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Food Consumption by Larval Fish

by

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Abstract

Fish population dynamics is used to develop a consistent model skeleton for larval fishes predation on nauplii. The problem is exemplified by considering simple environments comprising one size group of Atlanto Scandian herring (Clupea harengus) larvae and one size group of Artemia salina nauplii.

A data set on the exact number of nauplii before and after small scale predation experiments is presented and a technique for automatic nauplii counting with replacement is introduced.

The need for combined analyses of feeding, stomach content and digestion is emphasized and a preliminary queueing approach is presented.

1. INTRODUCTION.

Food consumption by larval fish is difficult to study directly in the marine environment.

We may at the very best obtain in situ data that gives adequate information on the food available (species, abundance, size and age distribution of zooplankton), and the stomach content of predators (species, age, size) at the moment of capture.

It is, however, not possible to utilize such assesment oriented data without a knowledge on the underlying biological processes or mechanisms. This is probably why quite a bit of research effort has been devoted to experimental studies of food consumption and digestion during the last decade.

In this study we attempt to deal with basic principles of food consumption by fish larvae and predation mortalities of nauplii. We concentrates on the simplest possible environment : one type of predator eating one type of prey.

A good deal of the study concerns the theoretical modelling, the design of the experiments and the interpretation of the results are then based on the models.

2. PROBLEM SPECIFICATION AND HYPOTHETICAL MODELS.

2.1. PREDATION MORTALITY OR FEEDING RATE.

In fish population dynamics (see for example Beverton and Holt 1957, Andersen and Ursin, 1977, and Beyer and Sparre, 198o) the reduction in stock size of a year-class is described by the differential equation

$$\frac{dN_a(t)}{dt} = Z(t)N_a(t) \qquad (1)$$

where N_a is the population size and the instantaneous coefficient of total mortality, Z, usually is partitioned into mortalities due to the various causes that characterizes the population and the environment it is occupying.

Eq (1) represents the starting point for this study where interest is focused on the quantification of predation mortality in a simple environment of volume V comprising only one type of prey (nauplii of the same species, age, precondition and size) and one type of predator (fish larvae of the same species, age, precondition and size).

Since there is no "fishing" in operation the individual prey is exposed only to natural mortality:

$$Z(t) = M1(t) + M2(t)\cdot N_b(t) \qquad (2)$$

N_b denotes the number of live predators each of which contributes with M2 to the total instantaneous coefficient of prey mortality. All other possible causes of mortality than predation are incorporated in the residual mortality M1.

Eq(2) represents a basis for modelling prey mortality. Any quantitative relationship that expresses M2 as a function of the past and/or present state of the prey/predator system defines a model of predation-mortality. The M2-mortalities, however, are caused by predators and the problem is here called food consumption.

Let R(t) denote the accumulated number of prey ingested by an individual predator and let (forgetting about differential problems) the feeding rate be defined as

$$f(t) = \frac{dR(t)}{dt} \qquad (3)$$

The fundamental requirement to consistency is that the total rate of feeding always equals the total rate of predation mortality, i.e. using Eqs. (1) and (2),

$$N_b(t)f(t) = N_b(t)M2(t)\cdot N_a(t)$$

or

$$M2(t) = f(t)/N_a(t) \qquad (4)$$

The partial coefficient of predation mortality M2 equals the fraction of the prey population that is consumed by the individual predator in one unit of time.

A model of food consumption by predators determines a model of predation. This, of course, is not surprising but still quite useful to keep in mind. We shall consider two simple models each of which may be applicable to feeding conditions at relative low prey densities.

First, however, a simplification is introduced. Due to the requirement of constant prey characteristics we choose to study the prey-predator system in a relative short period of time and assume:

(i) zero residual mortality (i.e. M1 = 0)

(ii) constant predator population size, N_b.

That is

$$\frac{dN_a(t)}{dt} = -N_b M2(t) N_a(t) \qquad (5)$$

2.1.1. FEEDING RATE PROPORTIONAL TO PREY DENSITY (EXPONENTIAL MODEL)

Assuming that the foraging behavior of a hungry predator remains the same when it is grazing down the food supply we get in a first approximation

$$f(t) = sq_a(t) \qquad (6)$$

where

$$q_a(t) = N_a(t)/V \qquad (7)$$

is the prey density and s is a constant which we refer to as the effective searching rate. The corresponding predation model is obtained from Eq. (4):

$$M2(t) = s/V \qquad (8)$$

Thus the coefficient of predation mortality is constant. The size of the prey population at time t is obtained from Eq (5):

$$N_a(t) = N_a(o)\exp(-N_b M2 \cdot t) \qquad (9)$$

If the prey population size is known at the start and at the end of the experiment the estimate of M2 becomes

$$\hat{M2} = \frac{1}{TN_b} \log\left[N_a(o)/N_a(T)\right] \qquad (10)$$

from which the estimate of the feeding rate is obtained:

$$\hat{f}(t) = \hat{M2}N_a(t) = \hat{s}q_a(t) \qquad (11)$$

2.1.2. CONSTANT FEEDING RATE (LINEAR MODEL)

If the feeding rate is constant, $f(t) = f_o$, we get

$$M2(t) = f_o/N_a(t) \qquad (12)$$

The coefficient of predation mortality increases as the prey density decreases because the predator must increase its rate of foraging in order to maintain a constant feeding rate when the available food is getting scarce.

Eq. (5) becomes

$$\frac{dN_a(t)}{dt} = -N_b f_o$$

or

$$N_a(t) = N_a(o) - N_b f_o t \qquad (13)$$

Thus the estimate of the feeding rate is

$$\hat{f}_o = \frac{N_a(o) - N_a(T)}{TN_b} \qquad (14)$$

2.1.3. MODEL TESTING.

Due to for example the sampling procedure it is often more convenient to express the grazing models in terms of prey density than population size. The exponential model, Eq. (9), takes the form

$$q_a(t) = q_a(o)\exp(-N_b M2t) \qquad (15)$$
$$= q_a(o)\exp(-q_b st);\ q_b = N_b/V$$

and the linear model, Eq (13), is

$$q_a(t) = q_a(o) - q_b f_o t \qquad (16)$$

One way to obtain data to test the models is to take prey-aliquots from the experimental tank (predator-prey system) at regularly intervals of time. Assuming this sampling procedure neither changes the prey density (i.e. sampling with replacement) or disturbs the predator-prey system in other ways, the aliquot-counts may be used to estimate the actual decline in the prey density during the predation experiment.

2.1.4. STOCHASTICITY

Since this study as most others laboratory studies deals with small populations the effect of (demographic) stochasticity cannot be neglected from the outset. We do not intend to present the complete stochastic formulations of the food consumption hypotheses here because of the preliminary nature of the experiments carried out. We restrict attention to some major differences between the stochastic and the equivalent (previous considered) deterministic approaches.

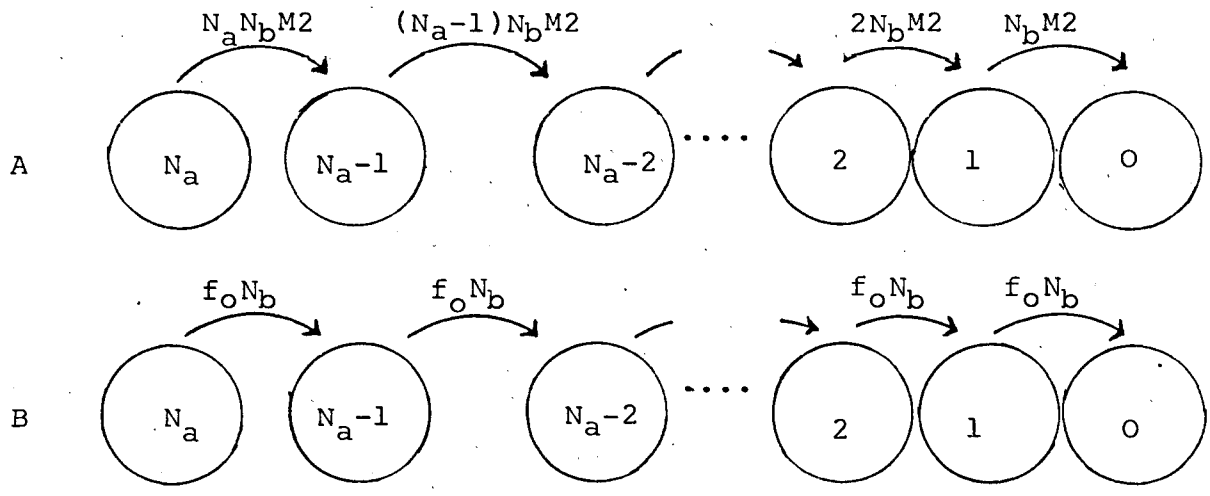

Figure 1: Transition intensity diagrams for stochastic processes governing reductions in the prey population size (state variable) due to predation by the N_b predators.
A: Constant mortality coefficient M2.
B: Constant average feeding rate, f_o, of the individual predator.

In the stochastic formulations of Eq. (1) a precise account of the prey population size is kept. Fig. 1A depicts the situation in the case of a constant coefficient of predation, $N_b M2$. Whenever one of the N_b predators eats a prey, the size of the population (i.e. the state variable)decreases by one. State zero, of course, is a trapping state (extinct population). In this model each of the $N_a(o)$ live prey in the initial population has an exponential lifetime distribution with mean $1/(N_b M2)$. The probability of still being alive at time t is thus $\exp(-N_b M2t)$ for each of the $N_a(o)$ prey. And, since it is assumed that the life-times are stochastically independent (i.e. the individual prey live and die as though its siblings did not exist), the number of live prey at time t follows a Binomial distribution, Bin $(N_a(o), \exp(-N_b M2t))$, i.e.

$$\Pr\{N_a(t)=x \mid N_a(o)\} = \binom{N_a(o)}{x} e^{-xN_b M2t}\left(1-e^{-N_b M2t}\right)^{N_a(o)-x} \qquad (17)$$

$$x = o,1,2,\ldots., N_a(o);$$

The expected population size and the maximum likelihood estimator of M2 are identical to the results obtained from the equivalent deterministic model, i.e. Eqs (9) and (1o), respectively.
The coefficient of variation is

$$CVAR(N_a(t)) = \sqrt{\frac{\exp(N_b M2t)-1}{N_a(o)}} \qquad (18)$$

Fig 1B depicts the intensity diagram in case of a constant predatory feeding rate. The elapse times between consequtive prey ingestions (by any of the predators) are exponentially distributed with a constant mean of $1/(f_o N_b)$. This is a simple Poisson process of rate $f_o N_b$ and the total number of prey eaten in the period of time t thus follows a Poisson distribution with mean $f_o N_b t$. We here assume a negligible probability of termination (i.e. last prey eaten at or before time t).

$$Pr\{N_a(o) - N_a(t) = x\} = \frac{(f_o N_b t)^x}{x!} \exp(-f_o N_b t) \qquad (19)$$

$$x = o,1,2,\ldots, N_a(o)$$

The expected population size and the maximum likelihood estimator of f_o are identical to the results obtained from the equivalent deterministic model, i.e. Eqs. (13)and (14), respectively.
The coefficient of variation is

$$CVAR(N_a(t)) = \frac{\sqrt{f_o N_b t}}{N_a(o) - f_o N_b t} \qquad (2o)$$

2.2. FEEDING, STOMACH CONTENT AND DIGESTION.

The basis for describing fish larvae as queueing systems has been given in FISH I & II (Beyer, 1976). In brief, prey organisms ("Customers") arrive individually at the larval stomach ("waiting room") where they stay until digestion ("service") can take place in the intestine. The queuing system is completely specified by the arrival process, the queue-discipline and the service mechanisms.

If the prey density is constant, q_a, then the simple feeding rate models considered in the previous section both imply that the fish larva encounter and eat prey in a Poisson process at rate

$$f = sq_a \qquad (21)$$

Once a prey is engulfed by the mouth it passes rapidly to the posterior end of the gut where digestion takes place (Blaxter, 1965)

Let us assume that digestion starts right away,i.e. newcoming nauplii do not wait in the gut (in contrast to the single server queueing considered in Fish I&II).Let d denote the digestion rate for a nauplius of weight W_a,i.e.

$$d = \frac{1}{h} \qquad (22)$$

where h is the time to complete digestion.

It is assumed that the digestion time of a nauplius of a given size is independent of the amount of food in the gut.

Figure 2 gives the transition intensity diagram for this queueing system.If the gut contains,say,two nauplii at time zero then the next event is either that a third prey is eaten in which case "the process jumps to state 3",or that one of the nauplii is fully

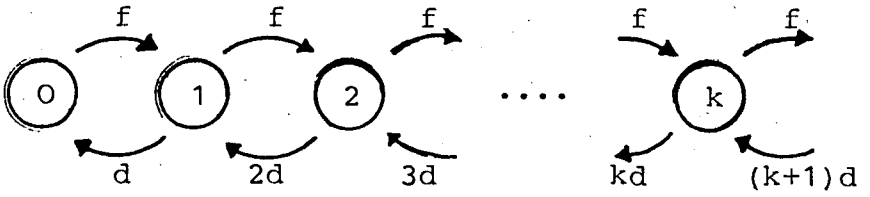

Figure 2 Transition intensity diagram for the number nauplii in the stomach of a herring larva assuming nauplii are eaten in a Poisson process at a rate f,and that digestion starts at once at rate d.

digested in which case the"process jumps to state 1".The number of nauplii in the gut,G,thus changes as time elapses.

We expect that G ultimately will fluctuate about a mean value of

$$g = \frac{f}{d} = f \cdot h \qquad (23)$$

because this situation represents a balance between feeding rate (f) and total digestion rate(d·g).

The process is said to reach statistical equilibrium and the gut content will follow a Poisson distribution with mean g,i.e.

$$Pr\{G=x\} = \frac{g^x}{x!} e^{-g} \quad ,x=o,1,2,\cdots \qquad (24)$$

This is a well known result in queueing theory and we omit the proof. It may be noted that this Poisson distribution is valid for the queueing system under any obscure distribution of individual digestion times.

That is,as long as individual prey are eaten in a Poisson process at a rate f,then the distribution of the gut content (in statistical equilibrium) is given by Eq(24) if the individual prey organisms are digested independently of each other with a average digestion time of d.Since we have related digestion time to prey size,the result implies that independent of changes in the shape of the size distribution of ingested prey the gut content is always Poisson distributed in the same way if the average prey digestion time remains constant.

If the average digestion time,h,is known ,the model may be used to estimate the feeding rate from the mean gut content,i.e. according to Eq(23),

$$f = \frac{g}{h} \qquad (25)$$

3. MATERIAL AND METHODS.

The experiments were carried out in May-June 1980 at the Danish Laboratory of Larval Fish Research, in Charlottenlund.
Grey, cylindrical PVC tanks, with a volume of 5 liter were used. A seawater supply of 0.1 liter/min and air blow (1 liter/min) on the watersurface created turbulence and prevented patchiness of the food organisms. The outlet tube was covered by a 100 µm plankton net. The salinity was 26 o/oo, the temperature was maintained at 10°C, and a constant lighting of 1000 lux was maintained at the water surface by two cool-white fluorescent tubes.

Food organisms were 1-3 days old Artemia salina nauplii grown to a length of 720-750 µm on a diet of dried Chlorella-powder.

At the start of an experiment a group of Atlanto-Scandian herring larvae was transferred to the tank which immediately before was supplied with the nauplii.

The prefeeding conditions of the larvae were approximately the same as in the experiments. The larvae were selected as homogeneous as possible by sorting by eye and a group consisted of 2-9 individuals, the actual number being determined according to expected grazing rates.

Two experimental series were conducted the first of which with focus on the effect of predation in continuous time.

A home-made glass tube (the transor) with a small hole (400 µm) at its apex was placed in the tank at a fixed position. The water was pumped through the aperture of the transor at a rate of 800 ml/hr, passed through the peristaltic pump and returned to the tank.
A generator maintained a constant current through the aperture of the transor between two platinum electrodes. When the individual nauplii passed through this opening the conductivity of the sea water dropped and the resultant changes in voltage was amplified and counted. A minicomputer was programmed to read total counts (on line) for a period of 30 minutes and restart the counter every 35 minutes. The individual sample size was thus 400 ml.

Before the larvae were transferred to the tank, Artemia were counted in a prolonged period of time in order to estimate both the mortality of other causes than predation and the start density that was offered to the larvae.

The second series of experiments was designed to provide information on rations over an extended period of time.
In these experiments the total number of Artemia was counted at the start and at the end of each experiment. The seeding was done with 1000 Artemia using the electronic counter, i.e. a start prey density of 200 Artemia/liter.

After an experimental period of about 22 hours the larvae were immediately measured on length (maximal length) and their stomach-contents were examined using the transparancy of the gut.
Finally the larvae were dryweighted after a short period in which their guts were emptied and a drying period of 24 hours at 55°C. The remaining Artemia within the tank were filtered and counted.

4. RESULTS AND DISCUSSION.

4.1. EXPONENTIAL OR LINEAR MODEL OR ?

Fig. 3 depicts the decline in Artemia density due to grazing by four herring larvae. The density level before the experiment does not show a downward trend indicating that the assumption of zero residual mortality cannot be rejected.

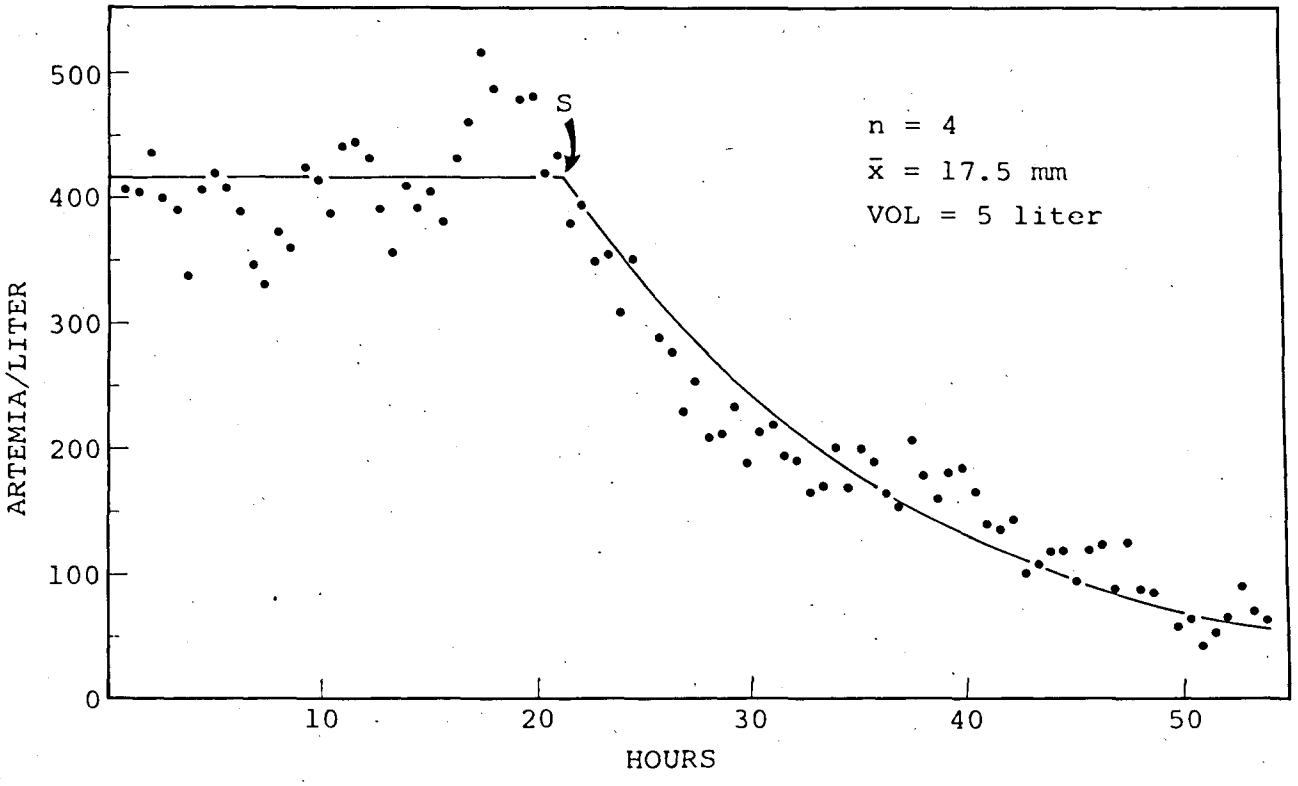

Figure 3.

Estimates of the Artemia density in the tank of 5 liter based on automatic counting in half-hour intervals (sample size 4oo ml.) The 4 herring larvae were transferred to the tank at time 22 hrs. Nonlinear least square fit to the exponential model is shown.

The mean density is 416 A/liter. Note the cyclic fluctuations which perhaps are due to turbulance. At any rate, the variations about the mean level are greater then what should be expected from a random distribution of nauplii (i.e. Poisson distributed sample counts).

The exponential model with $4 \cdot M2 = .062\ hr^{-1}$, Eq (15), from time 22 hrs. onwards gives a reasonable good fit to the decreasing density of Artemia. However, the variation about the exponential model cannot be explained by the effect of demographic stochasticity. Let us for example consider the situation at time 52 hrs., i.e. 30 hrs. after the start of the grazing experiment. With an instantaneous coefficient of predation mortality of $4 \cdot M2$ or $0.062\ hr^{-1}$ the expected prey density at t=30 hr is given by Eq.(15) as $416\exp(-0.062 \cdot 30)$ or 65 A/liter. The coefficient of variation, however, is only 5 % (Eq. 18). Thus, a 95 % confidence interval is approximately 59-72 A/liter and several of the points around 50 hrs on Fig. 3 fall outside this interval.

Note that the prey density at the start of the experiment has been assumed to be 416 A/liter. We do not really know. Forgetting about the cyclic trends, the data for 0-22 hrs. show a standard deviation of about 50 A/liter. This may explain part of the variability in densities during the grazing experiment. However, we do not want to go into an analysis of compound distributions based on these preliminary experiments.

A couple of similar grazing experiments (which are not presented here) with bigger larvae seem to indicate that an exponential decrease in Artemia density takes place until about 200 A/liter. Below this density level grazing is higher than is expected from the exponential model, indicating that bigger larvae increase their rate of foraging at low prey densities. However, further experiments are needed before a shift from exponential to linear grazing can be established as a general pattern.

According to the fish larval literature feeding rates are not surprisingly found to increase asymptotically with increasing prey densities. This of course is in accordance with the exponential model because we are not concerned here with satiation problems. However, few authors have dealt experimentally with densities of 100 nauplii/liter or less which seem to be the order of magnitude in the sea.

The experiment given by Fig. 3 represents the very first run of the automatic counting system. We clearly need to use the equipment with many replicates on both small-scale and large-scale systems. In this way we hope to be able to destinguish variation in fish larvae feeding from other sources of variation. The result is problably that the simple exponential model in its stochastic version cannot explain the variability observed among individual predators.

4.2 FEEDING RATES ESTIMATION UNDER A GIVEN MODEL

Data from the predation experiments are given in Table 1. Under the assumption of a constant mortality coefficient of prey during the experiment, M2 is calculated for different larval sizes (Eg. 10). The feeding rates at a given prey density is then calculated using Eq. (11). As an example Fig. 4 shows feeding rates at 100 A/liter against body-weight.

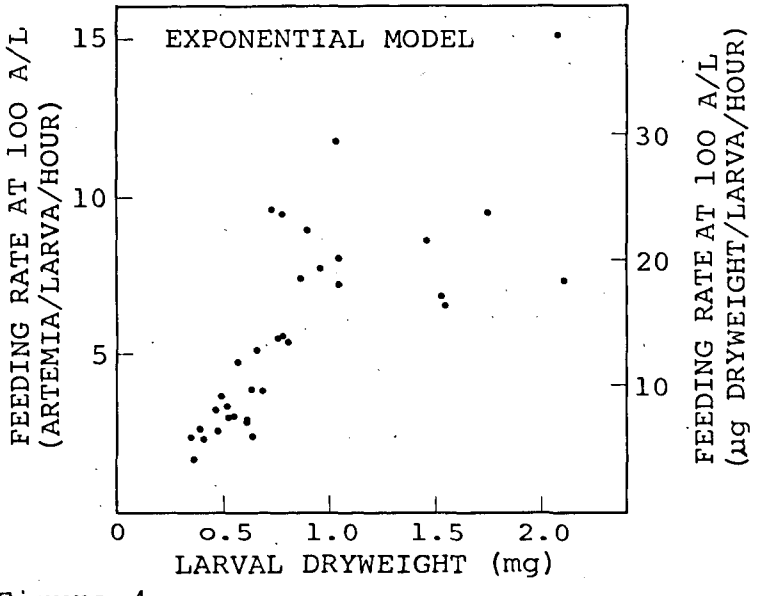

Figure 4.

Estimated feeding rates at 100 a/liter for herring larvae of 0.4 - 2.0 mg body-weight based on the exponential model, i.e. plot of the M2 column in table 1 multiplied by 500 against body-weight.

On the other hand, assuming that the feeding rate is constant during the experiment the last column in Table 1 is obtained from Eg. (14). These feeding rate calculations are plotted on Fig. 5.

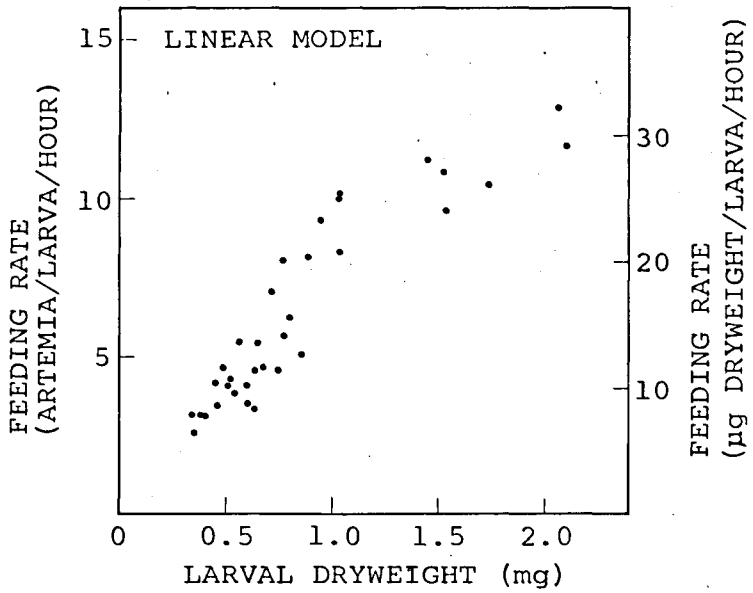

Figure 5.

Estimated feeding rates for herring larvae of o.4 - 2.o mg body-weight based on the linear model, i.e. plot of the f_o column in Table 1 against body-weight.

The smaller variability in feeding rate based on the linear model (Fig. 5) than in the feeding rate based on the exponential model (Fig. 4) cannot be used to reject the exponential model. In the exponential model, the compuation of M2 is very sensitive to the observed variations in the number of live nauplii at the end of those experiments that involved few big larvae.

Few estimates of the feeding rate of larval herring are reported in the litterature. On basis of food passage in the gut Rosenthal and Hempel (1970) estimates feeding rates for herring larvae of 13-14 mm in length to 4-5 A/hour. Our estimate at this larveal size is approximately 3 A/hour. But note again that the feeding rate is proportional to the prey density in case of the exponential model.

Fig. 4 and Fig. 5 both indicate a linear relationship between larval weight and the feeding rate until the larva reach a weight of about 1.0 mg whereafter the increase in feeding rate seems to level off.

This picture with the rate of increae levelling off at the bigger larval sizes is also found in experiments with other species (ex. Houde and Schekter, 1980 a). An increasing effect of the tank size can not be rejected, however, and further experiments incorporating this factor have to be done.

4.3 STOMACH CONTENTS

Fig. 6 depicts the frequency of stomach contents found at the termination of the predation experiments (solid line). The stomachs show a mean of 3.39 nauplii and a variance of 8.47. The expected Poisson frequency distribution, Eq. (24), obtained from the simple queueing model is also shown (shaded area). The variance of this distribution, however, is only 3.39 (equal to the mean).

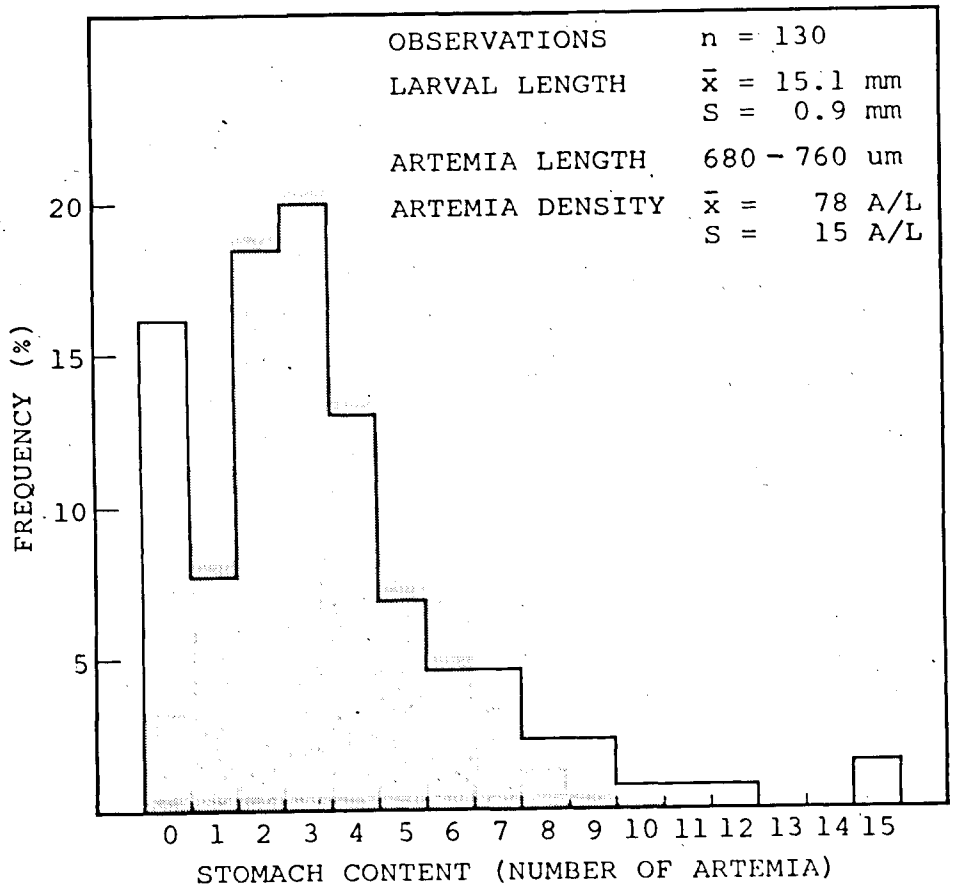

Figure 6.

Histogram of stomach contents for the herring larvae after the grazing experiments (heavy line) and the fitted Poisson frequency distribution (shaded area).

The unexpected high frequency of empty stomachs could be attributed to gut emptying of certain larvae that probably were stressed before they were caught. This pattern of a high frequency of empty stomachs is also reported by Houde and Schekter (1980 b) for lined sole at prey concentration of 100 nauplii/liter.

Not much information on digestion times for larval herring seems to be available. Rosenthal and Hempel' s (1970) work indicate that the digestion time of one Artemia nauplius is in the order of 1 hr. With d=1 hr. in Bajov's formula, Eq. (25), the feeding rate is estimated to 3.4 nauplii/hr. The average feeding rate according to Table 1 is about 3.5 nauplii/hr. for larvae of approximately 15 mm of length.

The queueing model described in this paper has been chosen with the purpose of emphasizing the importance of combining hypotheses on feeding rates, stomach contents and digestion into one consistent approach. An applicable model must incorporate feed back mechanisms such as satiation controls. It should also be noted that models cannot be tested exclusively on stomach distributions because different formulations governing food consumption and digestion may lead to the same type of distributions. We need more proces-oriented knowledge

5. ACKNOWLEDGMENTS

Purchase of the minicomputer and the electronic counter with adapter for nauplii counting,developed by Bjørn Rasmussen,were made possible by a grant from the Carlsberg Foundation.
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Table 1. Predation experiment.
$N_a(o)$ Artemia nauplii (mean weight $W_a(T) = 2.5$ µg) is grazed down to $N_a(T)$ by $N_b(T)$ larvae of a mean length and weight of $L_b(T)$ and $W_b(T)$. Volume of tank (V) is 5 liter. The coefficient of mortality and the feeding rate is calculated on basis of Eq (1o) and Eq (14) respectively.

Exp. no	Time of exp. T	Artemia number $N_a(o)$	Artemia number $N_a(T)$	Larvae number	Larvae length sample mean $L_b(T)$	Larvae length sample SD	Larvae dry weight $W_b(T)$	Coefficient of mortality $\hat{M2}$	Feeding rate $\hat{f}_o$
	hours				mm	mm	mg	hour^{-1}	Artemia /hour
1	22.67	1ooo	441	8	14.9	o.7	o.41	.oo451	3.o8
2	22.83	994	587	7	14.1	o.8	o.36	.oo33o	2.55
3	22.75	998	353	9	14.7	o.6	o.39	.oo5o8	3.15
4	23.oo	1oo1	421	8	14.3	o.6	o.35	.oo471	3.15
5	22.67	1o13	482	7	15.6	o.5	o.64	.oo468	3.35
6	22.83	1ooo	36o	8	15.7	1.o	o.61	.oo559	3.5o
7	23.2o	999	442	7	14.9	o.7	o.47	.oo5o2	3.43
8	22.5o	991	385	7	15.2	o.6	o.55	.oo6oo	3.85
9	22.67	1oo1	352	7	14.8	o.9	o.52	.oo659	4.o9
1o	22.83	1o52	385	7	15.o	1.o	o.46	.oo629	4.17
11	23.66	1oo2	339	6	16.2	1.3	o.68	.oo763	4.67
12	23.83	1o41	459	6	15.6	1.o	o.61	.oo573	4.o7
13	24.oo	1oo3	2o3	6	16.1	1.4	o.78	.o111	5.56
14	24.16	1oo1	12o	8	15.8	1.5	o.75	.o11o	4.56
15	22.58	1oo3	518	5	15.3	1.o	o.53	.oo585	4.3o
16	22.75	1oo2	374	6	14.9	1.2	o.5o	.oo722	4.6o
17	22.92	1o32	282	6	15.8	o.3	o.57	.oo943	5.45
18	23.o8	1o36	299	7	16.o	o.7	o.64	.oo769	4.56
19	22.42	1o52	141	5	16.9	1.4	o.89	.o179	8.13
2o	22.92	1o43	74	6	16.o	1.4	o.73	.o192	7.o5
21	23.o8	999	64	8	16.4	1.3	o.87	.o149	5.o6
22	22.67	993	248	6	15.8	1.3	o.66	.o1o2	5.48
23	22.oo	1o13	127	5	16.7	o.3	o.78	.o189	8.o5
24	22.oo	1oo6	127	4	17.9	o.7	1.o3	.o235	9.99
25	23.75	1o1o	219	4	18.1	o.5	1.o5	.o161	8.33
26	22.75	1oo5	297	5	16.8	1.o	o.81	.o1o7	6.22
27	22.75	1oo7	128	3	21.1	o.9	2.o7	.o3o2	12.9
28	23.58	1oo4	262	3	2o.2	1.1	1.74	.o19o	1o.5
29	17.67	1o21	511	3	19.7	o.8	1.55	.o131	9.62
3o	17.83	1oo8	465	3	19.2	o.7	1.39	.o145	1o.2
31	18.oo	1o25	6o4	2	21.2	o.6	2.11	.o147	11.7
32	18.17	1oo6	612	2	19.6	o.o	1.53	.o137	1o.8
33	18.33	1oo4	388	3	19.4	o.7	1.46	.o173	11.2
34	18.5o	1o12	321	4	17.5	1.1	o.96	.o155	9.33