit of energy (cal. or weight) are minimized (see for example the review paper by Pyke et. al. 1977). The development of such models requires of course comprehensive knowledge on the feeding behaviour of the predator in question. In case of larval herring no appropriate model seems to be available because most models assume that handling time is a function of prey size which it is not for clupeoid fish larvae. A step in the direction of developing models for the foraging strategy leading to optimal diet for larval herring has been given by Beyer (1980).

We here restrict attention to one of the results which seems to emerge from all theories of optimal diet. That is, increasing food abundance should lead to greater food specialization. In other words, if the relative abundance of each type of prey

$$p_i = \frac{A_i}{\sum A_i} = \frac{c_i}{\sum c_i}$$

remains constant when the absolute abundance (number A_i or density c_i) increases then the effect should be a size selection curve with less variability. This hypothesis was also put forward by Ivlev (1961). In the log-normal model, Eq. (21), the hypothesis imply that σ should increase when the food available decreases.

3. MATERIALS AND METHODS

Experiments of food selection by larval fish were carried out at the Danish Laboratory of Larval Fish Research in Charlottenlund, April-June, 1980.

Larvae of Atlanto-Scandian herring served as predators, *Artemia salina* nauplii as prey.

The herring larvae were grown on one day old *Artemia* of mean length 0.60 mm until the experiments were performed or until the prefeeding period of another food size adaptation was started. The *Artemia* nauplii had been fed dried *Spirulina*-powder.

Two types of experiments on food size selection were carried out. In both experimental series the larvae were offered equal numbers of *Artemia* from four different age groups. The mean size-at-age of these groups was 0.45 mm, 0.60 mm, 0.80 mm and 1.0 mm respectively in total length.

In the first type of experiments larvae of 10-20 mm standard length were transferred directly from the stocking pool to the experimental aquaria. The experiments were carried out at two nominal food concentrations of 4.0 A/ml and 0.4 A/ml, respectively.

In the other type of experiments 200 larvae of 14-20 mm standard length were allowed to adapt to different conditions of food size for seven days prior to the experiments. Half the larvae were offered the four size classes of *Artemia* (i.e. as in the experiments) and the other half only the largest size class of *Artemia*. During the adaptation period the larvae were fed once a day to a concentration of 0.4 A/ml and this concentration was also used in the experiments.

All experiments, including the adaptation controls, were carried out in cylindrical aquaria made of grey PVC. Aquaria holding 5 liter were used in case of high food concentration, 4.0 A/ml, and 20 liter systems were used for the low food concentration at 0.4 A/ml. During adaptation periods water was supplied to the aquarium at the surface and led out at the bottom through a perforated tube covered with 0.1 mm plankton net. Moreover an airjet was directed at the surface. The airjet itself created enough turbulence in the water column to keep *Artemia* suspended. During the experiments only the airjets were used.

The salinity of the water used was 26.5 o/oo. The temperature was 10-12.5°C. Two cool-white fluorescent lighttubes were placed above the aquaria. The light intensity at the water surface was about 1000 lux.

The experimental procedure was the same in both series. Approximately 100 larvae were used in each experiment. The larvae were starved in the experimental system for about 20 hours to empty their guts prior to the experiment. At the start of the experiment the aquarium was seeded with approximately 2000 or 5000 *Artemia* from each of the four age groups (i.e. 0.4 A/ml in 20 liter system or 4.0 A/ml in the 5 liter system). Aliquots from the *Artemia* age-pools to density estimation were taken with due caution to sampling errors (cf. Beyer and Laurence, 1979). After seeding with the needed volumes of the *Artemia* suspensions, the nauplii were distributed in the water column mixing well. A random subsample of 120 nauplii taken from each of the *Artemia* age-pools was preserved in 2 % Formalin in buffered sea-water to obtain the length distribution at age.

It may be noted that control experiments (the results of which are not presented here) showed that the airjet did not entirely prevent creation of nauplii aggregation (patchiness). However, based on these experiments we were not able to reject the hypothesis that patches were distributed at random in the body of water and that the four size classes of nauplii were evenly distributed within the patches.

After a feeding periode of about one hour the larvae were caught, anaesthetized in 20 % dissolved Urethan, and preserved in 2 % Formalin. The larvae were measured to standard length, and width of head and of lower jaw was measured (Fig. 3.A). Stomach contents prepared from the guts were measured to length. A relation between Artemia length and width was found by measuring 120 Artemia from each age group. The width was taken as the width in front of the first pair of appendages (Fig. 3.B).

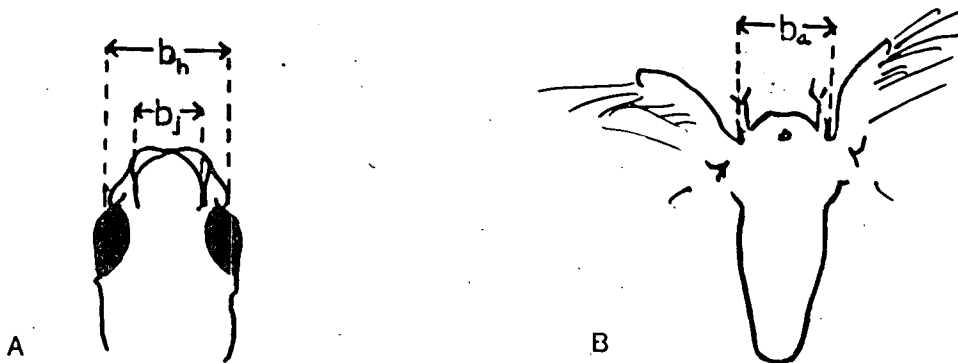


Fig. 3: A. Measures of width of larval head b_h and lower jaw b_j .
Larva seen from below.
B. Measure of width of Artemia b_a .

As Artemia apparently shrank due to the initial stage of digestion in the larval gut, controlled experiments were performed offering a narrow size range of nauplii to the larvae.

In one experiment, larvae of 16-20 mm standard length were offered one day old Artemia. Mean length and standard deviation of the size distribution offered were estimated by measuring 260 nauplii from a sample taken and preserved simultaneously with the start of the experiment. After a feeding period of one hour the larvae were preserved in 2 % Formalin and stomach contents measured to length.

The effect of size selection is likely to be negligible within the narrow size range of one day old Artemia. In any case, to eliminate a possible effect of size selection another experiment was set up. Newly hatched Artemia nauplii were measured and sorted to length prior to the experiment. Our very last herring larva (25 mm standard length) was then offered about 100 nauplii which had a total size range of only 0.02 mm live length. After a feeding periode of about one hour, the larvae and the remaining Artemia were collected and preserved in 2 % Formalin. The Artemia not-eaten and the stomach contents of the larva were measured to length.

4. RESULTS AND DISCUSSION

4.1 THE FOOD ORGANISM

4.1.1 SHRINKAGE EXPERIMENTS

The two experiments conducted on shrinkage of Artemia in the gut of herring larvae both showed a marked difference between Artemia lengths offered and lengths found in the gut.

The results of the experiments are shown in Table 1.

Table 1: Results of shrinkage experiments. All lengths are in mm and refer to conserved animals.

Experiment no	No. of larvae	Mean length	Artemia offered			Artemia eaten			
			Total	Meas ured	Mean lgth	St. Dev	Meas ured	Mean lgth	St. Dev
1	40	18	8000	260	0.678	0.051	262	0.570	0.064
2	1	25	100	40	0.456	0.021	14	0.349	0.040

The close agreement of shrinkage in the mean length of Artemia supports the linear digestion model. The mean shrinkage is 0.1075 mm and using ingestion MODEL II (cf. Eq. (8)) we obtain:

$$s_{\max} = 3/2 \cdot 0.1075 \text{ mm} = 0.161 \text{ mm}$$

using this value of s_{\max} and the observed variance of Artemia lengths offered the standard deviation of the length of the Artemia in the larval gut (L_d) is obtained from Eq (8) as 0.064 and 0.043 mm, respectively. These values are in good agreement with the observed standard deviation of 0.064 and 0.040 mm, respectively. The agreement is not so pronounced if ingestion MODEL I is used instead.

Note that the effect of mean shrinkage is in the order of 20 % although the feeding experiments only lasted for about 1 hour.

4.1.2 ARTEMIA LENGTH AND WIDTH

Prey width is usually considered as the critical dimension for fish larvae eating oblong prey.

The width of Artemia, however, is difficult to define and measure properly. Therefore length was used as a standard measure of Artemia size.

To be able to compare the width of prey to the mouth size of the fish larvae a relationship between Artemia length and width was derived from the measurement of 480 Artemia in the size range 0.4 to 1.3 mm. Relationships between length and width are often considered to be of the form:

$$\text{width} = a \cdot \text{length}^d \quad (a, d \text{ is constants})$$

In the narrow size range considered here it is however difficult to distinguish between this power function and a simple linear model.

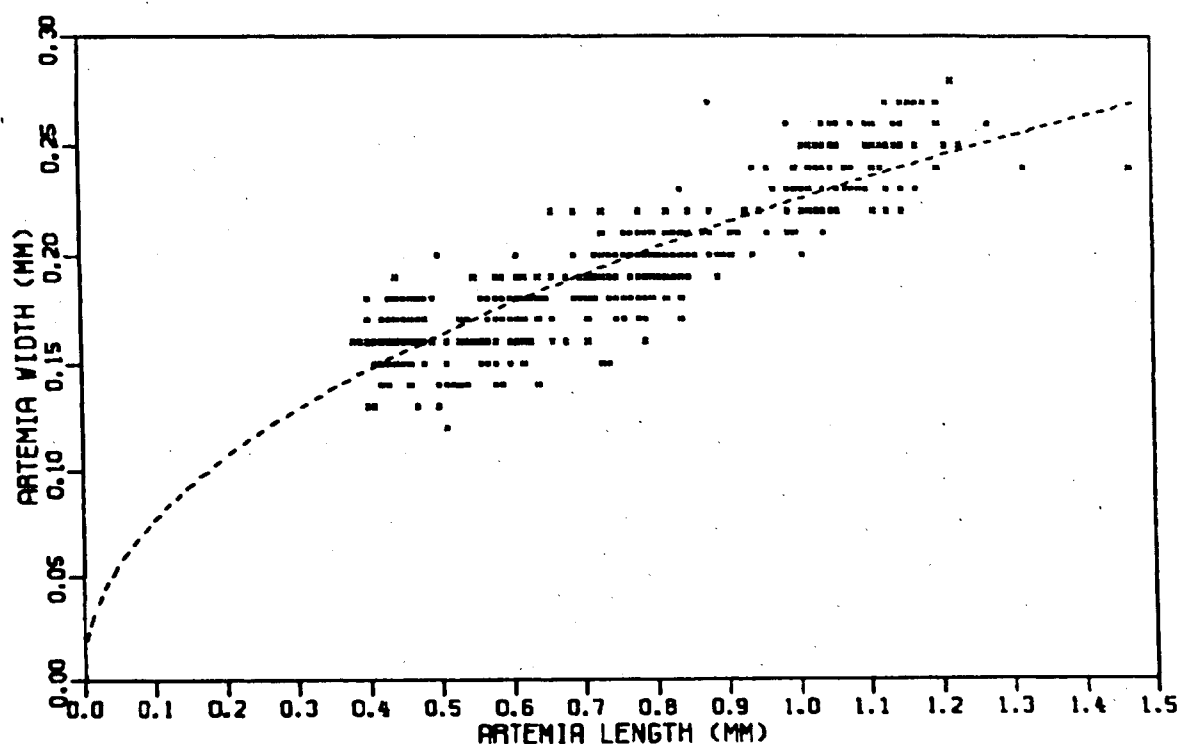


Fig. 4: Plot of width against length based on 480 measurements of individual Artemia nauplii. The fitted curve is obtained from non-linear least square regression.

The fit obtained (see fig. 4) is

$$\text{width} = 0.225 \cdot \text{length}^{0.466} \quad (\text{mm}) \quad (24)$$

The asymptotic 95 % confidence interval for a is (0.223, 0.227) and for d (0.443, 0.483). A linear fit gives ($r^2 = 0.782$)

$$\text{width} = 0.102 + 0.124 \cdot \text{length} \quad (\text{mm})$$

In relation to comparisons with the dimensions of larval mouth, this measurement of width (see fig 3.B) must be corrected for the additional width caused by appendages. The increase in maximum width of adult and copepodite stages of copepods by including the appendages ranges

from 0 to 50 % (Wiborg 1948). In the following we will adopt a value of 25 %.

4.1.3 ARTEMIA LENGTH AND WEIGHT

A length weight relationship for Artemia less than 1.5 mm does not seem to be available in the literature.

The following approach was adopted. Body-weight is assumed proportional to body volume which is approximated by a cylinder, that is

$$w_a = \beta \cdot l_a \cdot b_a^2 = \beta l_a^{1.93}$$

where the last equation follows from the width-length relationship given by Eq. (24). To determine β we need one good weight estimate for a given Artemia length.

On the basis of 40 weight determinations (200 nauplii in each) Benijts et. al. (1975) found a mean dry-weight of 1.85 ug for freshly hatched Artemia (1st Instar). The weight of Benijts et. al. have to be compared to our length measurements, as the length of Artemia depends upon treatment. On the basis of length measurements of 332 newly hatched Artemia of the same brand and using the same hatching procedure as in Benijts et al, we found a mean length of 0.452 mm.

From the requirement $1.85 = 0.452^{1.93}$ we obtain $\beta = 8.61$ ug-dry-weight \cdot mm $^{-1.93}$, that is

$$w_a = 8.61 \cdot l_a^{1.93} \quad (25)$$

An exponent of 1.93 may seem somewhat low. We were, however, able to find 9 mean weight at length data in the literature and they indicated a 95 % interval as extending from 1.65 to 3.4.

4.2 THE FISH LARVA

4.2.1 LENGTH OF LIVE AND PRESERVED HERRING LARVAE

The relationships between live and preserved length and width of larvae were determined by individual measurements of the same 40 larvae. The live larvae measured from 13.8 to 19.5 mm in length. The preserved from 13.3 to 18.3 mm. The linear least squares fit to the observations is:

$$\text{Length}_{\text{preserved}} = 0.95 \cdot \text{Length}_{\text{live}} \quad (r^2=0.9998) \quad (26)$$

$$\text{width}_{\text{preserved}} = 0.91 \cdot \text{Width}_{\text{live}} \quad (r^2=0.9952) \quad (27)$$

The results thus indicate a shrinkage in length of 5 % and in width of 9 % due to conservation.

4.2.2 WIDTH OF HEAD AND LOWER JAW OF HERRING LARVAE

On most larvae examined standard length, width of head and width of jaw lower jaw were measured (cf fig 3). Fig 5 shows the relation between width and length. As width of head is measured on 973 larvae and width of lower jaw on 1179 larvae only the means for each mm-length group is plotted. The standard error of the group means range for the two measures from 0.006 to 0.035 mm, and from 0.006 to 0.030 mm respectively. The same standard deviations within groups are smaller than 0.106 and 0.062 mm respectively. The increase in width of lower jaw is small compared to the increase in width of head.

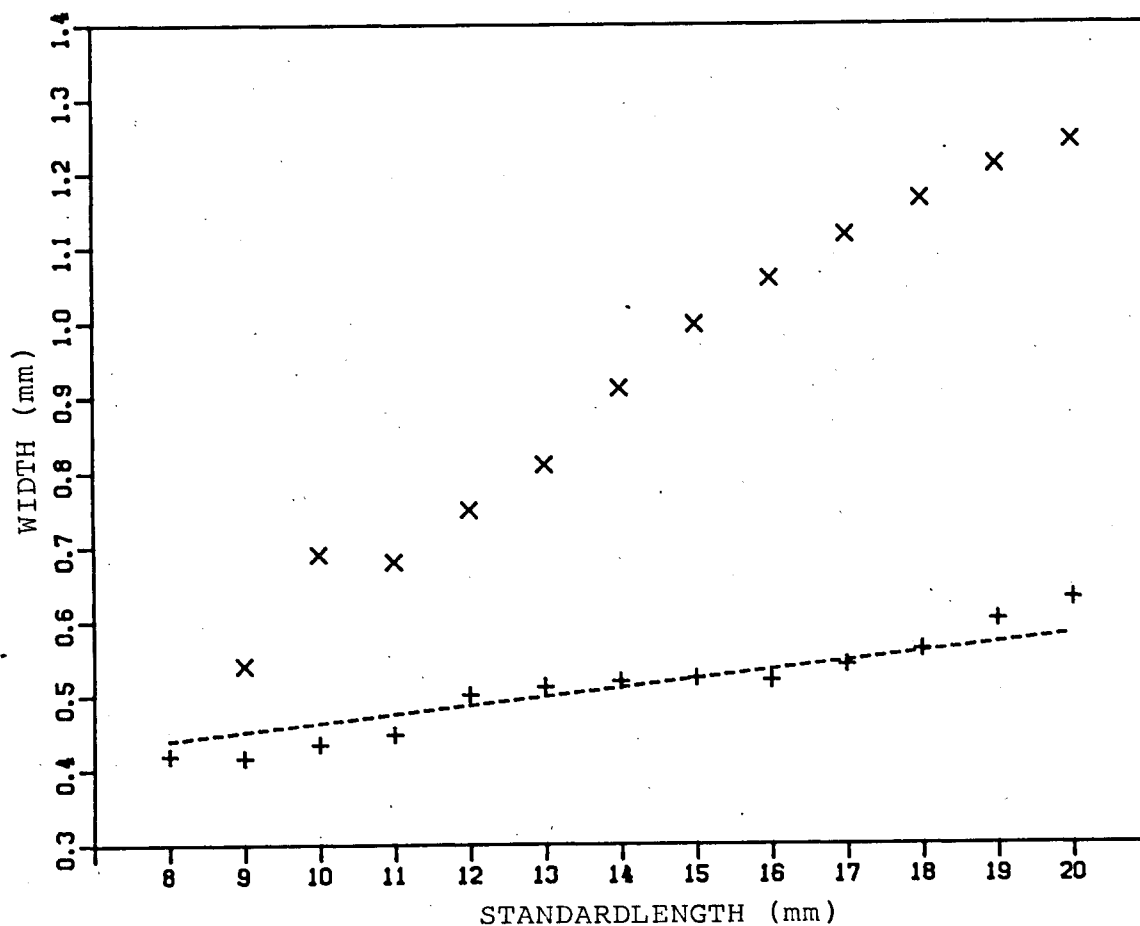


Fig. 5: Relation between larval standard length and width of lower jaw (+), and between standard length and width of larval head(x). Plots represent mean widths for each larval length group. (A total of 1179 and 973 larvae, respectively).

The width of the head and the width of the lower jaw represent two different measurements of mouth size. The critical mouth-size in respect to prey ingestion lies between these estimates, and probably closest to the width of the head.

The data do not permit us to distinguish between different length and width relationships. The data seem to indicate that a power function provides a reasonable good fit to the width-of-the-head-larval-length relationship.

The data on width of head (fig 5) are in agreement with data on larval lengths to size of mouth given by Shirota (1970) for larvae of *Clupea pallasii*. Shirota takes the mouth size to be the width of the gape when jaws are opened to an angle of 90° . The gape of jaws was about 0.70 mm at first feeding (9.5-10.5 mm length) increasing to about 1.2 mm for a larva of 17 mm length.

Blaxter (1965) gives the width of gape of Norwegian herring larvae, assuming an angle of 60° between upper and lower jaw. The gape of jaws at the end of yolk sac stage, app. 10 mm length, was about 0.4 mm, i.e. 55 % of the value given by Shirota for a larva of the same length. This value is closer to the value found of width of lower jaw.

4.3 AVAILABLE FOOD

The experimental food conditions as to sizes of food organisms were aimed kept as uniform as possible, by offering a diet comprising equal numbers of Artemia from four age groups. The variation in prey length, however, turned out to be too small in the youngest age groups to accept an assumption of uniformly distributed lengths. It is thus necessary to take account of the actual distribution of food sizes in a computation of size selection based on stomach content.

The sample distributions of length-at-age were reasonable well represented by Normal (probability) distributions. The estimated means and standard deviations are given in Table 2. The actual length distribution of Artemia offered to the larvae is then given by a weighted sum of the four length-at-age Normal densities; the weights being $\frac{1}{4}$ because the four age groups were equally represented in the experiments.

The only problem was that it turned out that the larval guts also contained Artemia of less length than the smallest of the Artemia offered. Anyway, that was the way our attention was drawn to the shrinkage problem. The correct way of adjusting for shrinkage in the gut is of course to adjust lengths in gut to lengths ingested. However, with the present lacking knowledge on the digestive processes it was difficult to decide on an appropriate way of making such an adjustment of the Artemia lengths in the larval gut.

Table 2: Available food in the experiments. That is, estimated and adjusted mean and standard deviations of length for Artemia age groups offered to the larvae. All lengths in mm.

Exp. with Age adapta- Group tion to	Age	Mean		Standard deviation	
		estimated	Adjusted	Estimated	Adjusted
SMALL	1	0.446	0.339	0.022	0.044
	2	0.580	0.473	0.050	0.063
	3	0.769	0.662	0.059	0.070
	4	1.038	0.931	0.125	0.131
ALL and LARGE	1	0.460	0.353	0.025	0.045
	2	0.697	0.589	0.056	0.068
	3	0.816	0.709	0.063	0.074
	4	0.968	0.860	0.088	0.096

In stead we have adjusted the size distribution of available food and kept the more accurate raw data on sample size distribution in guts. This adjustment of the available food was simply done by utilizing MODEL II on each agegroup, that is adjusting the mean by subtracting 0.108 mm (cf. 4.1.1) and the variance by adding 0.001445 mm².

Note that although this adjustment is questionable in several aspects: it is better than obtaining "an infinite index of selectivity" (Ivlev's first index) which would be the case if the predator eats prey that are not present in food environment.

The adjusted size distributions are shown on Figs. 6.A and 7.A.

4.4. FOOD SIZE SELECTION

Figs. 6.B and 7.B depict the frequency of Artemia lengths found in larval stomachs for the three types of experiments conducted.

The main purpose of the experiments was to investigate size selective feeding by herring larvae. The range of length variations of the larvae used in each of the experiments was about 5 mm. In all three cases comparing the frequency in stomach from the different mm-length groups of larvae, it turned out that a significant effect of larval size on prey size could not be detected. Therefore we do not distinguish between larval lengths within each of the three adaptive experiments.

In experiments with larvae adapted to Artemia of 0.55 - 0.65 mm length ("small") stomach data represent 543 Artemia from 110 larvae of mean length 13.7 mm. The effect of increasing the Artemia density available from 0.4 A/ml to 4.0 A/ml on size selection was insignificant so this representation (Fig 6.B) includes feeding at both densities.

In experiments with larvae adapted to Artemia of 0.45-1.1 mm length ("all sizes") data represent 1198 Artemia from 65 larvae of mean length 16.9 mm.

In experiment with larvae adapted to Artemia of 0.9-1.1 mm length ("large") data represent 1113 Artemia from 65 larvae of mean length 16,7 mm.

The computations of SUIT in Figs. 6.C and 7.C are based on Eq. (19). As described in connection with Eq. (14) SUIT is here interpreted as the prey size dependent factor, i.e. SIZE. The difference between the SUIT diagrams in Fig 7.C is small but there is a tendency that, larvae adapted to "large" Artemia show greater preference for larger Artemia than larvae adapted to the whole size range of Artemia lengths. The preference for large Artemia is relatively small in case of adaptation to small Artemia. It is easier to compare the preferences on an absolute scale and Fig. 8 gives the Ivlev's second index, Eq. (12) for all three experiments. The most pronounced effect is a strong avoidance against the smallest Artemia in all three cases.

A reasonable explanation for the selection patterns derived is an effect of the prefeeding conditions of the larvae, i.e. adaptation.

Herring larvae are reported by Rosenthal (1969) to react more often to prey which they have earlier been successful in catching. Rosenthal found that the larvae will not change to a new prey species (Artemia) as long as the usual (copepodnauplii) is present. After 3-4 days, however, the new prey type is taken as often as the usual prey type.

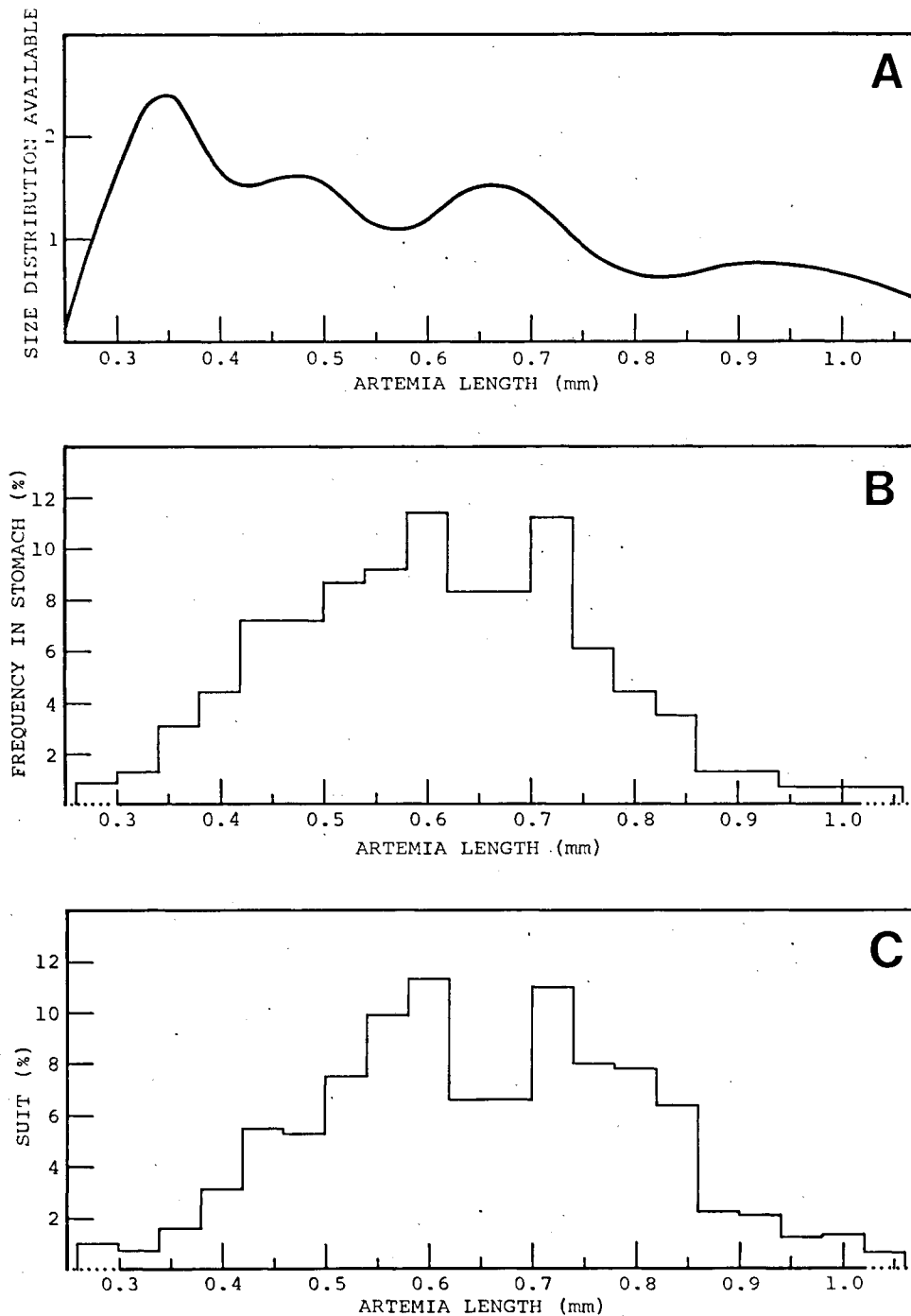


Fig. 6: Data on experiments with herring larvae adapted to small Artemia. A: length distribution of available food, adjusted to account for shrinkage in larval gut. B: Frequencies of Artemia found in larval gut, presented as percentage of Artemia within 0.04 mm length intervals. Based on 110 larvae with 543 Artemia. C: Calculated SUIT-index in percent based on A and B.

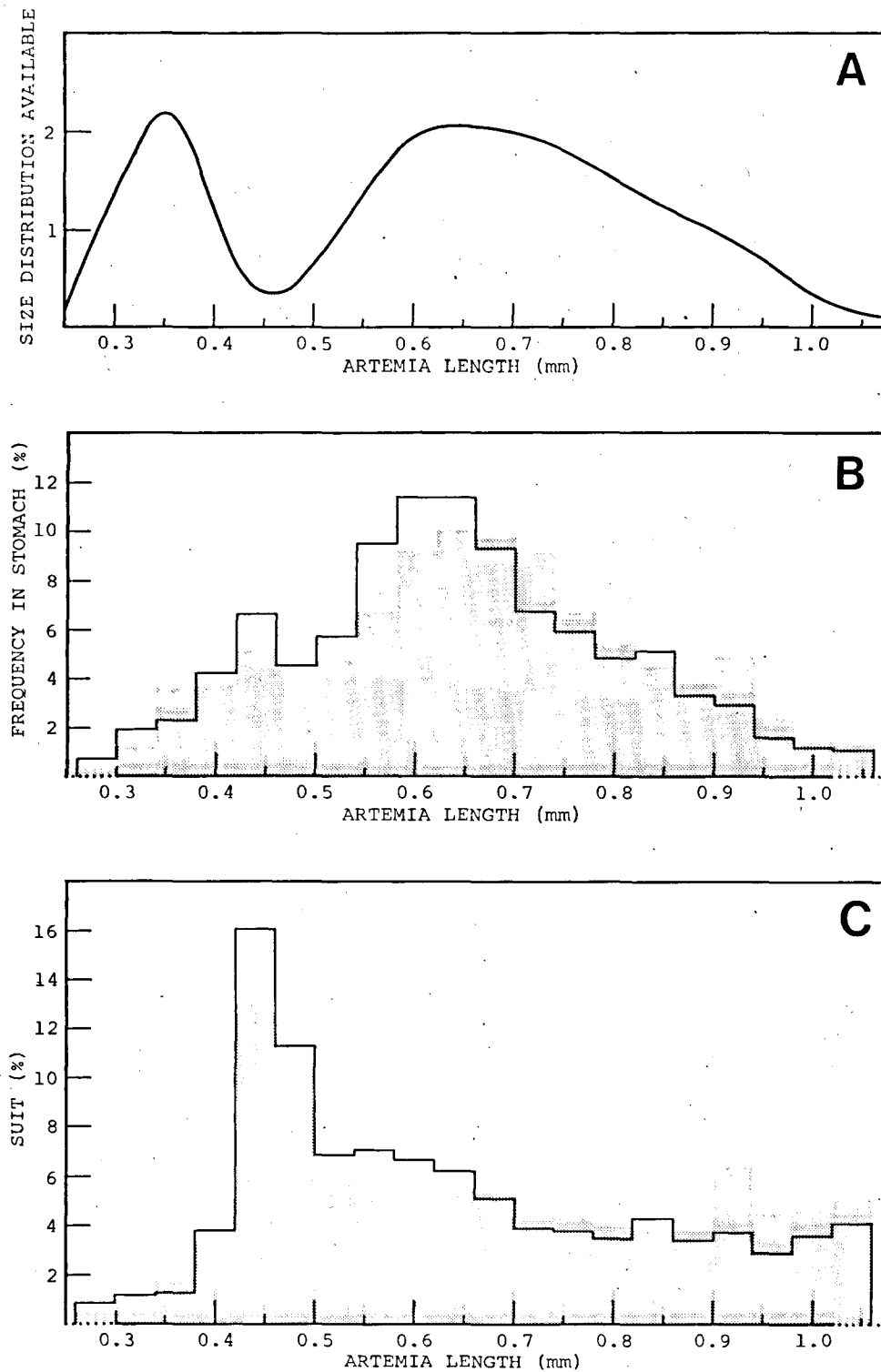


Fig. 7: Data on experiments with larvae adapted to total size range of Artemia (heavy outlined) and to the larger Artemia only (shaded). A; Length distribution of available food adjusted to account for shrinkage in larval gut. B: Frequencies of Artemia in larval stomachs presented as percentages of Artemia within 0.04 mm length intervals for the two experiments. Based on 65 larvae containing 1198 Artemia, and 65 larvae containing 1113 Artemia, respectively. C: Calculated SUIT-indices in percent based on A and B.

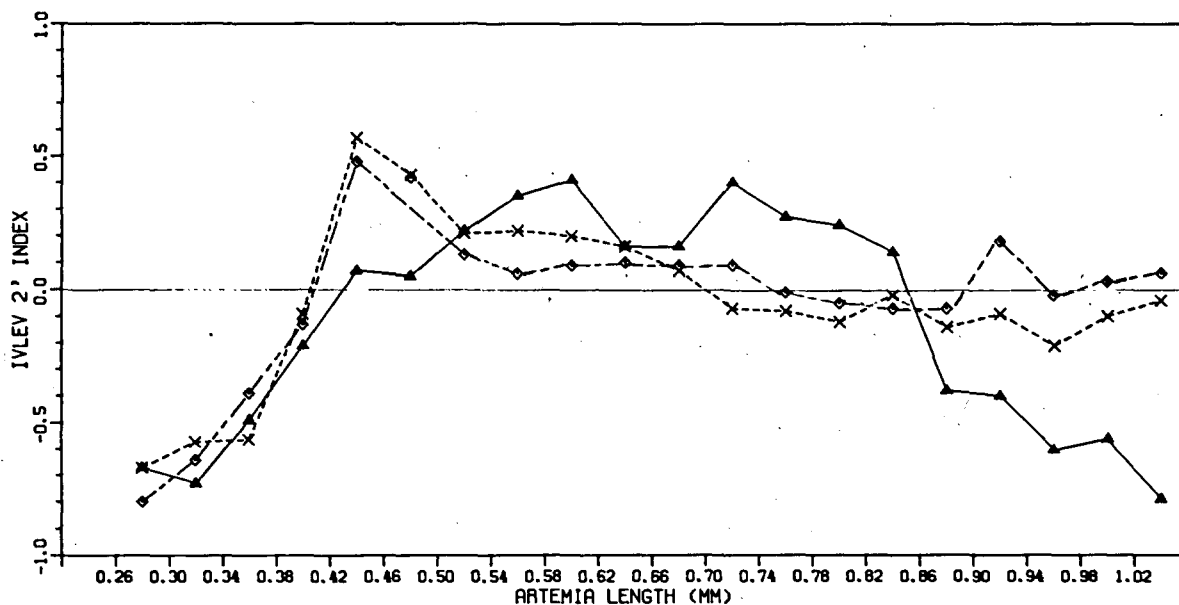


Fig. 8: Ivlev second index, E'' , for 0.04 mm length intervals of Artemia eaten. \blacktriangle : Larvae adapted to small Artemia; \times : larvae adapted to to total length range of Artemia; \diamond : Larvae adapted to large Artemia.

The present results indicate that an adaptation period of seven days may not be sufficient to change the selective patterns of the larvae in any conspicuous way.

Figs. 9-11 depict the result of a computation of SUIIT as in Figs. 6.C and 7.C, but on a log-length scale of Artemia. A Normal distribution (the Andersen and Ursin model, Eq. (18)) gives a reasonable good fit in case of adaptation to small Artemia (Fig.11).

Fig. 9: Calculated SUIIT histogram on a log-length basis for experiment with larvae adapted to small Artemia. Maximum likelihood fit of Normal(-0.553, 0.082) distribution is shown.

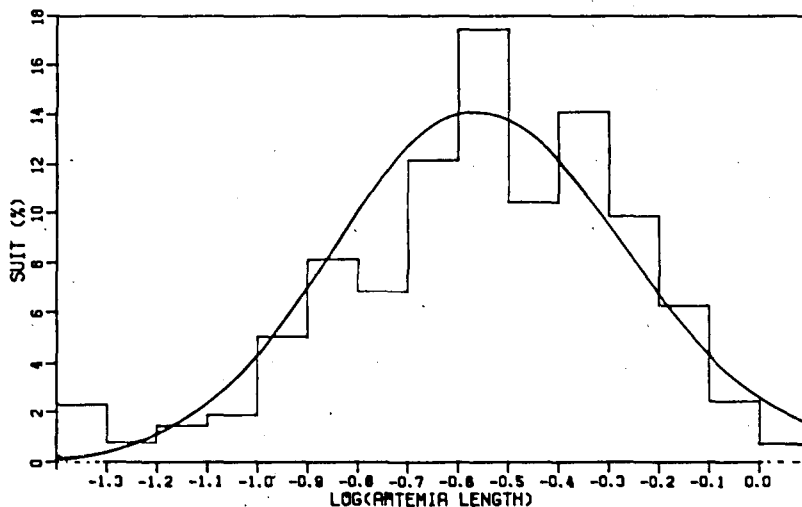


Fig. 10: Calculated SUIT histogram on a log-length basis for experiment with larvae adapted to all sizes of Artemia. Maximum likelihood fit of Normal (-0.589, 0.097) distribution is shown.

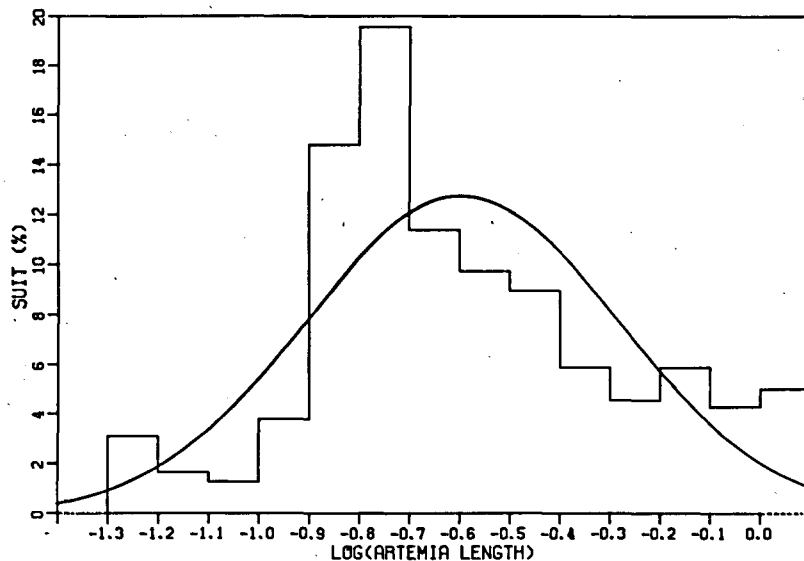
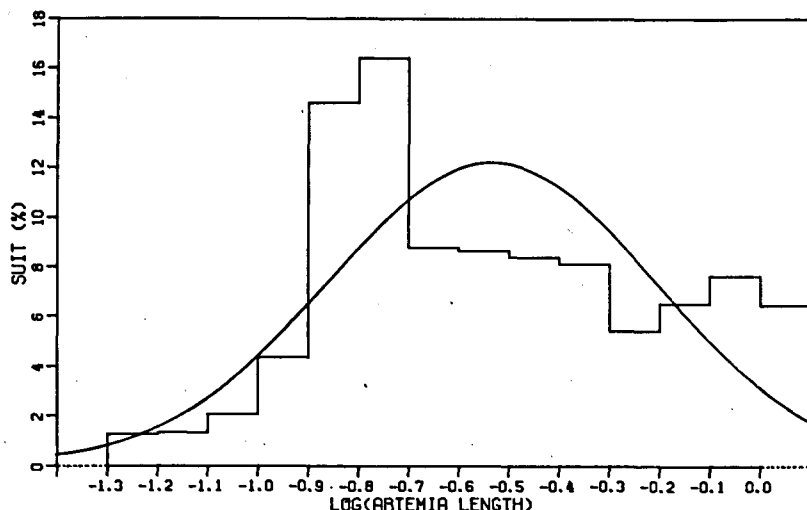


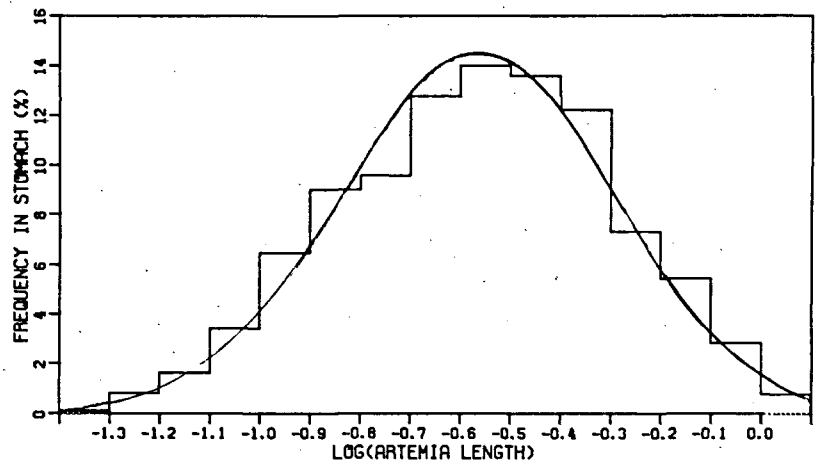
Fig. 11: Calculated SUIT histogram on a log-length basis for experiment with larvae adapted to large Artemia. Maximum likelihood fit of Normal(-0.536, 0.106) distribution is shown.



To simulate a situation of approaching size selection by sampling at the population level, Fig. 12 depicts the frequency in all larval stomachs on a log-normal scale (1200 larvae containing 7956 Artemia). Thus, this represents averaging over types of predators (length, adaptation) as well as averaging over varying feeding conditions. The average size distribution is a weighted mean of 20 size distributions including the two shown in Figs 6.A and 7.A. This size distribution of average food available is well represented by a straight line of negative slope (a smoothed-out version of Fig. 6.A) and after the logarithmic transformation in length an almost uniform distribution is obtained. This implies that Fig. 12 also may be interpreted as a SIZE selection diagram. A Normal distribution gives a good fit. The mean length of the 1200 larvae is 14.2 mm (range \pm 8-20 mm). According to the Normal model the preferred prey length is 0.56 mm in the gut or 0.67 mm when adjusted for shrinkage, i.e. the ratio of predator length to preferred prey length is 21. In weight this correspond to a ratio of 107 using the relation between larval length and weight for herring given by Laurence (1979):

$$w_1 = 0.0047 \cdot L_1^{4.3} \quad (\text{ug})$$

Fig. 12: Histogram of stomach contents on a log-length scale. Based on all the experiments, i.e. 1200 larvae containing a total of 7956 Artemia. Maximum likelihood fit of Normal($-0.568, 0.074$) distribution is shown.



5. CONCLUSIONS

The main conclusion as regard the present knowledge of selective feeding by marine fish is very short: incomplete data on the feeding behaviour of the predator, incomplete data on stomach content into prey length, incomplete data on the feeding environment of the predator can only result in very incomplete knowledge of the mechanisms governing predation and thus species interaction in the marine environment.

One of the limitations of the present work is that we were not able to use wild copepod nauplii as a controlled source of food. However, the study indicates that

- (1) when considering prey size selection of planktivorous fish larvae it may be necessary to compensate for shrinkage of the nauplii in the larval gut,
- (2) the effect of adaptation on prey size selection may be of importance, and
- (3) knowledge of available food and data on stomach contents are equally important for the study of food selection.

6. ACKNOWLEDGMENTS

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7. REFERENCES

- Andersen, K.P. and E. Ursin, 1977. A multispecies extension to the Beverton and Holt theory of fishing, with accounts of phosphorus circulation and primary production. Medd.Danm.Fisk. Havunders.N.S. Vol 7, 319-435.
- Anon., 1980. Report of the ad.hoc. working group on multispecies assesment model testing., ICES C.M. 1980/G:2.
- Benijts, F, E. van Voorden and P. Sorgeloos, 1975. Changes in the biochemical composition of the early larval stages of the Brine Shrimp, *Artemia salina*, L. 10'th European symposium on marine biology, Ostend, Belgium, Vol. 1:1-9
- Beyer, J.E., 1980: Feeding success of clupeoid fish larvae and stochastic thinking. Dana, Vol. 1. 65-91.
- Beyer, J.E. and G.C. Laurence, 1979. Modelling growth and survival of larval herring. ICES/ELH Symp./M:6. Available at National Marine Fisheries Service, Northeast Fisheries Center. Narragansett Lab., Narragansett R.I. 02882, USA. (mimeo, 150 p.)
- Blaxter, J.H.S., 1965. The feeding of herring larvae and their ecology in relation to feeding. Calif. Coop. Oceanic Fish. Invest., 10:79-88
- Ivlev, V.S., 1961. Experimental ecology of the feeding of fishes. New Haven, Yale University Press.
- Laurence, G.C., 1979. Larval length-weight relations for seven species of northwest atlantic fishes reared in the laboratory. Fish.Bull. 76:890-895.
- Pyke, G.H., H.R. Pulliam and E.L. Charnov, 1977. Optimal foraging: a selective review of theory and tests. The Quarterly Review of Biology, 52:137-154.
- Rosenthal, H., 1969. Verdauungsgeschwindigkeit, Nahrungswahl und Nahrungsbedarf bei der larven des herings, *Clupea harengus*, Ber.Dt.Wiss.Kommn Meeresforsch., 20:60-69.
- Shirota, A., 1970. Studies on the mouth size of fish larvae. (in Jap, Engl. summary). Bull.Jap.Soc.Sci.Fish., 36:353-368. (Transl. by Fish. Res.Board.Can.Transl. Ser.1978).
- Sparre, P., 1980. A goal function of fisheries (Legion Analysis). ICES, CM.1980/G:40.
- Ursin, E., 1973. On the prey size preferences of cod and dab. Medd.Danm.Fisk.Havunders., N.S. Vol.7:85-98.
- Werner, R.G. and J.H.S. Blaxter, 1980. Growth and survival of larval herring (*clupea harengus*) in relation to prey density. Can.Jour.of Fish.and Aquatic Sciences, 37:1063-1069.
- Wiborg, K.F. 1948: Experiments with the Clarke-Bumpus plankton sampler and with a plankton pump in the Lofoten area in northern Norway. Fiskeridir. Skr.Havundersøk. 9:32 p.