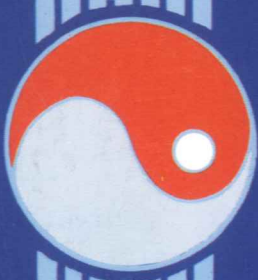# help

havforskningsinstituttets
egg - og larveprogram

Svein Sundby

Petter Fossum

Feeding conditions of Arcto-Norwegian
cod larvae compared to the
Rothschild-Osborn theory on small-scale
turbulence and plankton contact rates.

FORORD

I 1989 ble "Turbulens som rekrutteringsmekanisme" startet som prosjekt
under HELP. Formålet med dette prosjektet er å utforske virkningen av
småskala turbulens på fiskelarvenes næringsopptak. Bakgrunnen er en ny
teori som beskriver hvordan varierende turbulens, som i havet
hovedsaklig er generert av vind og tidevann, virker på kontakthyppig-
heten mellom plankton-organismer. I den følgende rapporten er denne
prosessen illustrert ved å studere kontakthyppigheten mellom torske-
larven og dens bytte (rauåte-nauplier). Men siden prosessen er av en
så grunnleggende karakter i det marine økosystemet, vil den også
belyse forhold omkring kontakthyppigheten mellom partikulær olje og
fiskelarver og raudåte. Denne rapporten gir den første dokumentasjonen
av teorien. Prosjektet "Turbulens som rekrutteringsmekanisme" er opp-
følgingen av rapporten. Det vil omfatte detaljerte målinger av verti-
kalfordelingen av fiskelarver og raudåte under varierende vindforhold,
og gi ny informasjon om blandingsprosessene i sjøens øvre lag.

HAVFORSKNINGSINSTITUTTETS EGG- OG LARVEPROGRAM (HELP)

FEEDING CONDITIONS OF 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 Arcto-norwegian cod larvae in Lofoten, northern Norway, sampled during the period 1976 - 1984, are examined to verify the theory on the influence of small-scale turbulence on the contact rate between predator and prey (Rothschild and Osborn, 1988). The number of prey per cod larval gut 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 a factor of 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 average increase in contact rate of 2.2 times for the same increase in wind speed. The data indicate that the turbulent velocity has a greater contribution to contact rate than the larval swimming speed, when wind speed exceeds 4 m s^{-1}. The larval period of Arcto-norwegian cod is an important period 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 must be an important regulatory mechanism for the formation of year class strength.

INTRODUCTION

Recent 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) developed a model which demonstrated how turbulence influences the contact rate, and 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 second one was developed from theory on random walk statistics.

In the present paper the theory of Rothschild and Osborn (1988), hereby called R & O, is tested by historical field data on first feeding Arcto-norwegian (also termed North-east arctic) 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 (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 small-scale turbulence.

Arcto-norwegian 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}. About 95 % of the diet of first feeding Arcto-norwegian cod larvae is nauplii of Calanus finmarchicus. In laboratory studies Solberg and Tilseth (1984) and Tilseth and Ellertsen (1984) measured a number of important parameters concerning the feeding and behaviour of Arcto-norwegian cod larvae, summarized in Table I.

The swimming speed of $\underline{C}$. $\underline{finmarchicus}$ nauplii has not been measured. Torres and Childress (1983) measured the swimming speed of adult $\underline{Euphausia}$ $\underline{pacifica}$ for different temperatures and pressures and for different metabolic rates. The swimming speeds ranged from 0 to 2 bodylengths s^{-1}. The average speed was about 0.5 bodylengths s^{-1}. If this value is applicable in general for crustaceans, the average swimming speed of $\underline{C}$. $\underline{finmarchicus}$ nauplii is less than 0.02 cm s^{-1}, which is about 10 % of the cruising speed of the cod larvae. (The body length of $\underline{C}$. $\underline{finmarchicus}$ nauplii is 1.2 times the carapax length, V.Melle, personal communication). The concentration of nauplii in the first feeding regions ranges from about 0.5 to 50 nauplii l^{-1}, which is roughly 10^3 times higher than the larval concentrations.

MATERIAL AND METHOD

Larvae and nauplii

The data in the present paper was sampled during surveys in the Lofoten first feeding regions in northern Norway 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 l^{-1} at each depth were counted manually. The larval gut content was examined. The number of prey organisms in each gut was identified and counted, and the feeding ratio for each sample was 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 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 l^{-1}, c, in the water column from 5 to 25

m depth, since cod larvae are mainly found at these depths. Table II 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 (Stations no. 1, 2, and 3 in Table 2) water bottles were used; in all other years Neil Brown CTD 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 Lighthouse.
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 were available. Figure 2 shows the positions of the meteorological stations at Skrova Lighthouse 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. There are also tidally energetic zones in sounds and shallow regions in Lofoten, but none of the stations were taken in those regions. Oakey and Elliott (1982) found that the turbulent energy dissipation in the mixed layer was proportional to the cube of the wind speed, W^3. The turbulent energy is modified by stratification. However, no universal functional relationship between turbulence and stratification has been found (e.g. Gargett, 1984). For the present data the parameter F is assumed to be proportional to the production of turbulent kinetic energy. It is used to describe the different situations of turbulent energy which the larvae are exposed to:

$$F = W_8^3 / N_{5-25} \qquad (1)$$

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 was lost after it was examined. Therefore only the processed mean values exist of the larval feeding ratio at the stations no. 16, 17, 18 and 20 (marked # in Table II). Only the mean nauplii concentration exists at the stations no. 6, 7, 9, 19 and 20 (marked * in Table II). Temperature and salinity were not measured at the stations 4 and 5 from Austnes-fjorden. 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 Austnesfjorden.

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 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, $A(c)$:

$$dA(c)/dc = b[A_{MAX} - A(c)] \tag{2}$$

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

$$A(c) = A_{MAX}[1 - \exp -(b \cdot c)] \tag{3}$$

Equation (3) is now applied to the data on feeding ratio of first feeding cod larvae. Table III 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.

The data in Table III 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: 90 < F < 227. The three data

sets are fitted to Equation (3), and the coefficient b is estimated. The results are shown in Table IV. 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 l^{-1}. In Figure 3 the three data sets and their regression lines are drawn. The ratio b_3/b_1, which indicates 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? We use the results of of Oakey and Elliott (1982) on the empirical relation between the wind speed and the mixed layer turbulent energy dissipation rate per unit volume, $\epsilon = (W/91)^3$. Then we use the equations of R & O to calculate the corresponding turbulent mean-square-velocity, w^2, based on ϵ and r, where r is the distance of separation. For the present data the distance of separation ranges from 3 to 9 cm. We now assume that a separation of 5 cm represents well the average length scale that contributes to turbulence dependent contact rate. In Figure 4 the equation of R & O expressing the velocity component of the contact rate, B, where

$$B = \frac{(u^2 + 3v^2 + 4w^2)}{3(v^2 + w^2)^{1/2}} \qquad (4)$$

is drawn as a function of the predator (cod larvae) speed, v, for three different values of root-mean-square turbulent velocity, w. The prey (nauplii) speed, u, is set to 0.02 cm s^{-1}, as outlined in the introduction. The vertical lines indicate the observed mean cruising speed, and the standard deviation according to Solberg and Tilseth (1984). The three turbulent situations in Figure 4 are:

A) Laboratory conditions without turbulence, which implies that w = 0.
B) Wind conditions equal to Set no. 1 in Table 4 (W = 2 m s^{-1}) which implies that w = 0.08 cm s^{-1}.
C) Wind conditions equal to Set no. 1 inTable 4 (W = 6 m s^{-1}) which implies that w = 0.30 cm s^{-1}.

It follows from equation (4) that the turbulent velocity becomes more important for the contact rate than cod larva velocity already when w equals v. At typical r-values for nauplii in Lofoten, it implies that

the turbulent component of the contact rate becomes more important than the larval speed component already at wind speeds of about 4 m s^{-1}. When cod larvae are cruising at mean speed (v = 0.17 cm s^{-1} according to Table I), 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. For r = 3 cm the corresponding increase of the contact rate is 1.9, while for r = 9 cm the increase is 2.5. At cod larval cruising speed of 0.09 cm s^{-1} the corresponding increase of the contact rate is 3 when r = 5 cm. Consequently, the calculated increase of the contact rate by the R & O 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 requirement 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 has been 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 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 Arcto-norwegian 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, cod larvae in the field 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 (velocity dependent component of the contact rate) to some extent may be counteracted by another effect of increasing turbulence, namely through the reduction of peak prey concentrations by vertical mixing (density dependent component of the contact rate). This may be an important process if in general there is co-occurrance between the predator and prey. However, reduction in the peak prey concentrations implies that the prey concentration becomes higher at other depths, and since there are as often lack of co-ocurrance between predator and prey, the change of vertical concentration of predator and prey may as well contribute to increase the density component of the contact rate. This is often the situation for larval cod and their prey, 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 successful attacks on the prey. Above such a level the residence time of the prey within range of attack will be shorter than the reaction time of the predator, and the prey will pass the predator before it is able to react. The present study indicates that this optimal level must occur at higher wind speeds than those recorded here (>6 m s^{-1}). Is it possible to evaluate from laboratory data on larval behaviour where this level occurs for the cod larvae? Gerritsen and Strickler (1977) assumed that the encounter radius was reduced exponentially as the predator speed increased. The "reactive perceptive distance" as measured by Solberg and Tilseth (1984), was defined as "the distance from the larval eye to the prey organism when the larva altered its swimming pattern to chase its prey". Consequently, information was not provided on what time it takes to do the four consecutive operations: perception of the prey, stop, change direction and attack, and therefore we are unable to quantify the optimum level of turbulence. Behavioral studies in the laboratory of larval reaction are required to quantify this process.

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. 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 (which is the squared ratio between the Brunt-Vaisala frequency and the vertical current shear). Continuous measurements of wind and waves should be done at all stations. Lastly, the small-scale turbulence should have been measured directly, though this is a difficult task. However, the present study strongly supports the theory of R & O that small-scale turbulence is an important process in marine and aquatic ecology. The mixed layer is the habitat for the early stages of Arcto-norwegian 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 are the most characteristic features of the mixed layer, and therefore small-scale turbulence and contact rate would be important regulatory mechanisms in the formation of year class strength.

ACKNOWLEDGEMENTS

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Table I. Parameters of feeding of first feeding Arcto-norwegian 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^{-1} (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

Table II. The present data set. Positions of stations are shown in
Figure 1. For stations marked "*" only the mean value of the nauplii
concentration exists. For stations marked "#" only the mean value of
the feeding ratio exists.

Station Number	Date		Region	Number of larvae	Number of wind observations
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

Table III. Mean feeding ratio (no. of prey gut^{-1}), A, and standard deviation, mean nauplii concentration (no. of prey l^{-1}) in the water column from 5 to 25 m depth, c_{5-25}, and the standard deviation, mean wind speed (m s^{-1}) during the past 8 hours, W_8, mean Brunt-Vaisala frequency (s^{-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

Table IV. Ranges of the turbulence parameter, F, ranges and mean wind speed of the past 8 hours, W_8, the calculated coefficient, b, in equation (3) and the coefficient of determination, R^2, for the three sets of data appearing in Figure 3.

Set no. 1 $0 < F < 30$ $0.9 < W_8 < 3.3$ $\overline{W}_8 = 2.0$ $b_1 = 0.034$ $R^2 = 0.96$

Set no. 2 $30 < F < 90$ $2.7 < W_8 < 4.8$ $\overline{W}_8 = 3.7$ $b_2 = 0.072$ $R^2 = 0.97$

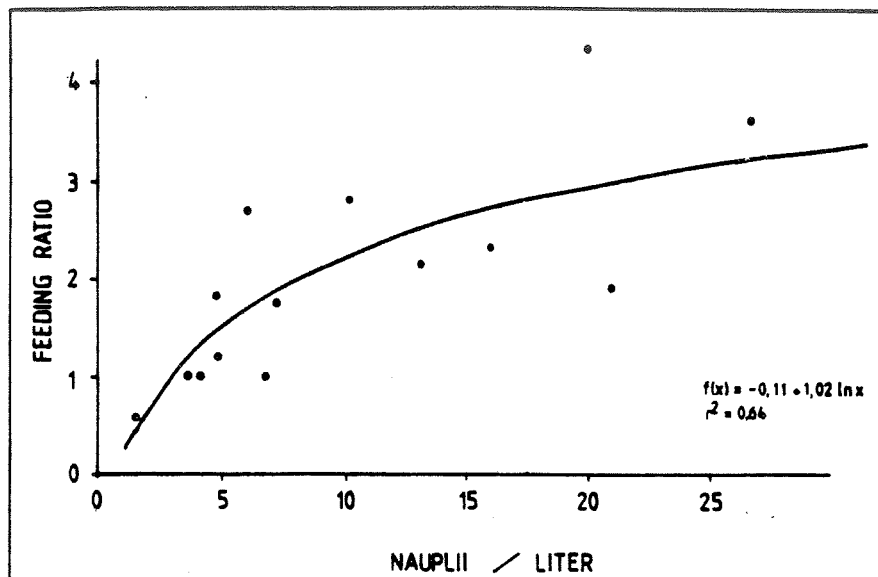Set no. 3 $90 < F < 227$ $5.2 < W_8 < 6.6$ $\overline{W}_8 = 6.0$ $b_3 = 0.095$ $R^2 = 0.98$

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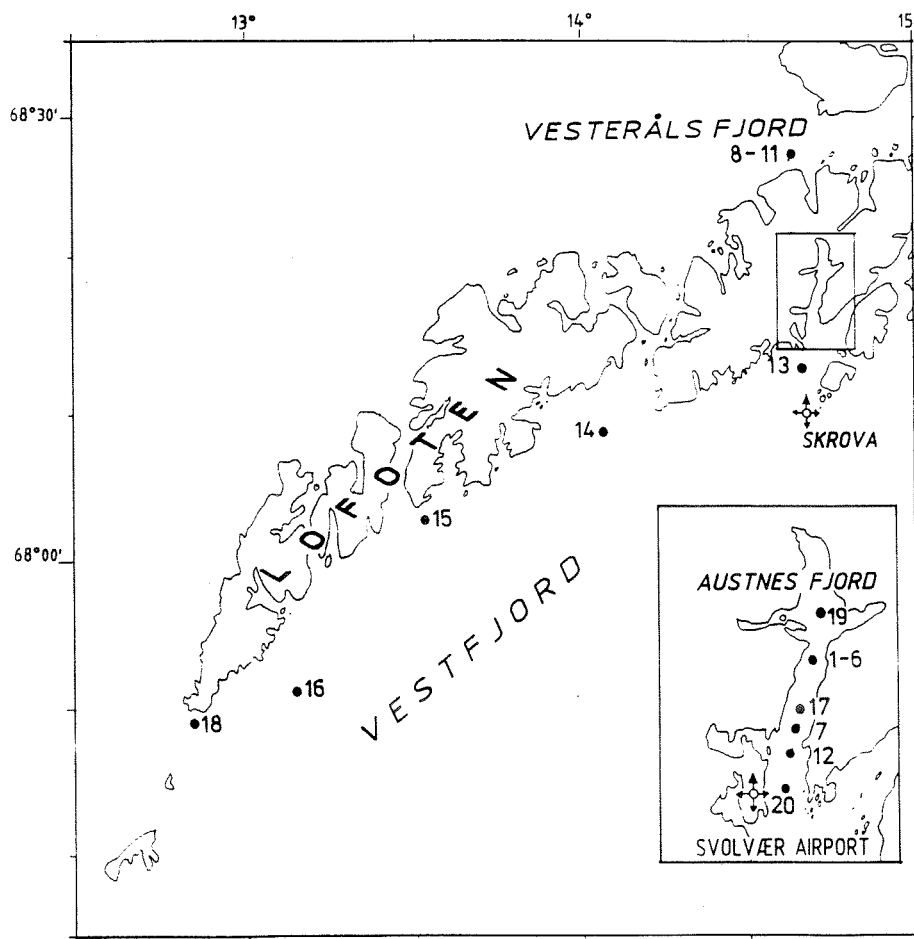to 25 m depth (From Ellertsen et al. 1989).

Fig. 2. Positions of the cod larvae stations (dots) and the
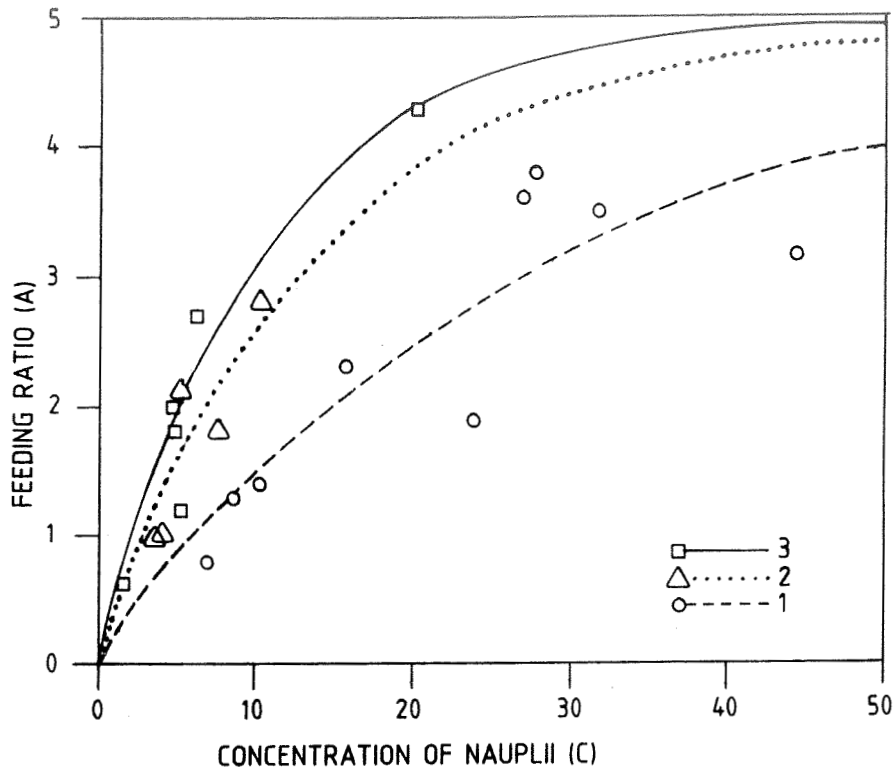meteorological stations (compass roses).

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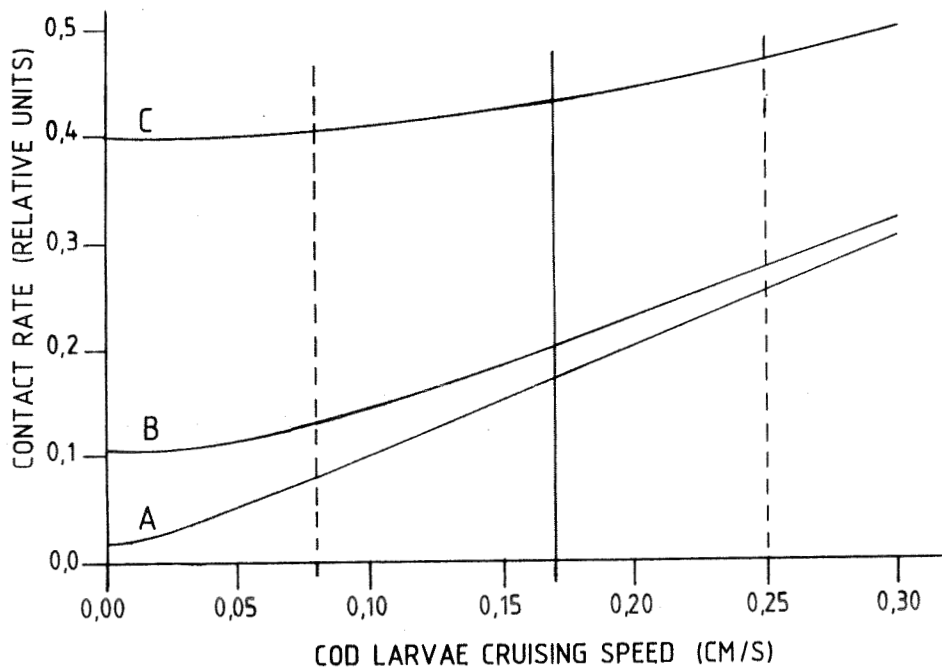

Fig. 4. Contact rate as a function of the cod larvae cruising speed for distance of separation, r = 5 cm, between nauplii.
A: For root-mean-square velocity, w = 0 (equivalent to laboratory conditions without turbulence).
B: For root-mean-square velocity w = 0.08 cm s^{-1} (equivalent to conditions for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

Oversikt over tidligere utkomne rapporter.

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