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The effects of maternal status of Arcto-Norwegian cod on egg quality and vitality of early larvae. II. Preliminary results of the experiment in 1992

by

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Abstract
The stage of spawning of females of the Arcto-Norwegian cod caught during peak spawning in Lofoten had a profound effect on several vital parameters of the eggs and larvae. Significant negative correlations were demonstrated between stage of spawning and size of eggs and larvae and total content of non-protein amino compounds (NPS). Reduced larval activity was recorded in groups from cod females at the end of spawning. Investigations on the bacteriological status and the fatty acid profiles of the eggs are also included. The results are proposed in order to demonstrate a recruitment mechanism and are discussed in this connection.

I. Introduction

The recruitment mechanisms on the early larval stages are caused by two processes working simultaneously:

1) The varied annual degree of synchronization of the early fish larvae to it's food. This idea was first put forward by Hjort (1914).
2) The maternal effects on egg quality and the vitality of early larvae resulting from female size, condition and the stage of spawning. The pioneer investigations on the maternal effect were carried out by Soviet investigators (see Nikolskii 1962a).

Nikolskii (1962b) tried to put the two processes together: "The better the supply both of yolk, and of external food for the fry at this stage, the higher the survival rate".Temperature is the factor directing both processes. Since temperature variations are a large scale phenomenon, covering both spawning and nursery areas of the Arcto-Norwegian cod, a model of an adaptive larval production has been put forward (Ellertsen & Solemdal 1990).

The present results aim to measure the effect of the stage of spawning on the egg quality and the vitality of the early larvae.

In general two types of studies were carried out to solve this problem:

1) Comparative experiments on survival, feeding, growth and behaviour of larval groups from females of different stage of spawning (Solemdal *et al.*, 1991).
2) From basic knowledge of the chemical components (amino and fatty acids), larval groups from females of different stage of spawning can be evaluated.

The present paper tries to some extent to combine these types of studies, restricting the experiments to the period from hatching to the end of larval endogenous energy resources.

In addition to the stage of spawning, both size and condition of the cod female are included in the analysis. The next step will be to collect a homogenous material according to stage of spawning to analyze effect of female size and condition specifically.

II. Material and Methods

The data on the spawning cod females used in the egg and larvae experiments are described in Table 1 taken from Solemdal *et al.* (1992).

Egg parameters

Egg diameter from 50 eggs were measured manually according to Kjesbu (1989). Egg dry weight was calculated on the basis of 50 eggs dried for at least 48 hours at 70 °C. Weighing was performed with a Cahn microbalance.

Egg stress experiment

The eggs were stressed by bubbling air through the water from day 3 to day 7 after fertilization. About 500 eggs were incubated in tanks of 6 l UV-sterilized and filtered (0.2 µm) sea water with a temperature of 5°C and a salinity of 32‰. The air was filtered through a 0.22 Millipore filter and bubbled into the tanks at a rate of 1.5 l min^{-1}. Dead eggs were removed and counted every day.

Respiratory studies and analysis of non-protein nitrogen

For respiratory studies and analysis of non-protein nitrogen, groups of eggs from the various batches were incubated in thermostated glass aquaria at 5 ± 0.05 °C and a salinity of 34.5 ‰. No stirring or aeration was applied.

Samples of 50 pooled eggs (four parallels) were extracted in 6% trichloro-acetic acid, and the supernatant analysed for total content of non-protein amino compounds (NPS) by the ninhydrin procedure of Moore and Stein (1948) using nor-leucine as the reference standard. The embryonic oxygen consumption and ammonia excretion were determined by closed respirometry and polarographic measurements of oxygen tension in test (5 parallels) and blank (4 parallels) respirometers as described by Finn *et al.* (1991). Ammonia was determined by the salicylate-hypochlorite method of Bower and Holm-Hansen (1980).

Larval parameters

Dry weight
Before drying ten larvae were rinsed twice in distilled water. Drying and weighing procedure as for eggs.

Developmental stages
The early larvae were staged according to the system by Fossum (1986).

Behaviourial studies

At day 1 after hatching (50 % hatching refers to day 0), 20 larvae from each experimental group were transferred to observation chambers holding 100 ml filtered (0.2 µm), 34 ‰ sea water. The temperature was 5°C and the larvae were kept in darkness. The activity level was measured by means of an ultrasound system (Scanner 450, linear array scanner). A 7.5 MHz transducer was placed at the top of the observation chamber in such a way that the plane of registration made a section of the water column from the top to bottom. The ultrasonic registrations were video taped. The number of swimming larvae through the ultrasonic plane per unit was defined as the activity level. For each larval group, the measuring of the larval activity was conducted for one hour in darkness and for one hour in light (30 lux) at day 3 and 6.

Bacteriological studies

The eggs were washed three times in autoclaved 25‰ sea water (SSW) and homogenized in an autoclaved homogenizer. From a dilution series in SSW, the homogenate was plated onto petri dishes with Difco 2216 Marine Broth (Difco, Detroit, USA) with 15 % agar (MBA) and Tryptone Citrate Bile Salt agar (TCBS) (Oxoid, Basingstoke, U.K.). After an incubation period of 14 days at 10°C, the number of colony-forming units (CFU) were assessed on both media. 32 isolates from the MBA plates of each group were randomly chosen as representatives for

the composition of the adherent microflora, and were subjects to phenotypical characterization.The tests performed were: Gram staining (Bacto Gram stain set, Difco, Detroit, U.S.A.), oxidase (API 7046, Bio Merieux, France), catalase (measured with 3% H_2O_2) and growth on TCBS agar. In addition, each strain was morphologically examined by a Nikon microscope operated with phase contrast at 600 or 1200X. The strains were regarded rods or cocci. Further studies are in progress.

Fatty acid studies
Ten eggs from 15 cod were analysed separately by methanolysis followed by gas chromatography of the resulting methyl esters according to the method described by Ulvund & Grahl-Nielsen (1988).

III. Results

Egg and larval parameters
Fig.1 shows the relation between egg diameter and stage of spawning. Linear regression analysis showed this relation to be significant (P = 0.001). Multiple regression using egg diameter as dependent variable and stage of spawning, female weight and percentage of dry white muscle as independent variables showed no significant (P > 0.05) contribution of the latter two.

In Fig.2, the dry weight of eggs is plotted against stage of spawning. In this case the regression analysis also showed a significant value (P = 0.007). The other female parameters did not contribute significantly.

Standard length of larvae in development stage 6 was also significantly (P = 0.009) related to the stage of spawning (Fig.3). The dry white muscle of the cod female was found to contribute significantly (P=0.024), but not the other female parameters.

Dry weight of larvae of stage 6 is plotted against stage of spawning in Fig. 4. The multiple regression analysis showed a significant contribution by the stage of spawning (P = 0.001), and also by female weight (P= 0.024) and female dry white muscle (P= 0.004).

Fig.5 shows the relation between egg diameter and larval standard length at stage 6. These parameters are highly correlated (P <0.001). The relation between dry larval weight and egg dry weight is shown in Fig.6, showing also a highly significant (P < 0.001) relation.

Egg stress experiments
In Fig. 7 the results from the egg stress experiment is plotted against stage of spawning of the cod females. Relatively high egg mortality is found in the very beginning and end of spawning, while lower egg mortality is noticed in the early

middle part of the spawning period.

Respiratory studies and analysis of non-protein nitrogen
The egg content of soluble non-protein amino compounds (NPS), correlated negatively with the stage of spawning (Fig. 8). Mostly, the NPS represent freely dissolved amino acids.
Ammonia excretion but not oxygen uptake of the eggs at day 11 after fertilisation correlated with the stage of spawning. Taking the ratio between the ammonia production to the oxygen consumption the nitrogen quotient (NQ) is obtained (Gnaiger 1983). The NQ is a measure of the proportional use of amino acids in the aerobic energy dissipation of the cod embryo. When the energy dissipation is fully based on amino acid catabolism, the NQ equals 0.27 while a strict carbohydrate or lipid catabolism results in an NQ of zero. In the present study the NQ values for the cod embryos on day 11 after fertilisation, ranged between 0.17 and 0.12, and a negative correlation existed between the NQ and the spawning status of the mother fish (Fig. 9).

Behaviourial studies
In Fig. 10 the activity of the cod larvae in one hour of darkness and in one hour of light at day 3 and 6 after hatching are shown. Development of activity from day 3 to day 6 are also shown in the figure. These values result from subtracting the total activity at day 3 from the total activity at day 6. Thus, a value below zero indicates a decrease in activity from day 3 to day 6. The larval groups are sorted after the stage of spawning of the cod females, with stage 1 first. The larval groups from the latest stage of spawning show a decrease in activity from day 3 to day 6 after hatching, in other words from before to after the point where the larvae are able to start feed.

Bacteriological studies
The number of colony-forming units on the MBA and TCBS media, and the results from the phenotypical characterization are given in Table 2. Practically all isolates were Gram negative, and most were rod-shaped. However, some of the tested parameters showed high variation among the different egg groups. Whereas the assessed number of CFU on TCBS agar was close to, or equal to zero in most of the groups, group 4864 had $3.5 \cdot 10^3$ CFU egg^{-1}, 43 times higher than the second highest number. This group also showed atypical results regarding the oxidase test, as only one of the isolated strains were oxidase positive. Group 4855 and 4973 also had relatively high numbers of oxidase negative tests (33% and 30%, respectively) whereas all other groups were dominated by oxidase positive strains. Another fish not included in Table 1 had 35% catalase negative strains, whereas all other groups were dominated by catalase positive bacteria. The frequency of isolates that could grow on TCBS agar varied from 31 % to 90 %, and apparently no covariation with the assessed number of CFUegg^{-1} on the same agar.

Fatty acid studies
Table 3 shows the composition of fatty acids of eggs from the investigated cod

females. A principal component plot of the relative values of the fatty acids in the eggs from the investigated cod females is shown in Fig.11, and in Fig.12 a similar plot of the absolute amounts of the fatty acids are shown.

IV. Discussion

Egg size is to a large extent a species characteristic, but is found to vary both with spawning time (Hiemstra 1962; Kjesbu 1989) and female size (Zastrow *et al.* 1989; Buckley *et al.* 1991a,b). For cod, a batch spawner, it is obvious that the stage of spawning is the parameter responsible for most of the egg size variation, the effect of female size being completely masked in the present material. Few authors have taken the stage of spawning into consideration when investigating maternal effects on eggs and larvae. However, Hislop (1988) used a six point scale based on visual, external inspection of the gonad. He selected haddock females in early stages of spawning to study the maternal effects. Many fisheries laboratories use similar methods for staging spawning, but laboratory experiments have proved them to be unreliable (Kjesbu, unpublished data). Buckley *et al.* (1991,b) investigated the combined effect of spawning time and female size on egg size in *Pseudopleuronectes americanus*. These parameters amounted to 61 % of the total variability in egg size. A general method for describing the stage of spawning in this species was not developed, but batch spawning was described.

The results on mortality of stressed eggs from cod females in different stages of spawning (Fig7) fit well with the results given by Kjesbu *et al.* (1991) demonstrating a cycle of protein mobilization during the spawning of cod. The spawning stage showing lowest egg mortality corresponds to the period of maximum influx of yolk protein. The same cycle applies also for the production of chorion material (Kjesbu *et al.* 1992), indicating a tougher chorion to stress in the same period.

Free amino acids are typically found in high amounts in marine fish eggs at spawning, and have been implicated as an important energy substrate during embryogenesis of marine fishes (Fyhn 1990). In a study of successive egg batches of captive Atlantic cod, the egg content of free amino acids was found to decrease during the spawning season (Mårstøl *et al.* 1992). The present egg data for cod caught during spawning in the ocean agree with that finding.

The bacteriological tests showed large differences among groups in the frequencies of positive scores. This demonstrates that the composition of the adherent microflora varied among the groups. No systematic differences with respect to the maternal fish were, however, detected.
The analytical method used on the fat in the eggs does not discriminate between the different lipid classes, e.g., triglycerides, phospholipids and free fatty acids. The results express the total fatty acids in the cod eggs. The fatty acids in the eggs

are dominated by the saturated acid 16:0, the monounsaturated acid 18:1n9 and the two polyunsaturated acids 20:5n3 and 22:6n3 (Table 3). The composition found in the present investigation corresponds closely to those found in cod eggs collected in Lofoten in 1985 by Klungsøyr *et al.* (1989). The relative amounts of the fatty acids, and the total amount of fatty acids, differed among the cod females. By performing a multivariate principal component analysis of the data, the differences in all fatty acids are considered simultaneously. Differences among the 15 cod are seen in the PC-plot (Fig.9). The plot is a projection which shows only 55% of the total variance among the samples. The cod overlapping in the plot were found to be different by constructing new PC-plots based on samples from fewer cod. A principal component analysis of the absolute amounts of fatty acids also showed differences among the individual cod (Fig.10). Among the 10 eggs from each cod female, the differences were larger in absolute amounts than on relative amounts. No correlation between the fatty acid composition in the eggs and size of the respective cod females were found. Taking the stage of spawning into consideration, eggs from 3 cod females in the beginning of spawning were tested against eggs from 3 cod females at the end of spawning. No systematic difference was detected, in contrast to the results from individually spawning cod (Ulvund 1988, Ulvund & Grahl-Nielsen 1988). It is concluded from this preliminary study that each cod female has egg with distinct fatty acid composition. Possible differences caused by stage of spawning, size etc, are completely masked by the individual differences.

Stage of spawning affects the size of larvae, the size decreasing significantly at the end of the individual and general spawning period. As seen from the activity studies, larvae from advanced stages of spawning showed reduced activity during the very important period of first feeding.

The viability of an early fish larvae is a very complex term and is extremely difficult to investigate experimentally, with a certain amount of realism. The most realistic experiments are to bring the larvae through a certain period under the most natural environmental and feeding conditions. The different growth and survival relations of the groups are then related to various characteristics of the early larvae: dry weight, standard length, RNA/DNA and chemical and biochemical parameters. In this way Buckley *et al.* (1991b), on the basis of experiments with *Pseudopleuronectes americanus*, concluded that high dry weight of the newly hatched larvae increased the survival. In general dry weight described the survival and growth relations in their material better than the other parameters. No compensatory growth were found during similar experiments with larvae of striped bass (*Morone saxatilis*) (Monteleone and Houde, 1990).

The present results have implications for the recruitment of the Arcto-Norwegian cod in the following way: The smallest eggs come from the latest spawned batches, this would be of importance for the reproductive success of the cod. Ellertsen & Solemdal (1990) put forward a hypothesis combining the year to year variation in peak spawning of *Calanus* and the cod egg size reduction

throughout the spawning season. During warm years peak spawning of *Calanus* are ahead of the peak hatching of cod larvae, giving the best start feeding to the largest, presumably most viable larvae. On the contrary, during cold years peak spawning of *Calanus* is significantly delayed and coincides with the small sized, probably less viable, larvae hatched at the end of the season due to exhaustion of the cod female.

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Table 1. Data on the cod females selected for different stage of spawning.

Stage of spawning	Fish nr.	Length cm.	Weight g.	Dry muscle %	Age	Type	Spawning zones
1	4842	84	7850	17.59	7	4	0
1	4961	113	17750	18.16	9	5	2
1	4577	86	6250	18.16	9	5	2
1	4973	126	19950	17.27	10	4	1
1/2	4838	70	3250	17.22	9	4	1
1/2	4868	111	16950	17.35	8	4	1
2	4595	85	5050	18.28	7	5	0
2	4855	91	6000	16.6	9	5	1
2	4864	78	4150	17.53	6	1	0
3	4834	71	3050	17.02	9	4	2
3/4	4965	85	4500	15.52			
4	4590				9	2	0
4	1	122	16400	17.63			
4	2	89	8750	17.14			
4	4	90	7500	17.59			
4	5	48	950	16.6			

The scale of stage of spawning is as follows:

1- early in spawning (0-25 % of all eggs spawned)
2- midway (25-50 %)
3- approaching the end (50-75 %)
4- end of spawning (75-100 %)

The code for the cod types are as follows:

1. Coastal cod
2. Uncertain coastal cod
3. Svalbard cod
4. Uncertain Arcto - Norwegian cod
5. Arcto - Norwegian cod.

Table 2. Number of colony-forming units per egg, and results from the phenotypical characterization of the isolated bacteria (percentage of positive tests). NM = not measured.

Egg group	CFU on TCBS (CFU • egg^{-1})	CFU on MBA (CFU • egg^{-1})	Gram (% pos.)	Oxidase (% pos.)	Catalase (% pos.)	TCBS (% pos.)	Rod (% pos.)
4577	$2.6 \cdot 10^{1}$	$3.3 \cdot 10^{4}$	0	91	100	68	100
4973	$8.0 \cdot 10^{1}$	$9.9 \cdot 10^{4}$	0	70	87	57	100
4961	0	$9.2 \cdot 10^{3}$	0	90	65	90	100
4842	0	$3.5 \cdot 10^{3}$	0	100	100	52	95
4838	0	$3.5 \cdot 10^{2}$	0	100	100	59	100
4864	$3.5 \cdot 10^{3}$	$2.4 \cdot 10^{4}$	0	5	100	53	100
4855	$1.4 \cdot 10^{1}$	$1.8 \cdot 10^{5}$	0	67	96	67	100
4595	$1.3 \cdot 10^{1}$	$2.4 \cdot 10^{4}$	0	94	100	84	100
4965	0	$1.5 \cdot 10^{4}$	0	100	100	44	97
4834	NM	NM	0	100	100	41	100
4590	$7.0 \cdot 10^{0}$	$1.6 \cdot 10^{4}$	6	100	100	53	83

Table 3. Composition, given as percent of sum ± SD, and total amount, given as µg/egg, of fatty acids in total lipid in ten eggs from each of eight cod from Lofoten as well as the average values from 15 cod.

	COD NO								
Fatty acids	4577	4590	4595	4834	4842	4855	4871	4973	AVERAGE
14:0	3.0±0.4	3.3±0.6	3.5±0.5	3.2±0.3	4.1±0.3	4.2±0.6	2.4±0.3	2.6±0.4	3.5±0.8
15:0	0.6±0.1	0.6±0.1	0.7±0.1	0.7±0.1	0.7±0.0	0.6±0.1	0.5±0.0	0.6±0.1	0.6±0.1
16:0	21.5±1.7	22.0±0.9	27.0±1.8	23.8±1.6	24.1±0.8	21.5±1.5	22.1±1.3	23.8±1.5	22.9±2.0
16:1n9	1.4±0.1	1.5±0.1	1.2±0.1	1.3±0.1	1.3±0.1	1.3±0.1	1.4±0.1	1.3±0.1	1.4±0.2
16:1n7	3.1±0.3	3.4±0.4	2.9±0.1	3.1±0.1	1.9±0.1	3.8±0.3	2.1±0.2	3.1±0.1	3.0±0.6
16:1n5	0.4±0.1	0.5±0.1	0.4±0.0	0.4±0.0	0.4±0.0	0.6±0.1	0.3±0.0	0.3±0.0	0.5±0.1
17:0	0.3±0.1	0.3±0.0	0.5±0.1	0.4±0.1	0.4±0.0	0.3±0.1	0.4±0.1	0.4±0.1	0.4±0.1
18:0	2.4±0.4	2.8±0.7	3.4±0.9	4.9±0.5	5.1±0.6	2.4±0.7	4.2±1.0	3.5±0.7	3.6±1.2
18:1n9	8.3±0.7	8.8±0.7	8.3±0.5	8.0±0.3	8.4±0.4	7.5±0.5	10.5±0.4	10.3±0.6	8.6±1.1
18:1n7	3.2±0.3	4.0±0.7	3.0±0.2	4.0±0.4	2.0±0.2	2.8±0.3	4.1±0.4	5.0±0.7	3.5±1.0
18:1n5	0.4±0.0	0.4±0.0	0.4±0.0	0.4±0.0	0.3±0.0	0.4±0.0	0.2±0.0	0.4±0.0	0.4±0.1
18:2n6	1.0±0.2	1.3±0.4	1.1±0.1	0.9±0.0	0.9±0.0	1.6±0.8	0.6±0.0	1.1±0.3	1.1±0.4
18:3n3	0.5±0.2	0.6±0.2	0.5±0.1	0.6±0.2	0.7±0.1	0.6±0.1	0.5±0.1	0.4±0.1	0.6±0.1
18:4n3	0.9±0.2	0.7±0.1	0.6±0.1	0.5±0.0	0.9±0.1	1.0±0.1	1.1±0.1	0.4±0.1	0.8±0.3
20:4n6	1.8±0.0	1.8±0.2	1.6±0.1	3.0±0.1	1.1±0.0	1.1±0.0	4.9±0.2	3.4±0.1	2.0±1.0
20:4n3	0.4±0.0	0.4±0.1	0.3±0.1	0.3±0.0	0.5±0.1	0.4±0.1	0.6±0.1	0.3±0.0	0.4±0.1
20:5n3	18.2±1.7	14.7±0.7	14.9±1.2	15.7±0.9	15.6±0.7	18.8±1.5	15.5±1.2	12.8±0.8	15.9±2.0
22:5n3	1.3±0.3	1.2±0.2	1.0±0.2	1.2±0.1	1.0±0.1	1.3±0.3	1.3±0.2	1.3±0.2	1.2±0.2
22:6n3	30.1±1.0	30.5±1.4	27.4±2.0	26.5±1.3	29.7±0.7	28.9±1.4	26.7±1.4	27.1±1.6	28.9±1.9
24:1n9	1.1±0.2	1.3±0.3	1.4±0.2	1.0±0.2	0.8±0.1	1.1±0.3	0.8±0.2	1.8±0.3	1.1±0.3
µg/egg	11.3	10.6	9.2	10.0	8.6	12.8	12.6	10.9	10.4

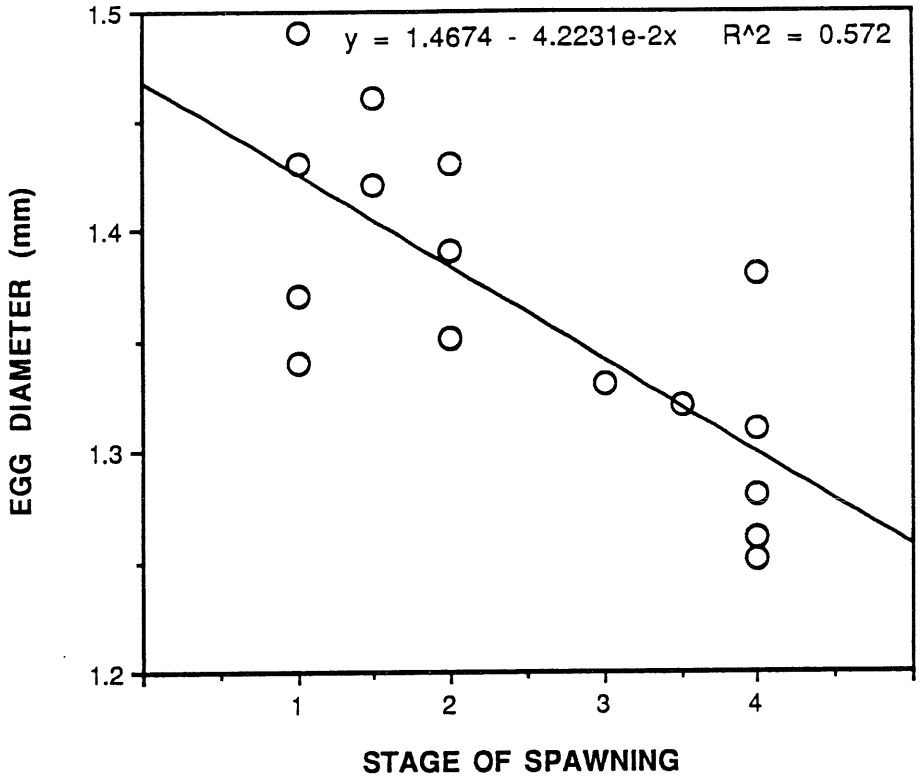

Fig. 1. The relation between stage of spawning of the cod females from Lofoten (scale given in table 1) and their egg diameter.

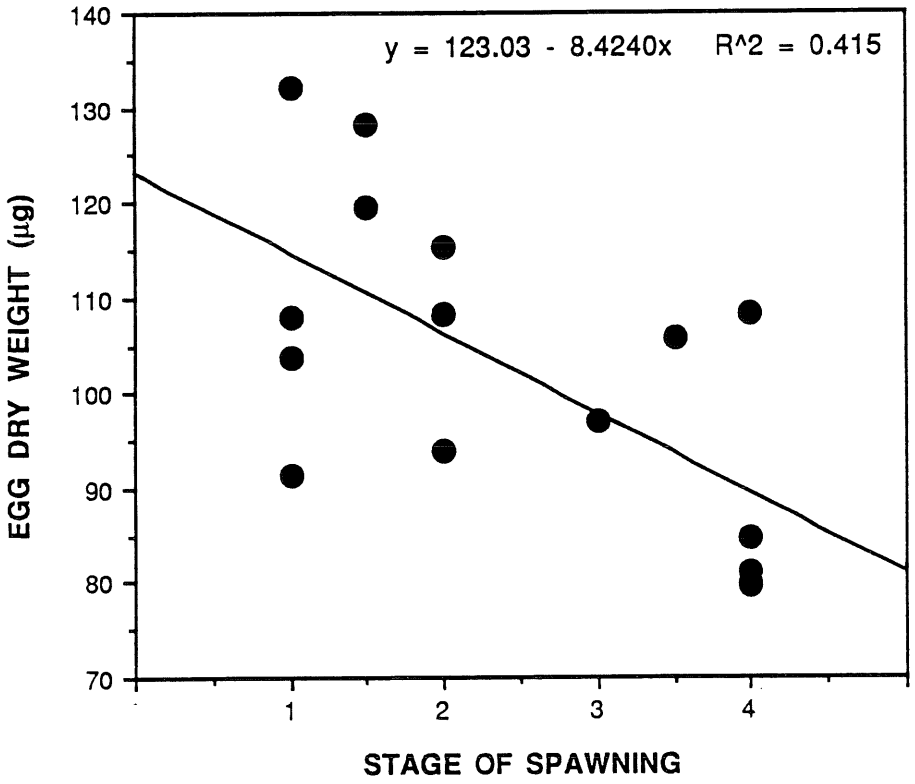

Fig.2. Relation between stage of spawning of the cod females from Lofoten (scale given in table 1) and the dry weight of their eggs.

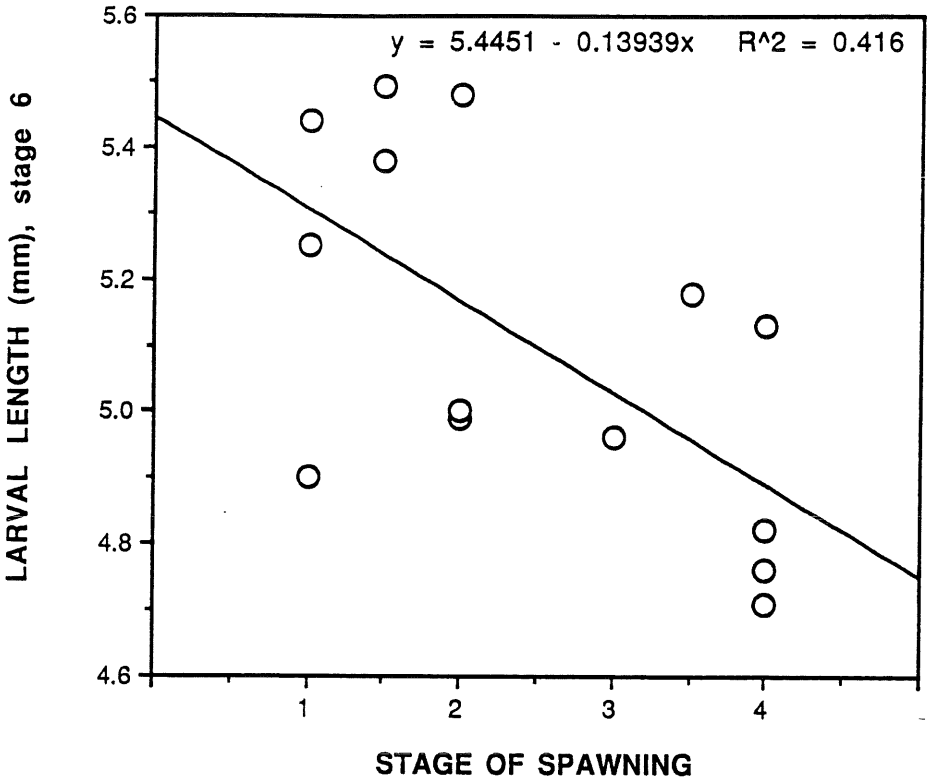

Fig. 3. The relation between the stage of spawning of the cod females from Lofoten (scale given in table 1) and the standard length of their larvae in developmental stage 6 (Fossum 1986).

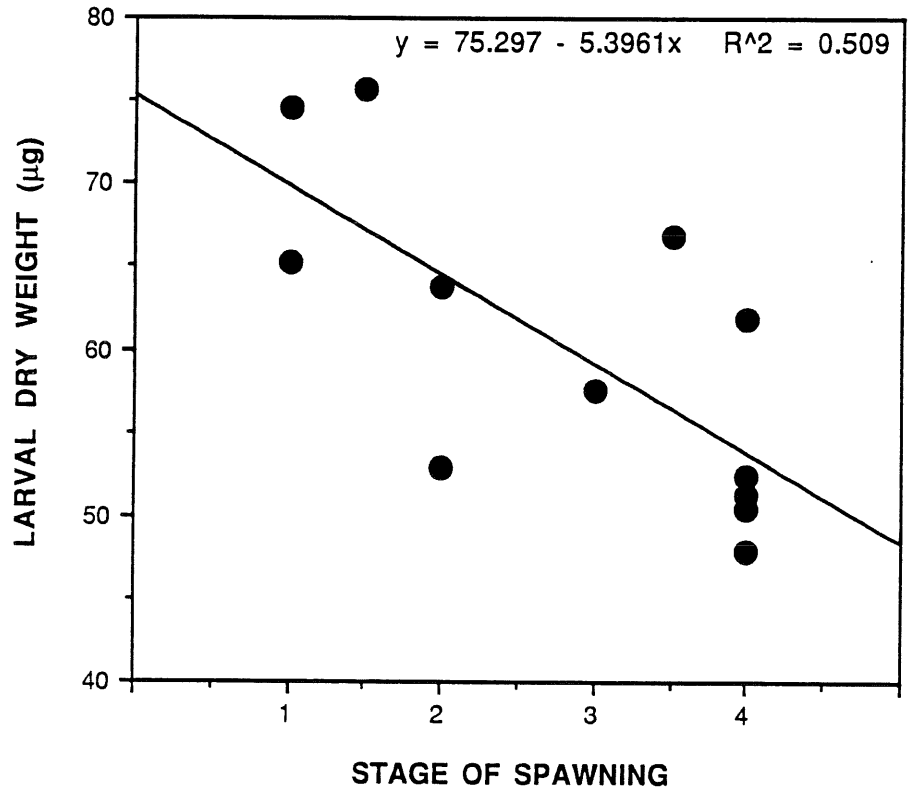

Fig. 4. The relation between stage of spawning of the cod females from Lofoten (scale given in table 1) and the dry weight of larvae in developmental stage 6 (Fossum 1986).

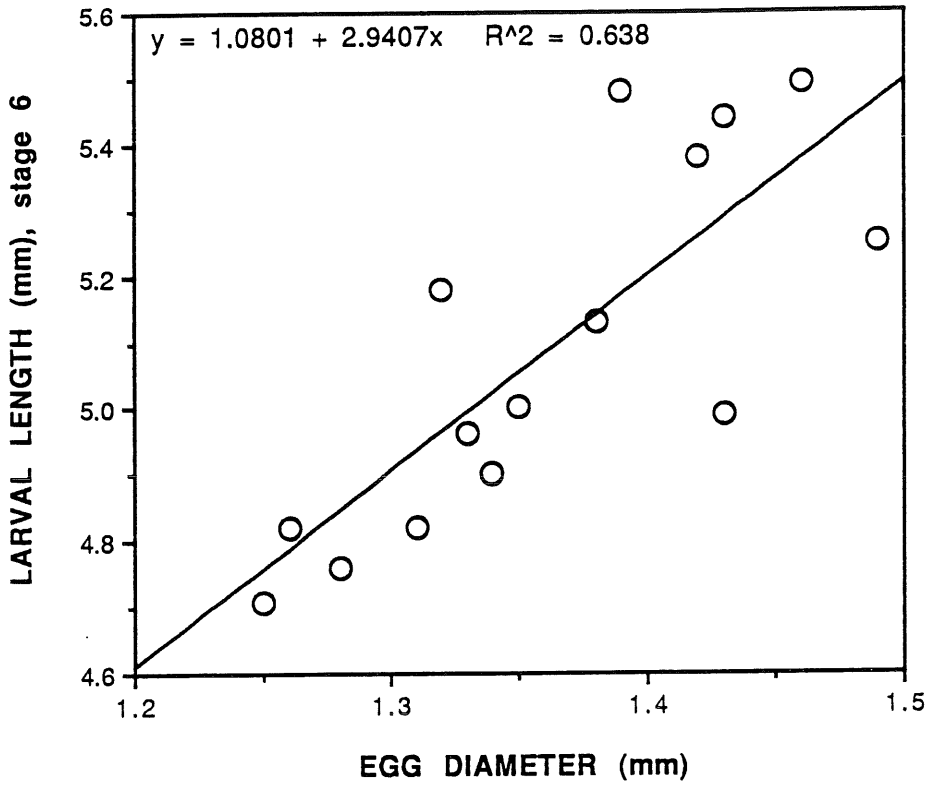

Fig. 5. The relation between egg diameter and the standard length of larvae in developmental stage 6 (Fossum 1986).

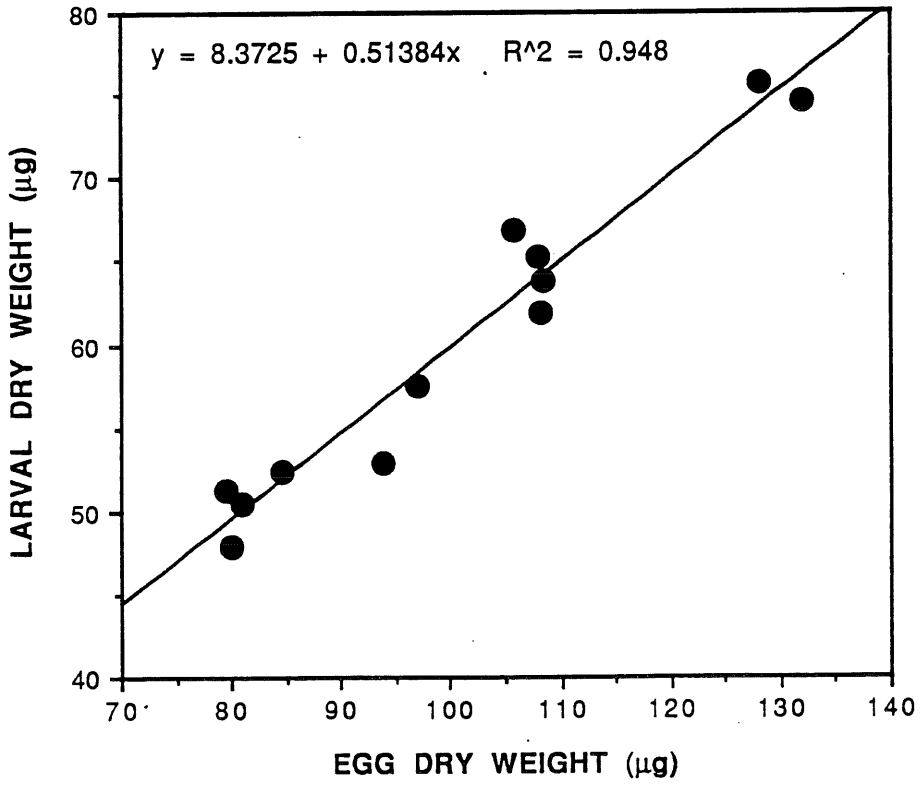

Fig. 6. The relation between egg dry weight and dry weight of larvae in developmental stage 6 (Fossum 1986).

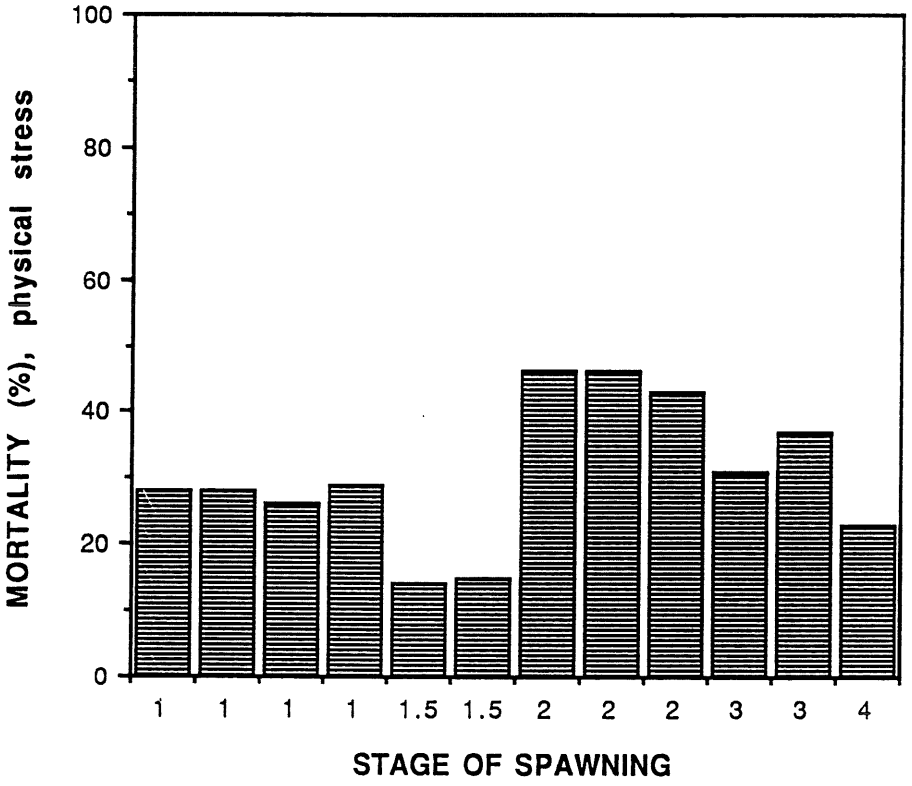

Fig. 7. Mortality, %, in the egg stress experiment plotted against stage of spawning of the cod females from Lofoten (scale given in table 1).

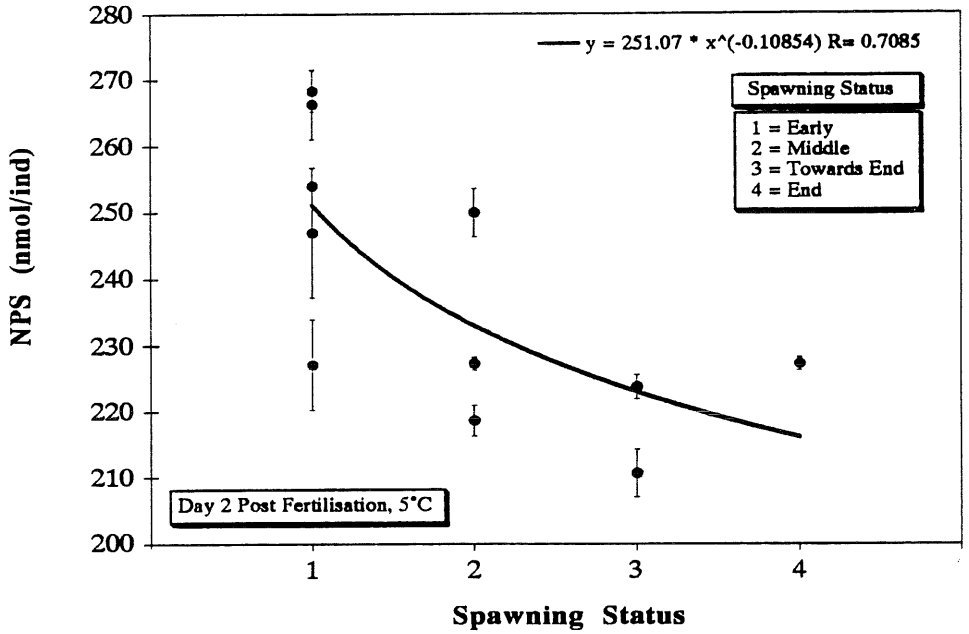

Fig. 8. NPS content of Lofoten cod eggs as a function of the stage of spawning.

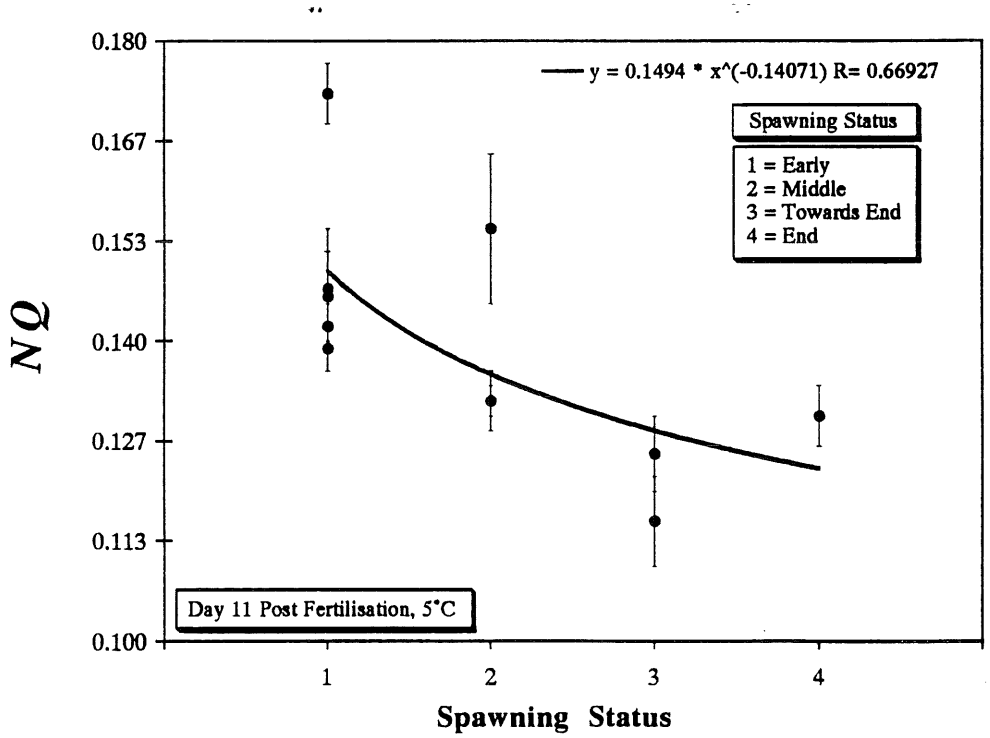

Fig. 9. Apparent NQ of Lofoten cod eggs as a function of the stage of spawning.

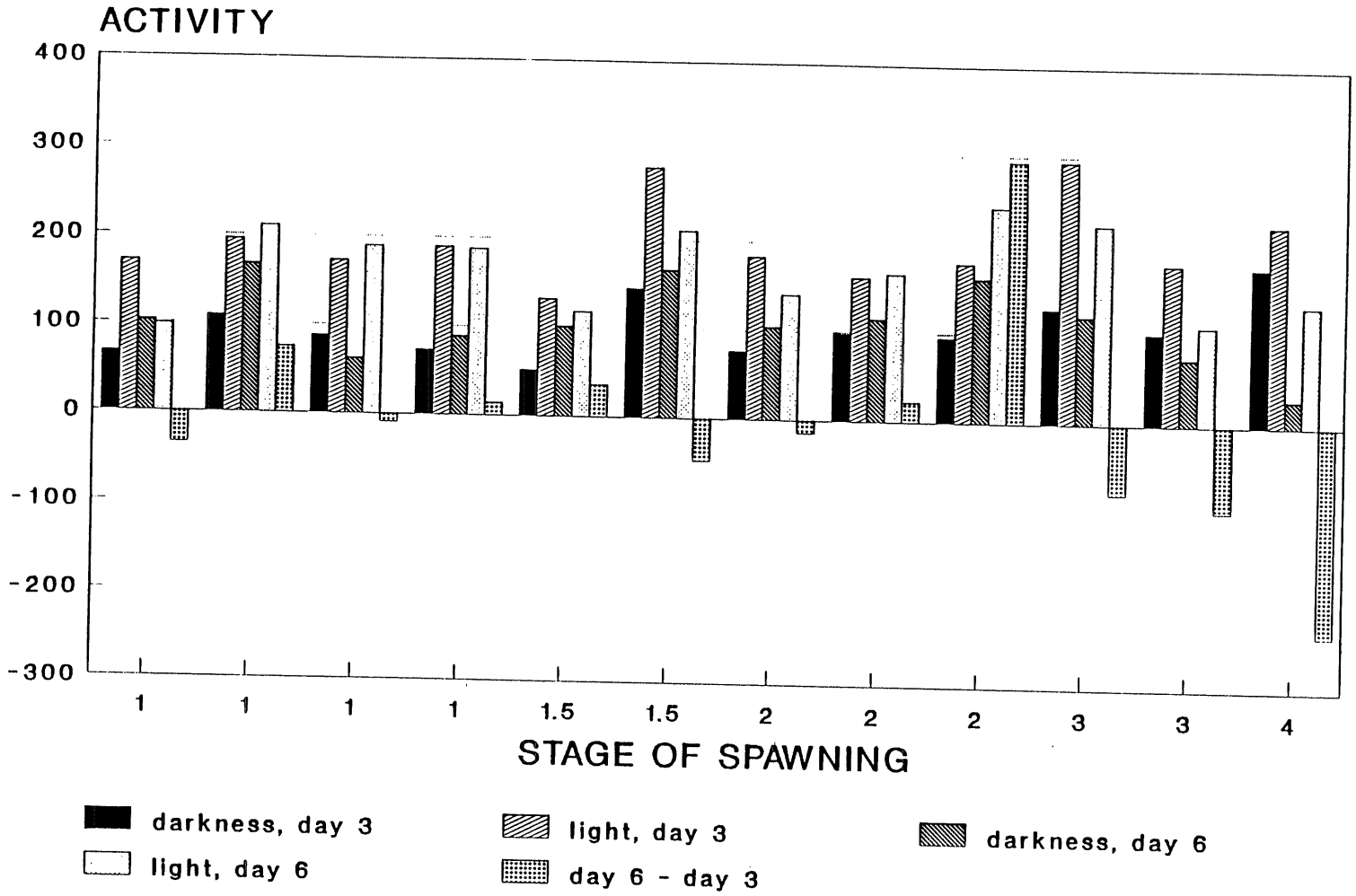

Fig. 10. Activity of cod larvae during hour of darkness and 1 hour of light. The activity was measured by a ultrasound system, and the activity was measured as nos. of larvae swimming through the ultrasonic plane.

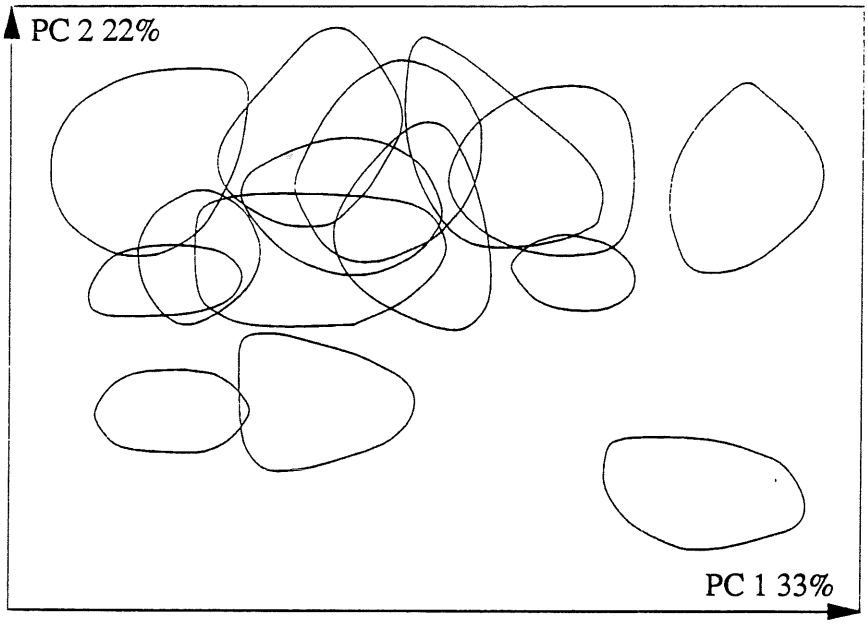

Fig.11. PC-plot of the relative values of fatty acids in cod eggs. Within each encircled area, which represents one cod, are ten samples of individual eggs (not shown).

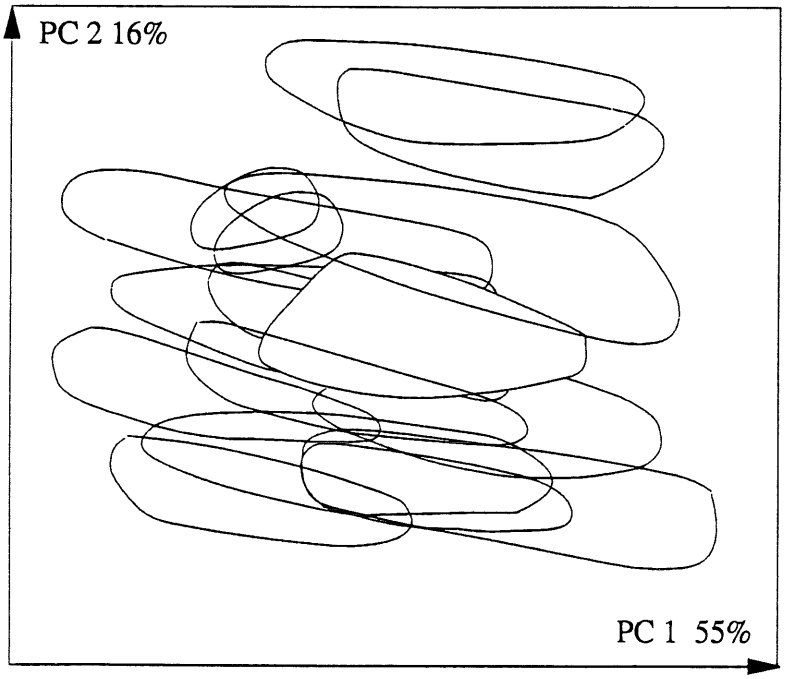

Fig. 12. PC-plot of the absolute amounts of fatty acids in cod eggs. Within each encircled area, which represents one cod, are ten samples of individual eggs (not shown).