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FEEDING CONDITIONS OF NORTH-EAST ARCTIC (ARCTO-NORWEGIAN) COD LARVAE COMPARED TO THE ROTHSCHILD-OSBORN THEORY ON SMALL-SCALE TURBULENCE AND PLANKTON CONTACT RATES

by

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ABSTRACT

Data on first feeding North-east arctic cod larvae in Lofoten, sampled during the period 1976 - 1984, are examined to verify the theory on the influence of microturbulence on the contact rate between predator and prey (Rothschild and Osborn, 1988). The number of prey per gut of the cod larvae are compared to the concentration of prey, Calanus finmarchicus nauplii, and to data on wind speed and static stability of the upper layer. The data indicate that the contact rate increases by 2.8 when the average wind speed increases from 2 m s^{-1} to 6 m s^{-1}. Independent data on cod larval cruising speed, the velocity and concentration of prey organisms, inserted into the model of Rothschild and Osborn (1988) show a comparable increase of the contact rate of 2.2 for the same increase of wind speed. Larval stages of North-east arctic cod are important for the formation of the year class. Larval stages are confined to the mixed layer, and therefore the variable contact rate induced by wind mixing is an important regulatory mechanism for the formation of year class strength.

INTRODUCTION

During recent years papers dealing with the influence of the relative motion between predator and prey on the encounter rate has thrown considerable light on feeding conditions for predators. Simple relations for the encounter rate, considering only the prey concentration, swimming speed of the predator and the escape rate of the prey at encounter, have been followed by more realistic models. Gerritsen and Strickler (1977) demonstrated by a mathematical model how random movement of the prey increases the encounter rate. Rothschild and Osborn (1988), developeing a model which demonstrated how turbulence influence the contact rate, arrived at two different equations which quantify the increased contact rate induced by turbulence. The first one was developed from the Gerritsen and Strickler (1977) equation, and the other one was developed from random walk statistics.

In the present paper the theory of Rothschild and Osborn (1988) (hereby called R & O (1988)) is tested by historical field data on first feeding North-east arctic (Arcto-Norwegian) cod larvae from the Lofoten nursery grounds. The feeding ratio (number of prey organisms per gut) of first feeding cod larvae (predator) are studied together with the nauplii (prey) concentration, and the rate of wind induced turbulence. The data were originally analysed to find the relation between the feeding ratio of first feeding cod larvae and the naupliar concentration. These results were presented by Ellertsen et al. (1989), Figure 1. The data, however, showed large variations from the regression line. On this background it was of interest to reanalyse the data to see if this variation could be explained by variable levels of contact rate induced by the microturbulence.

North-east arctic cod larvae are confined to the wind mixed layer. Normally, during calm and moderate wind conditions, they are found between 5 m and 25 m depth with the highest concentration at approximately 15 m depth (Ellertsen et al., 1984). The highest concentrations of first feeding larvae are found during the first half of May and ranges from 0.5 to 10 larvae/m^3. The main prey organism of first feeding North-east arctic cod larvae is nauplii of *Calanus finmarchicus*. About 95 % of the diet consists of this species. In laboratory studies Solberg and Tilseth (1984) and Tilseth and Ellertsen (1984) measured a number of important parameters concerning the feeding and behaviour of North-east arctic cod larvae. Table 1 shows some of their results, which are important for the present study.

Table 1. Parameters of feeding of first feeding North-east arctic cod larvae relevant for the present study (After Solberg and Tilseth (1984) and Tilseth and Ellertsen (1984)).

Standard length at hatching:	0.45 cm
Cruising speed :	0.08 - 0.25 cm/s (average 0.17)
Reactive perceptive distance:	0.23 - 0.45 cm
Feeding success:	11 - 22 %
Gut clearance rate:	~ 2 hours
Mean prey size (carapax length of nauplie):	250 µm

The swimming speed of *C. finmarchicus* nauplii have not been measured. Torres and Childress (1983) measured the swimming speed of adult *Euphausia pacifica* for different temperatures and pressures and for different metabolic rates. The swimming speeds ranged from 0 to 2 bodylengths per sec. The average speed was about 0.5 bodylengths per sec. If this value is applicable in general for crustaceans, the average swimming speed of *C. finmarchicus* nauplii is less than 0.02 cm/s, which is about 10 % of the cruising speed of the cod larvae. (The body length of *C. finmarchicus* nauplii is 1.2 times the carapax length, Melle, pers. comm.). The concentration of nauplii in the first feeding regions ranges from about 0.5 to 50 nauplii/liter, which is roughly 10^3 times higher than the larval concentrations.

MATERIAL AND METHODS

Larvae and nauplii

The data in the present paper was sampled during surveys in the Lofoten first feeding regions during the period 1976 - 1984. Figure 2 shows the positions of the stations. The surveys were conducted in late April and early May when maximum larval concentrations occur. The larvae were sampled by a plankton net, 0.5 m^2 opening, 375 µm mesh size, vertically hauled from 50 m depth to the surface. The nauplii were sampled at 5 and 10 m depth intervals from the surface to 40 m depth with a plankton pump, mesh size 90 µm. Both larvae and nauplii were preserved in sea water of salinity 10 added 4 % formaldehyde.

The number of nauplii per liter at each depth were counted manually. The larval gut content was examined, the number of prey organisms in each gut was identified and the feeding ratio calculated. Only stage 7 larvae, 8 - 10 days old (Fossum 1986) are considered in this material. These larvae show small variation with respect to physical size and condition, they are very active feeders and show the most variable response to variable prey concentrations. Samples during night time, from 23 hours to 05 hours, are also excluded from the study, since the larvae have a reduced feeding activity around midnight. The feeding ratio, A, of the larvae is compared to the mean number of nauplii per liter, c, in the water column from 5 to 25 m depth, since cod larvae are mainly found at these depths. Table 2 shows the number of larvae analysed for each of the 20 stations. Altogether 639 larvae were analysed.

Hydrography and wind

Temperature and salinity were measured at all stations except for no. 4 and 5. In 1976 (No. 1, 2, and 3) water bottles were used; in all other years Neil Brown CTD's were used. Wind data were supplied from

1) ship observation at the stations at intervals varying from 15 min to 1 hour.
2) observation every third hour from the meteorological station at Skrova Island
3) continuous recordings of 10 min wind velocity average from Svolvær Airport.

The data from the airport were applied only to stations in Austnesfjorden because of the local wind conditions in the fjord. The wind data from the meteorological station at Skrova are representative for most of the stations taken in Vestfjorden. For the stations to the north of Lofoten only ships observations could be used. Figure 2 shows the positions of the stations at Skrova and Svolvær Airport.

No measurements of the turbulence were made during the surveys. However, since the larvae are confined to the mixed layer, the energy input by the action of wind is the main factor for the production of turbulent energy. Oakey and Elliott (1982) found that the turbulent energy dissipation in the mixed layer was proportional to the cube of

Table 2. The present data set. For stations marked "*" only the mean value of the nauplii concentration exists. For stations marked "#" only the mean value of the feeding ratio exists.

St. No	Date	Region	No larvae	No of wind obs.
1	3 May 1976	Austnes Fjord	19	continuous
2	3 May 1976	Austnes Fjord	32	continuous
3	3 May 1976	Austnes Fjord	36	continuous
4	18 May 1977	Austnes Fjord	37	continuous
5	19 May 1977	Austnes Fjord	36	continuous
6*	9 May 1981	Austnes Fjord	105	continuous
7*	27 April 1982	Austnes Fjord	14	12
8	7 May 1982	Vesteråls Fjord	27	12
9*	10 May 1982	Vesteråls Fjord	8	11
10	10 May 1982	Vesteråls Fjord	10	12
11	11 May 1982	Vesteråls Fjord	91	8
12	15 May 1982	Austnes Fjord	8	continuous
13	15 May 1982	Vest Fjord	12	7
14	15 May 1982	Vest Fjord	12	7
15	16 May 1982	Vest Fjord	5	12
16 #	16 May 1982	Vest Fjord	11	14
17 #	15 May 1983	Austnes Fjord	26	5
18 #	17 May 1983	Vest Fjord	9	13
19*	6 May 1984	Austnes Fjord	33	3
20*#	6 May 1984	Austnes Fjord	?	continuous

the wind speed, W^3. It is to be expected that the turbulent energy is modified by stratification in the mixed layer. For the present data the parameter F is assumed to be proportional to the rate of turbulent energy dissipation. It is used to describe the different situations of turbulent energy which the larvae are exposed to:

$$F = \frac{W_8^{\ 3}}{N_{5-25}}$$

where N_{5-25} is the average Brunt-Vaisala frequency, $\sqrt{(g/\varrho\ \delta\varrho/\delta z)}$, in the water column between 5 and 25 m depth, and $W_8^{\ 3}$ is the average cube of the wind speed during 8 hours previous to the sampling.

Some of the original material on larvae and nauplii have been lost. Therefore only the processed mean values exist of the larval feeding ratio at the stations no. 16, 17, 18 and 20 (marked # in Table 2). Only the mean nauplii concentration exists at the stations no. 6, 7, 9, 19 and 20 (marked * in Table 2). Temperature and salinity were not measured at the stations 4 and 5 from the Austnes Fjord. The turbulence parameter for the two latter stations were calculated by applying the mean Brunt-Vaisala frequency, N_{5-25}, for the other 9 stations from the Austnes Fjord.

RESULTS

In analogy to the equation by Ivlev (1961) the change of feeding ratio, dA(c), for the larvae with respect to nauplii concentration, c, (by R & O, 1988 called density component of the contact rate and denoted D) is proportional to the difference between the maximum feeding ratio, A_{MAX} (full gut), and the actual, A(c):

$$dA(c)/dc = b[A_{MAX} - A(c)] \tag{1}$$

where b is a constant (which include the velocity component of the contact rate denoted A by R & O (1988)). Integrating the equation gives

$$A(c) = A_{MAX}[1 - \exp -(b\ c)] \tag{2}$$

Equation (2) is now applied to the data on feeding ratio of first feeding cod larvae. Table 3 shows the mean feeding ratio, A, for each station, the mean nauplii concentration between 5 m and 25 m depth, c_{5-25}, the average wind speed for the 8 hours period previous to the station, W_8, and the mean Brunt-Vaisala frequency between 5m and 25 m depth, N_{5-25} and the turbulence parameter, F.

Table 3. Mean feeding ratio (no./gut), A, and standard deviation, mean nauplii concentration (no./l) in the water column from 5 to 25 m depth, c_{5-25}, and the standard deviation, mean wind speed (m sec^{-1}) during the past 8 hours, W_8, mean Brunt-Vaisala frequency (sec^{-1}) in the water column from 5 m to 25 m depth, N_{5-25}, and the calculated turbulence parameter, F.

St. no.	No. larvae	Feeding ratio A	st.dev.	Nauplii conc. c_{5-25}	st.dev.	Wind W_8	Stability N_{5-25}x10^2	Turb. Fx10^2
1	19	2.1	1.47	5.1	0.5	5.8	1.26	155
2	32	1.8	1.22	4.7	0.5	5.6	1.26	139
3	36	2.0	1.31	4.6	1.0	4.8	1.26	88
4	37	3.5	2.18	26.7	5.3	3.3	-	21*
5	36	3.8	2.26	27.5	10.1	2.0	-	5*
6	105	3.2	1.30	44.3	-	1.8	1.05	6
7	14	4.1	2.87	20.0	-	6.6	2.21	130
8	27	1.4	1.13	10.2	5.3	2.9	1.46	17
9	8	2.5	1.94	6.0	-	5.2	1.42	99
10	10	1.3	0.90	8.6	1.4	1.4	1.33	2
11	91	0.9	1.03	6.9	2.8	1.0	1.57	0.6
12	8	1.9	1.17	23.7	13.7	3.1	1.95	14
13	12	1.0	0.91	4.0	2.1	2.6	1.51	60
14	12	1.8	1.86	7.6	3.6	3.9	1.29	71
15	5	1.2	0.98	5.2	2.4	5.3	1.16	128
16	11	1.0	-	4.1	3.8	3.8	1.53	36
17	26	2.3	-	15.6	2.8	1.4	2.06	4
18	9	0.6	-	1.6	1.0	6.3	1.10	227
19	33	3.3	1.56	31.5	-	0.9	2.04	0.4
20	-	2.8	-	10.3	-	3.6	1.94	47

The data in Table 3 are grouped into three separate data sets depending on the value of the turbulence parameter. For set 1: F < 30, for set 2: 30 < F < 90 and for set 3: F> 90. The three data sets are fitted to equation (2), and the coefficient b is estimated. The results are shown in Table 4. The highest correlation coefficient for the data sets was found when using A_A equal to 5. This corresponds to the maximum feeding ratio recorded for larval groups in the laboratory reported by Tilseth and Ellertsen (1984). Their maximum feeding ratio was 5.1 for a larval group which was fed in an aquaria containing 500 prey organisms per liter. In Figure 3 the three data sets and their regression line are drawn.

Table 4. Ranges of the turbulence parameter, F, ranges and mean value of the past 8 hours wind speed, W_8, and the calculated coefficient, b, in eq. (2) for the three sets of data and the coefficient of determination, R^2.

Set no. 1	$0 < F < 30$	$0.9 < W_8 < 3.3$	$W_8 = 2.0$	$b_1 = 0.034$	$R^2=0.96$
Set no. 2	$30 < F < 90$	$2.7 < W_8 < 4.8$	$W_8 = 3.7$	$b_2 = 0.072$	$R^2=0.97$
Set no. 3	$90 < F < 227$	$5.2 < W_8 < 6.6$	$W_8 = 6.0$	$b_3 = 0.095$	$R^2=0.98$

The ratio b_3/b_1, which indicate the increase of the contact rate between the low turbulence (Set no. 1) and the high turbulence (Set no. 3), is 2.8.

How does this result compare to the theory of the influence of turbulence on the contact rate? In Figure 4 the theory of R & O (1988) is applied to cod larvae and their prey. The graphs are based on their approach developed from Gerritsen and Strickler (1977) and show the increase of contact rate as a function of the swimming speed of cod larvae for three different levels of turbulent dissipation rate:

1) complete absence of turbulence
2) mixed layer turbulence corresponding to a wind speed of 2 m s^{-1} (as in Set no. 1)
3) mixed layer turbulence corresponding to a wind speed of 6 m s^{-1} (as in Set no. 3)

The speed of the nauplii was set to 0.02 cm s^{-1}. The distance of separation between the nauplii was set to 5 cm, which corresponds to the typical concentration found at the first feeding grounds. Taking the mean cruising speed of cod larvae (0.17 cm s^{-1}) the figure shows that the contact rate (relative units) increases from 0.2 at wind speed of 2 m s^{-1} to 0.43 at wind speed of 6 m s^{-1}. Consequently the contact rate increases by 2.2 . At cod larval cruising speed of 0.09 cm s^{-1} the corresponding increase of the contact rate is 3. Consequently, the calculated increase of the contact rate by the R & O (1988) theory is comparable to the increase calculated from the field data.

DISCUSSION

Laboratory investigations on first feeding cod larvae (Solberg and Tilseth, 1984) show that the larval food density requirements is considerably higher than in the field (Ellertsen et al., 1989). Gamble and Houde (1984) found higher survival of first feeding cod larvae in 300 m^3 enclosures than in 30 l tanks. Øiestad (1985) reviewing different experiments on the larval cod survival also found lower critical food requirement in ponds and basins than in the laboratory. This is not special for larval cod. It seems to be a general feature for several fish larvae. Houde and Schekter (1983) , investigating first feeding larvae of sea bream, bay anchovy and lined sole, pointed out that the required minimum prey levels were higher in the laboratory than observed in the field. This discrepancy may be explained by several factors: Effects from the walls of the aquaria, patchy prey distribution, food quality and larval concentrations. The turbulence theory by R & O (1988) and the present field comparison demonstrate that the influence of "natural" turbulence on the contact rate must be added to this list. At least for the above mentioned laboratory experiments on North-east arctic cod larvae, the aquaria were practically without turbulence. In the beginning of May the mean wind speed at the Lofoten first feeding grounds is 5.6 m s^{-1} (Sundby, 1982). Under such wind conditions in the field, cod larvae cruising at mean speed of 0.17 cm s^{-1} will experience a contact rate which is a factor of 2.2 higher than the contact rate in a laboratory tank free of turbulence. The wind speed can be considerably higher during shorter periods of 1 - 3 days duration. During about 10 % of the time (in the beginning of May) the wind speed exceeds 10 m s^{-1}, increasing the contact rate by more than 4 times compared to conditions free of turbulence.

In general, it is possible that the increased contact rate by turbulent action to some extent may be counteracted by breaking down high prey concentration gradients. For the interaction between larval cod and their prey, this effect may act in the opposite direction, since nauplii are found at highest concentration in the surface layer, above 5 m depth during calm wind conditions, while at higher wind speeds they are mixed down to greater depth where cod larvae are found. There should exist an optimal level of turbulence with respect to the number of successfull attacks. Above this level the residence time of the prey within range of attack will be shorter than the reaction time of the predator. The present study indicate that this optimal level occurs at higher wind speeds than those recorded here (>6 m s^{-1}). The highest cod larval cruising speed recorded in the laboratory by Solberg and Tilseth (1984) was 0.25 cm s^{-1}. The burst speed, which should be much higher, was not measured. The root mean square turbulent velocity at wind speed of 6 m s^{-1} for typical distances of nauplii separation, is about 0.3 cm s^{-1} according to R & O (1988). It is reasonable to believe that cod larvae are adapted to a reaction time comparable to the time it takes to burst through the reactive perceptive distance, which is 0.25 - 0.45 cm.

The "historical" data presented in this paper were not sampled with the aim to investigate the influence of turbulence on the contact rate between larvae and nauplii. Many things concerning the sampling would have been done differently if this process had been known. Cod larvae should have been sampled at discrete depths, just as the nauplii. The vertical current profile should have been measured at each station to calculate the Richardson number. Continuous measurements of wind and waves should be done at all stations. Lastly, the microturbulence should have been measured directly, though this is a difficult task. However, the present study strongly support the theory of R & O (1988) that microturbulence is an important process in marine and aquatic ecology. The mixed layer is the natural environment for the early stages of North-east arctic cod from the egg stage until the 5 - 6 months old juveniles settle towards the bottom. During this period the year class strength is established (Sundby et al. 1989). Wave action and turbulence is the most characteristic feature of the mixed layer. It is therefore impossible to exclude the concepts of microturbulence and contact rate as important regulatory mechanisms in the formation of year class strength.

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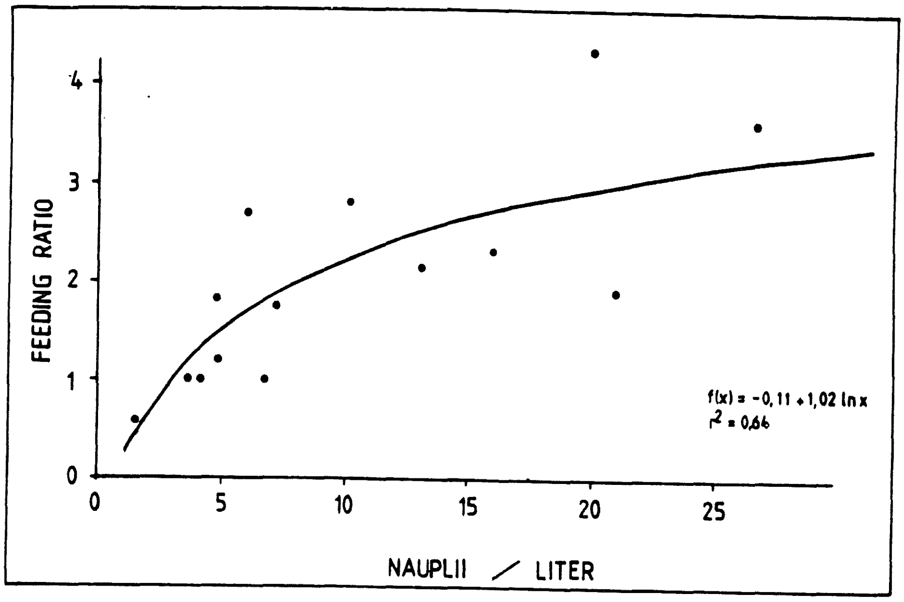

Figure 1. Relation between the feeding ratio of first feeding cod larvae and the mean nauplii concentration in the water column from 5 m to 25 m depth (From Ellertsen et al. 1989).

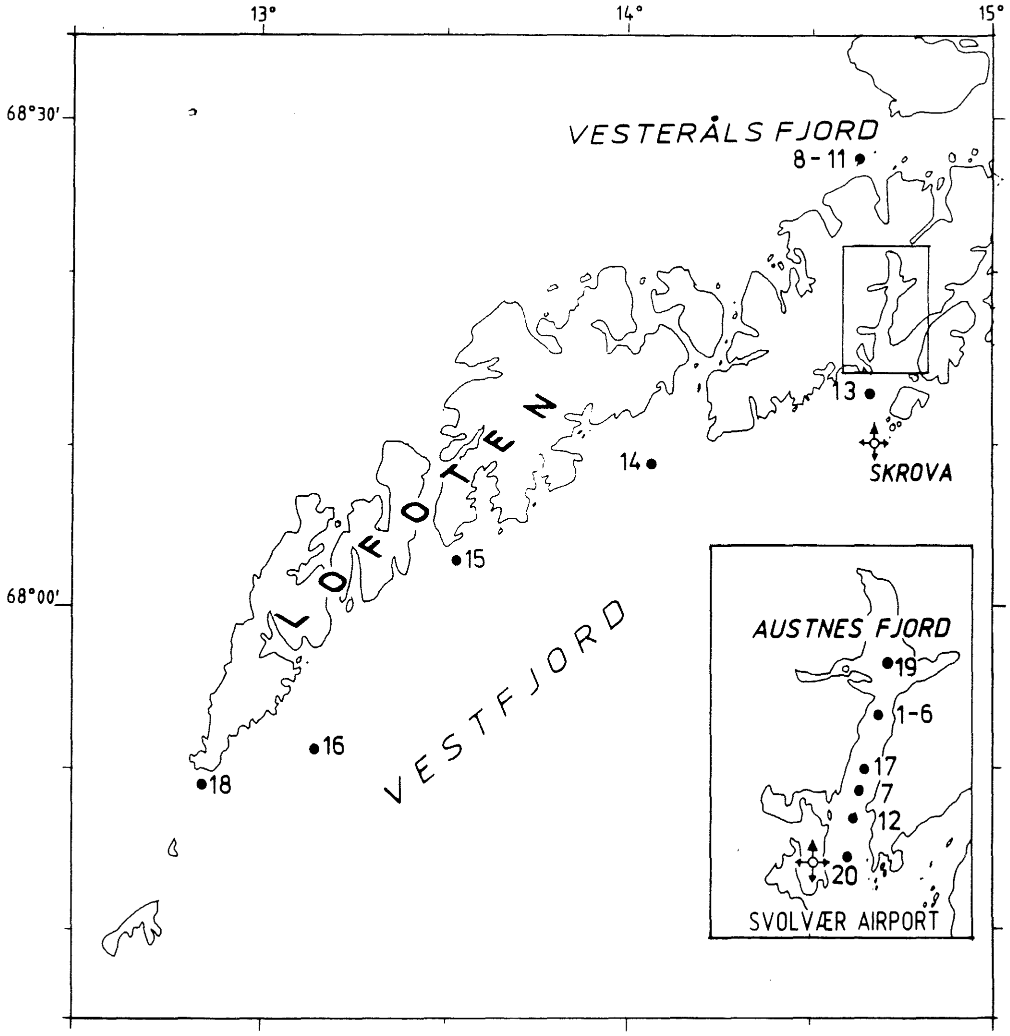

Figure 2. Positions of the cod larva stations, • , and the meteorological station, ✥ .

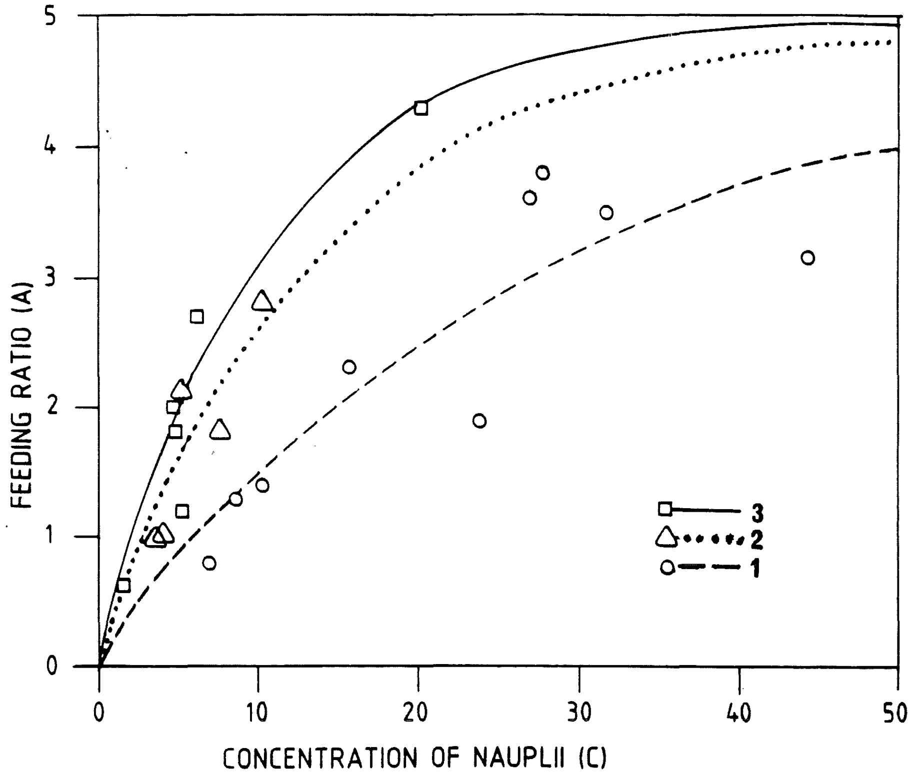

Figure 3. Relation between the feeding ratio and the nauplii concentration for the three sets of data and their regression lines with respect to eq. (2).

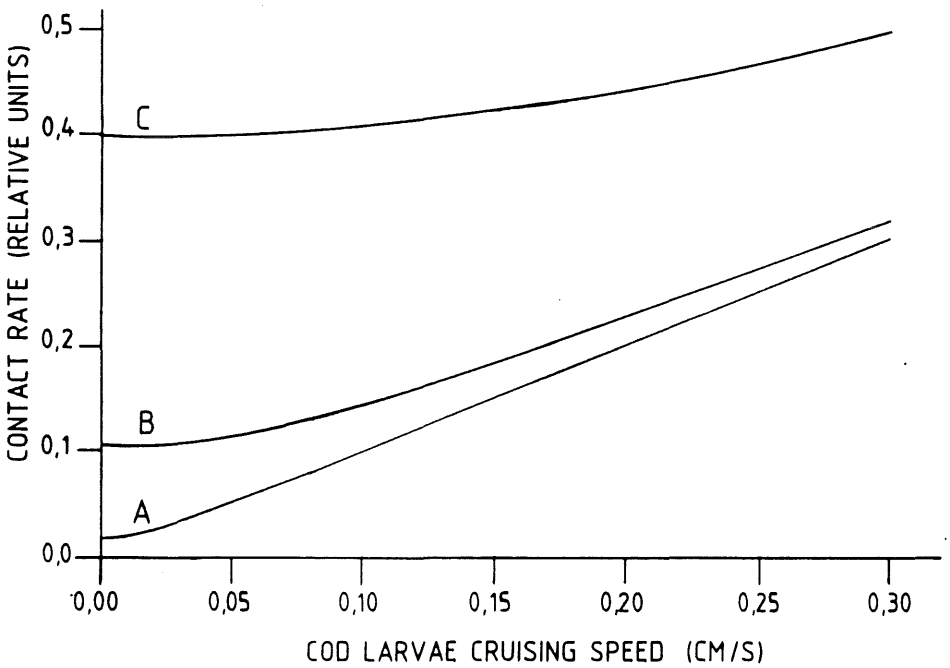

Figure 4. Contact rate as a function of the cod larvae cruising speed for distance of separation, r = 5 cm, between nauplii.
A: For root mean square (r.m.s.) velocity w = 0 (equivalent to laboratory conditions without turbulence).
B: For r.m.s. velocity w = 0.08 cm s^{-1} (equivalent to conditions for data set no.1).
C: For r.m.s. velocity w = 0.30 cm s^{-1} (equivalent to conditions for data set no. 3).