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SIZE OF EGGS AND NAUPLII OF CALANOID COPEPODS IN THE BARENTS SEA; INFLUENCE OF ENVIRONMENTAL AND MATERNAL FACTORS

by

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ABSTRACT

During the years 1986 to 1988 eight cruises were conducted in the central and western parts of the Barents Sea. The cruises, together spanning the time period from January to July, covered most developmental stages of the phytoplankton spring bloom. Temperature, salinity, nutrients, chlorophyll *a*, and zooplankton were generally sampled at each station.

Size frequency distributions of eggs and nauplius stages of the copepods *Calanus finmarchicus, C. glacialis, C. hyperboreus, Pseudocalanus sp., and Metridia sp.*, are given. Cluster analysis and a subjective method of classification grouped the sampling stations into environmental regions on the basis of environmental variables. The environmental variables were related to size of eggs (diameter) and nauplii (carapax length) of *C. finmarchicus* by a linear method of canonical ordination (Redundancy Analysis). A significant overall difference in size of eggs and nauplii between environmental regions was demonstrated. The size of eggs and nauplius stages N1 to N3 were positively correlated with distance from the Norwegian Sea, and the size of the females were positively correlated both with distance from the Norwegian Sea and egg size. Egg size was negatively correlated with temperature. It was concluded that advection of smaller sized adult females into the Barents Sea gave rise to a population of small sized eggs and young nauplii. The maternal effect may be a direct process where bigger females spawn bigger eggs, or more indirectly where the females spawn bigger eggs at low temperatures. The feeding stages N4 and N6 were positively correlated with chlorophyll content (assumed to represent food supply), and negatively correlated with temperature. Chlorophyll and temperature were inter-correlated, and the contribution of each particular variable to the relationship could not be estimated. Thus, after the nauplii start to feed, food supply and/or temperature have greatest influence on size, and soon mask size patterns due to maternal effects.

Introduction

Patterns in distribution of temperature and salinity, the current system, and characteristics in the onset and development of the spring phytoplankton bloom, are used to distinguish between ecological regions of the Barents Sea (Skjoldal & Rey 1989). The Barents Sea can be divided into three main regions according to water masses. In the south-west the Norwegian Coastal Current enters the Barents Sea forming a zone of Coastal water along the Norwegian coast, which towards east gradually mixes with the "older" Barents Sea water (Figure 1). Atlantic water from the Norwegian Sea is penetrating into the Barents Sea north of the Coastal Current. Towards east this water mass is cooled and mixed with Barents Sea water. North of the polar front Arctic water flows southward. At the polar front northward flowing Atlantic water dives under the Arctic water. Atlantic Water are gradually converted into Arctic water by freezing and formation of high-salinity bottom water. Arctic water is generally cold and with low salinity, while Atlantic Water is warmer and with high salinity (e.g. Skjoldal & Rey 1989). Early in the season coastal water is colder and less saline than Atlantic water, later the temperature is generally higher than in the Atlantic water. In addition to the three water masses described above, there is the Melt water area which is of a more mixed origin. This area consist of Atlantic water covered with cold low salinity water from melting sea ice south of the polar front. Later in the summer when the retarding ice edge have passed the polar front, the Melt water region consist of Arctic water below the melt water. This situation, however, was not encountered during the cruises considered here.

The spring phytoplankton bloom tend to start first in the highly stratified Melt water region, and in the frontal areas between Atlantic water and Coastal water. In the central areas of homogeneous Atlantic water and in the Coastal water, the initiation of the spring bloom is dependent of the slower process of stratification due to atmospheric warming of the surface waters. Therefore the development of the spring bloom in the Barents Sea is neither directly related to time nor a south-north gradient. Within the melt water region were the bloom is short and vigorous, the development of the spring phytoplankton bloom can be mapped by either moving along a north-south transect (or perpendicular to the retreading ice edge), or by sampling at one geographically fixed position over time (Skjoldal & Rey 1989). Probably this is also true within the homogeneous parts of Atlantic and Coastal water masses,

although weaker gradients can be expected.

According to this general pattern of physical and biological characteristics the Barents Sea have been classified into a set of sub-areas, which have proved to be useful for ecological interpretations (Melle & Skjoldal in prep.): **Arctic water**, **Melt-water**, **Atlantic water**, and **Coastal water**. Each water type are further classified according to the state of the phytoplankton bloom: **pre-bloom**, **early bloom**, **bloom**, and **post-bloom**. The latter classes being both geographically and temporarily defined.

The copepods *Calanus finmarchicus* and *C. glacialis* are the dominant zooplankton species of the Barents Sea, south and north of the polar front, respectively. Other important copepods are *C. hyperboreus*, *Pseudocalanus sp.* and *Metridia sp.*, which are found both north and south of the polar front. The two genera listed are probably represented by more than one species each in the Barents Sea. This is, however, not discussed here. Except *Pseudocalanus sp.* that carry their eggs in clusters attached to their body, these copepods have pelagic eggs. After hatching they develop through six nauplius and six copepodite stages. All stages are easily recognized on morphological characters. *C. finmarchicus*, the main subject of this article, has a one year life-sycle, that is one generation a year in most of the Barents Sea (Tande *et al.* 1985). In the southern parts, two generations a year may be started, if not completed (Manteufel 1938). Copepodite stage 5 is the over-wintering stage, and the females start to spawn in the beginning of the phytoplankton spring bloom (Melle *et al.* 1987). Feeding in the new generation starts at nauplius stage 3.

Size of zooplankton is the result of growth and size at the start of the growth period. Growth is a function of feeding rate, which is a function of several variables; light, temperature, food quality, food size, food abundance, feeding history, and body weight (Huntley 1988). Laboratory and field experiments have proved temperature and quantity and quality of food supply to be the most important factors governing growth and size of copepods. Temperature and food supply are directly related to growth and developmental rate in calanoid copepods. Size at each developmental stage is directly related to food supply, but inversely related to temperature (Deevey 1960, Evans 1981, Klein Breteler & Gonzales 1982, Durbin *et al.* 1983, Klein Breteler *et al.* 1982,1990, Uye 1987).

After the eggs hatch the nauplii of copepods develop through one or two non-feeding stages where developmental rate is a function of temperature. Laboratory rearings of copepods have given rather conflicting results on the influence of temperature and food supply on growth and size of feeding nauplius stages. In several species there have been found no difference in size of nauplius stages reared at different temperatures and/or food concentrations (Klein Breteler & Gonzales 1982, Peterson 1986). In *Calanus sinicus* only the fifth nauplius stage showed a significant relationship with temperature (Uye 1987). In other laboratory and field experiments, however, growth rate is shown to be dependent of temperature and food supply in the naupliar stages as well (Mullin & Brooks 1970, Klein Breteler *et al* 1982, 1990).

The size of a life stage also depends on the size of the preceding stages, ultimately the size of the eggs. It is reasonable to think that the effect of egg size is greatest on the early naupliar stages, when growth governed by external factors still have had little influence on size. Egg size is related to mother size in *Pseudocalanus* (McLaren 1965), however, only between generations or geographical locations.

In the present study typical size distributions of eggs and nauplius stages of the most common copepods of the Barents Sea, are given. The sampled stations are grouped into what is interpreted as ecological units by cluster analysis based on environmental variables. The significance of the clusters is evaluated by a comparison with a subjective classification of the same stations. The relationships between size of eggs and nauplii of *Calanus finmarchicus* and the environment, as well as differences in size between ecological regions defined by the cluster analysis, are explored. Possible maternal effects on size of eggs and subsequent naupliar stages are included in the analyses. Multivariate statistical methods are used to relate size to environmental factors, and to test for size differences between ecological regions.

Material and methods

Field sampling

Eighth cruises, over the years 1986 to 1988, covered a majority of the water masses and phytoplankton bloom situations of the Barents Sea. Two cruises in April 1986 were carried out with two ice going vessels

from the coast guard, the other cruises were limited to open sea. At each station simultaneous samples of eggs and larvae and adult stages of zooplankton, phytoplankton, nutrients, and physical parameters were obtained. During a cruise in June 1988 (M/S "Odin Finder") no samples of chlorophyll and nutrients were taken. The position of the stations are shown in the map of Figure 1.

Eggs and nauplii were sampled with 30 l Niskin water bottles at about 8 depths from the surface to 100 or 150 m. The samples were sieved off on 30 µm (1986) or 90 µm nets. On the cruise with R/V "Endre Dyrøy" eggs and larvae were sampled with a Juday net, 36 cm opening and 90 µm meshes. The net was towed vertically from 150 m (or bottom) to the surface. These samples are assumed to be comparable to the water bottle samples. Whether catch efficiency, as a function of avoidance and clogging, differ between the two gears is not known. However, the net was only used during pre- and early bloom situations, when the abundance of algae is generally low, and clogging of the net probably a minor problem. Copepodites were collected with a pump as described in Melle & Skjoldal (1989), or a WP-2 net, 52 cm opening and 180 µm meshes. The net was towed vertically from 100 m to the surface. Zooplankton was fixed in seawater with 4% formaldehyde.

Sampling procedures for temperature, salinity and chlorophyll are given by Melle & Skjoldal (1989). Nutrients were usually taken from the whole water column from surface to bottom, at intervals of about 10 m down to 50 m, of about 25 m below 50 m, and of 25 or 50 below 100 m.

Laboratory and data analyses

Size measurements were done on formaldehyde fixed animals. Egg size was measured as diameter. Nauplius stages 1 and 2 were measured as total length of the body, while nauplius stages 3 to 6, and copepodites were measured as length of cephalothorax. Eggs and nauplii were measured at 100x magnification, copepodites were measured at 25 or 16x magnification, under a stereo microscope. All eggs and nauplii in the water bottles were measured except on some rare occasions when the total number of one stage exceeded 100 specimens. Then a subsample of about 50 specimens was measured. The measurements of copepodites were usually done on subsamples, and the numbers measured at each station were usually less than 50.

Species of eggs were identified according to size and morphological

characters given in the literature (Sømme 1934, Marshall & Orr 1972, Alshuth 1989), and new information based on the present material. The eggs of *Pseudocalanus sp.* were in most cases rather irregular in shape, probably because they had been packed in egg clusters attached to the females. They were also smaller, <0.15 mm, than the eggs of *Calanus finmarchicus*, 0.14-0.16 mm. The eggs of *C. hyperboreus* were bigger, >0.16 mm, than those of *C, finmarchicus*, and were found to be darker, nearly black after fixation. The eggs of *C. glacialis* were distinguished from the others by an outer, spiny membrane.

The six nauplius stages were easily recognized on morphological characters (Sømme 1943, Ogilvie 1953). Stages 3 to 6 of *Metridia sp.* were identified by the rectangular form of the last segment of the antenna. Stage 6 of *Pseudocalanus sp.* was identified by a lower number of bristles on the antenna (Ogilvie 1953). The other species of various stages had to be identified using size differences between the species (Sømme 1934, Wiborg 1948, Ogilvie 1953). The size measurements of nauplii reported in the literature were sparse and mostly obtained under environmental conditions different from those in the Barents Sea. Therefore, the reported sizes used to distinguish between the species were thoroughly evaluated against the modes in size the present data. The identification of the size modes was always evaluated against the occurrence of species with well defined morphological characters. Eggs or nauplii of a size equal to the size of division, were allocated to the species on either side relative to the number of nauplii in the neighboring size classes. When obviously only one species were abundantly present, and tails of the size distribution stretched across the size of division, a few specimens were included in that species, rather then eliminated from the analyses.

This procedure was followed for each sample (water bottle). The size distributions of each species was averaged over all depths to get the station means. Sampling by vertical net hauls was assumed to represent the same averaging process. Means for geographical areas were also averaged over samples and not the station means.

Statistical methods for identifying normal distributions in a size frequency distribution were tried. For these methods to converge, however, a lot of measurements are needed, and they had to be used on the combined samples at a station. It was observed that the species often had different vertical distributions. To combine the samples before the analyses, therefore reduced the chances of identifying the

species. It was decided to use the more subjective method, working on single samples as described above.

Samples for phytoplankton pigments (chlorophyll) were stored and analyzed as described by Rey & Loeng (1985). Nutrients were usually analyzed onboard using autoanalyser according to the procedures described by Føyn *et al.* (1981). On the cruises with R/V "Endre Dyrøy" the nutrient samples were preserved with chloroform and kept in the dark in the refrigerator until they were analyzed using an autoanalyser onland (Hagebø & Rey 1984).

By a subjective method of classification sampled stations are pooled into groups according to type of water mass and stage of spring bloom (Hassel pro mare, Melle & Skjoldal 1989). The distinction between the water types Coastal water, Atlantic water, Melt water, and Arctic water is based on a judgment of the parameters: temperature, salinity, density, and an index of water column stability (Loeng, in press). The four stages of the spring bloom (pre-bloom, early bloom, bloom, and post-bloom), are characterized by the vertical profiles of chlorophyll and nutrients, and their derived variables (Table 1) (Skjoldal & Rey 1989, Melle & Skjoldal 1989). A cluster analysis was performed on the underived variables, that is; vertical profiles of temperature and salinity (each 5 m), nutrients and chlorophyll content (each 10, 25 or 50 m). If measurements at a depth were missing, they were replaced by linear interpolation.

Principal Component Analysis (PCA) represent the total variation in the data in a reduced number of dimensions, and thereby simplifies the interpretation. The derived environmental variables (see Table 1) were analysed to search for environmental gradients within the investigated area, and to relate environmental variables to the clusters of stations produced by the cluster analysis and the PCA itself. On some of the cruises with "Endre Dyrøy" the measurements of salinity were uncalibrated. Therefore both the cluster analysis and the PCA were performed both with and without salinity. There was no difference between the results. Here the results without salinity are given.

PCA was also used to find relationships in size between the egg and nauplius stages of *Calanus finmarchicus*, and gradients in size among the sampled stations (Jongman *et al.* 1987). All size measurements were introduced as stations averages in the analyses. Redundancy Analysis (RDA) was used to investigate the influence of biological and

physical environmental factors (Table 1) on size of eggs and nauplii, and to test for differences in size patterns between different areas (Jongman *et al.* 1987). RDA was also preferred in tests of the response in single stages to environmental factors. The relationship between size and the environmental factors was assumed to be linear and therefore the linear method RDA was chosen as a proper method. Some of the environmental variables were log-transformed prior to analysis, after a graphical test of normal distribution (Table 1) (Wilkinson 1989).

Table 1. Derived variables used in multivariate analyses. Methods of calculation and variable names. Names of log-transformed variables in brackets.

Variables	Calculations
T5	Temperature at 5m depth
TPYC	Temperature at MAXPDT
T100	Temperature at 100m depth
TEGG	Temperature at depth of maximum concentration of eggs of *C. finmarchicus*.
S5	Salinity at 5m depth
SPYC	Salinity at MAXPDT
S100	Salinity at 100m depth
DSIG (LNDSIG)	Difference between water density at 5m and density below the pycnocline (100m)
MAXPYC	Maximum increase in density over 5m, within the pycnocline.
MAXPDT	Depth of MAXPYC
INTCHL	Integrated concentration of chlorophyll *a* in the upper 100m
CHLMAX (LNCHLM)	Maximum concentration of chlorophyll *a* in the water column
N10	Nitrate concentration at 10m depth
N100	Nitrate concentration at 100m depth
NCONT	Integrated concentration of nitrate in the upper 100m of the water column
NCONSU (LNNCNS)	Difference between pre-bloomm concentration of nitrate above 100m (assumed to equal concentration at 100m) and NICONT
MAXNCL	Maximum increase of nitrate over 10m within the nitracline
NCLDT	Depth of MAXNCL
NORTH	Latitude
EAST	Longitude
ATLANT (LNATLA)	Distance from position of the station to Atlantic water of the Norwegian Sea
DATE	Number of days from 1 January to date of sampling

The calculation of the environmental variable ATLANT (Table 1) needs further description. A transect south of the Bear Island, directed north-south, was assumed to represent the boarder between the Barents Sea and "pure Atlantic water" of the Norwegian Sea. The shortest distances from the sampling stations to the transect were measured "down stream" according to the general circulation pattern of surface currents in the Barents Sea (Midttun & Loeng 1987). The distances were measured

in cm on a map of the stations plotted in UTM-projection (Knutsen & Westgård 1988). The variable was assumed to represent "the influence of Atlantic water".

The multivariate methods used here do not accept missing data. Therefore only stations with a complete set of size of eggs and nauplii of *Calanus finmarchicus* and environmental variables were included in the analyses. This limited the number of stations, from a total of more than 60 to 17. Substitution of missing values was not considered. Other relationships, that for different reasons could not be tested by the multivariate methods, were tested using simple correlation analysis. All correlation analyses were Pearson correlations performed on SYSTAT (Wilkinson, 1989).

The cluster analyses were done using the SYSTAT statistical package (Wilkinson, 1989). Before clustering the environmental variables were standardized to a mean of 0 and a variance of 1 to eliminate the effect of different scales. Ordinary Euclidian distances were used as measures of dissimilarity and the stations were linked using Ward's method (Wilkinson, 1989).

Principal Component Analysis and Redundancy Analysis were performed on CANOCO 3.11 (TerBraak, 1988, 1990). Environmental factors were standardized to a mean of 0 and variance of 1. In the RDA some variables were log-transformed prior to standardization, to meet the requirements of normal distribution (Table 1). The variables were tested for normal-distribution using normal probability plots on SYSTAT. Size of eggs and nauplii were log-transformed as this gave the best correlations with the environmental variables. Size data were also centered to zero mean, but not standardized to variance of 1. These transformations means that ordination was performed on a covariance-matrix between size of the stages (Ter Braak 1988).

Results

The classifications of the investigated area by cluster analysis and the subjective method of classification based on the environmental variables, were quite similar (Figure 2). By both methods the same main groups were identified, but with some discrepancies in the internal grouping of the pre- and early-bloom stations from especially the Atlantic and Coastal areas. Principal Component Analysis (PCA) related

the environmental variables to the clusters and displayed environmental gradients within the sampled stations. To get a simpler plot redundant variables were eliminated before the analysis by a test run of the PCA. The results of the PCA given here is limited to the qualitative presentation in the "covariance bi-plot" in Figure 3. In this plot the angle between the arrows, representing the scores of the response (here environmental) variables approximates the pair-wise correlation coefficient between variables. The direction of the arrow indicates the direction of steepest increase in the variable, and the length of the arrow indicates the rate of change in that direction (Jongman *et al.* 1987). The PCA showed that Atlantic bloom stations, Melt-water bloom and post-bloom stations were characterized by high chlorophyll contents and low temperatures (Figure 3). The Arctic early-bloom stations were characterized by low temperatures and relatively high concentrations of nitrate. Atlantic post-bloom stations showed low nitrate concentrations and relatively high temperatures and water column stability. The pre-bloom stations on the left side of the plot typically showed high concentrations of nitrate and low water column stability. Axis 1 and 2 of the PCA accounted for 41 and 27% of the total variation, respectively. The groups produced by the cluster analysis were adopted for the following statistical analysis.

Egg diameter and carapax lengths of nauplius stages 1 to 6 of *Calanus finmarchicus* , *C. glacialis, C. hyperboreus and Pseudocalanus sp.* may be of general interest, and are reported here. The size measurements are presented as length frequency histograms for all specimens measured, including all stations (Figure 4).

The result of the PCA of the size of eggs and nauplii at 17 of the sampled stations are shown in Figure 5. Axis 1 and 2 of the PCA accounted for 55 and 21% of the total variance, respectively. The sizes of the pre-feeding stages (egg, N1 and N2) were positively pair-wise correlated (Figure 5). N3, the first feeding stage, was positively correlated to the younger stages. The feeding stages N5 and N6 were positively correlated to each other, while N4, in an intermediate position, were correlated both to the younger and older stages. The smallest specimens of eggs and nauplius stages 1,2 and 3 were found in the western areas, mainly pre-bloom areas in Coastal and Atlantic water; that is in the lower right part of the plot. The size of the young stages increased towards east and north, where the more developed stations with respect to the phytoplankton bloom, were found (cf. map of stations; Figure 1). The largest feeding stages were found in the high

chlorophyll content areas; that is on the left side of the plot. These stations were classified as "Atlantic bloom" and "Melt-water post-bloom" areas. The smallest feeding stages were found in low chlorophyll and high temperature areas, on the right side of the plot; pre- and post-bloom waters of Atlantic and Coastal origin. Although some similarity in pattern of stations can be seen between the formation of clusters of stations based on environmental factors (Figure 2) and the PCA bi-plot (Figure 5), more powerful analyses were required to be able to relate biological to environmental factors.

As a first step towards relating the environmental variables to the size of eggs and nauplii, the differences in size between classes obtained by the cluster analysis of environmental variables, were tested. In a Redundancy Analysis (RDA) 4 environmental clusters (which were the maximum number of clusters represented among the 17 stations) were introduced as 4 nominal dummy variables. The four clusters were named ATCOPR: Atlantic and Coastal pre-bloom waters (joined in one group since the cluster analysis was not able to distinguish between them), ATLBLO: Atlantic bloom water, ATLPBL: Atlantic post-bloom water, MELPBL: Melt water post-bloom. A Monte Carlo test, 99 unrestricted permutations (TerBraak 1988, 1990) showed that there was a significant overall difference in size of eggs and nauplii between the clusters, $P< 0.01$. Figure 6 shows the relationship between the clusters and the size of eggs and nauplii. Generally ATCOPR is characterized by small eggs and young nauplii (N1-N3), while MELPBL and ATLBLO is characterized by large N4, N5, and N6.

Redundancy analysis (RDA) was used to explore and quantify the relationships between size of eggs and nauplii and environmental factors. To minimize the problems of redundancy and multicollinearity, the environmental variables to be included in the Redundancy Analysis were first evaluated on the basis of general knowledge of the ecosystem in the Barents Sea. Excess variables that were known to represent the same phenomenon were excluded. The remaining variables were evaluated by computing a correlation matrix (Table 2). The variables showed some degree of pair-wise correlation. Therefore the variables were grouped into sets of inter-correlated variables, and one representative variable was chosen from each set (Table 2). Three sets of significantly correlated variables were formed, in addition to DATE that was not correlated to any other variable. The variables TEGG, LNCHLM, LNATLA, LNDSIG, and DATE were chosen to represent the groups. From the first group both TEGG and LNCHLM was selected since

temperature and food supply are known to be the most important factors determining growth in zooplankton. This, however, introduced two problems in the analysis. First, the possibility of multicollinearity in the RDA. A test run of RDA with the selected variables showed that this was not a problem, the inflation factors were low for all variables (Table 3). Secondly, the fact that TEGG and LNCHLM were correlated limited the possibility of determining the relative importance of the two in governing size of eggs and nauplii.

Figure 7 shows a so called "tri-plot" (joint plot of size of stages, stations and environmental factors) produced by the RDA. Tri-plots of the covariance type are interpreted

Table 2. Correlation matrix of environmental variables, and groups of inter-correlated variables with significant Bonferroni probabilities.

	TEGG	S5	NORTH	LNDSIG	LNCHLM	LNNCNS	LNATLA	DATE
TEGG	1.00							
S5	0.42	1.00						
NORTH	-0.88	-0.51	1.00					
LNDSIG	-0.16	-0.92	0.36	1.00				
LNCHLM	-0.76	-0.08	0.68	-0.13	1.00			
LNNCNS	-0.20	-0.19	0.50	0.33	0.41	1.00		
LNATLA	-0.38	-0.28	0.51	0.40	0.39	0.74	1.00	
DATE	-0.23	0.16	0.05	-0.34	-0.07	-0.51	-0.38	1.00

GROUP 1		GROUP 2		GROUP 3		GROUP 4
	TEGG		LNATLA		LNDSIG	DATE
TEGG	0.00	LNATLA	0.00	LNDSIG	0.00	
LNCHLM	0.02	LNNCNS	0.03	S5	0.00	
NORTH	0.00					

as described earlier for the PCA bi-plots. The only difference is that both response factors (size of eggs and nauplii) and determinant factors (environmental variables) are represented by arrows. The representation of the size of eggs and nauplii in the RDA (Figure 7) are much like the result of the PCA (Figure 5). This indicates that no major environmental factors were overlooked (Jongman *et al.* 1987).

Table 3. Inflation factors of environmental variables and Intraset correlations of environmental variables with axes 1 and 2.

	Infl. factors	Intraset correlations Axis 1	Axis 2
TEGG	4.96	-0.63	0.19
LNDSIG	2.13	0.24	-0.47
LNCHLM	4.54	0.71	0.06
LNATLA	1.69	0.33	-0.77
DATE	2.19	-0.34	0.13

The size of eggs and the young nauplius stages, N1, N2, and N3, showed a positive correlation with LNATLA (distance to Atlantic water masses). The older stages, N4, N5, and N6, showed a positive correlation with LNCHLM (chlorophyll content). TEGG also showed a strong relationship with size, especially stages N4, N5, and N6. As already mentioned, TEGG and LNCHLM were negatively correlated. DATE showed a weak and negative correlation with size, that is; the specimens got smaller during the season. LNDSIG, an index of water column stability, showed a weak and positive correlation to egg size and the nauplius stages N1-N3. LNDSIG was not strongly positively correlated to neither DATE nor LNCHLM. The stations clustered into three groups; two "warm" groups, that each could be characterized as a western early-bloom group and an eastern late-bloom group, and a third "cold" group from the polar front region with rather high chlorophyll content. The tri-plot thus seems to give an ecologically reasonable representation of the data, both with respect to the size of the eggs and the nauplii relative to the environmental variables, and the relationships between the stations.

The features of the tri-plot were statistically tested by a Monte Carlo test, 99 unrestricted permutations (Ter Braak 1988, 1990). Axis one and two of the RDA were both significant, $P<0.01$. The intra-set correlations of environmental variables with the axis (Jongman *et al.* 1987), showed that the first axis mainly represented a gradient in chlorophyll content, LNCHLM. The second axis was interpreted to be a gradient in distance to Atlantic water, LNATLA (Table 3). Intra-set correlations were preferred to canonical correlation coefficients due to problems with the latter when any of the environmental variables are correlated (Jongman *et al.* 1987). Axis1 and 2 accounts for 43 and 16% of the variation in the size of eggs and nauplii, respectively. RDA with forward selection of environmental variables (TerBraak 1988, 1990), showed that LNCHLM

and TEGG were the two variables that explained most of the total variation in size of eggs and nauplii, 31 and 25%, respectively, P< 0.01 (Table 4). Following the procedure of forward selection, the best variable (LNCHLM) was included as covariable in the next run. Since TEGG and LNCHLM were correlated this reduced TEGG to the least fitted variable in the next output (Table 4). The next best fitted variable were LNATLA, 15%, P= 0.04. Non of the other variables were significantly related to the response variables.

The single stages were related to environmental variables by repeated runs of RDA where all but one stage were treated as passive variables (given weight of 0.01), and the major environmental variables were identified by forward selection as described above (Ter Braak 1988, 1990). The size of the eggs and the nauplius stages 1, 2, and 3 were significantly and positively related to the environmental variable LNATLA, P<0.01, P=0.04, P<0.01, and P<0.01 respectively. The size of stages 4 and 6, after the start of feeding at stage 3, were both significantly positively related to LNCHLM, P<0.01. The second best variable was TEGG, and, again, since TEGG and LNCHLM were correlated the effect of the particular variables could not be singled out. Stage 5 was not significantly related to any of the measured environmental variables, but was closest related to TEGG, P=0.11. The direct relationship between size of feeding stages and $\log_e$ maximum chlorophyll content (LNCHLM) can be interpreted as a response to the availability of food.

Table 4. Extra fit = proportion of variation in size of eggs and nauplii explained by an environmental variable, if that was the only one in the analysis.

Run 1		Run 2	
Variable	Extra fit	Variable	Extra fit
LNDSIG	0.08	TEGG	0.05
DATE	0.08	DATE	0.07
LNATLA	0.19	LNDSIG	0.11
TEGG	0.25	LNATLA	0.15
LNCHLM	0.31		

The causal basis of the relationship between LNATLA and the size of the stages egg to N3, may be related to typical properties of the Atlantic water masses like high temperature, and a generally smaller size of zooplankton individuals (see Discussion). Two possible causal

relationships were tested. First, that egg size is inversely related to temperature, and secondly, that small females drift in from the Norwegian Sea and spawn smaller eggs which hatch to smaller nauplii.

The two possible causal relationships could not be analysed by the multivariate methods for different reasons. Temperature is already shown to be significantly correlated to the total size distribution of eggs and nauplii, though most closely to the feeding stages. The lack of significant relationship between the size of eggs and prefeeding nauplius stages and temperature were based on the analysis of only 17 stations, that covered a rather narrow range of temperatures compared to the total material. Therefore were 30 additional stations included in a simple correlation analysis. Females were measured at only 8 of the 17 stations analyzed by multivariate methods. Therefore were female size related to environmental variables or egg size by simple correlation analyses where several additional stations could be included. The correlations involving LNATLA were limited to the stations outside the Norwegian Coastal Current, since a reliable index of influence of Atlantic water is more difficult to obtain within this water mass (cf. definition of LNATLA).

The test of the first possible causal relationship showed that egg size were negatively correlated with temperature (TEGG), $r=-0.565$, $N=47$, $P<0.001$ (Figure 8). Routinely copepodites of *Calanus finmarchicus* and *C. glacialis* are separated using differences in size (e.g. Tande *et al.* 1985). The size distributions of the two species overlap (Jashnov 1972), creating a problem when mean size are to be estimated at stations where both occur. The abundance of *C. glacialis* generally increase towards the polar front, that is; in most areas an increase towards north. A significant relationship between the variable NORTH (latitude) and female size was found, $r=0.41$, $N=51$, $P=0.003$. Because of the problem with *C. glacialis* possibly contributing to the mean size of *C. finmarchicus* it was decided to reduce the size of division from the usual 3.2 mm to 3.0 mm, a size smaller than the smallest expected size of *C. glacialis*. The "mean size" obtained after this was considered as an index of mean size of the pure stock of *C. finmarchicus* females. As expected this new statistic showed a weaker relationship with NORTH, $r=0.30$, $N=51$, $P=0.034$, and was significantly related to LNATLA, $r=0.42$, $N=35$, $P=0.013$. The index of female size was significantly correlated to egg size, $r=0.36$, $N=35$, $P=0.033$ (Figure 9), indicating a possible causality behind the correlation between LNATLA and size of eggs and subsequent pre-feeding nauplius stages. The index of female size also

showed a significant negative correlation with mean temperature between the pycnocline and 100m depth (TPC100), r=-0.421, N=42, P<0.001. This mean temperature was assumed to represent the over-wintering temperature of the females. The female size index was not significantly correlated with TEGG.

Discussion

In studies of reproduction of copepods in boreal and Arctic environments, the timing of the spawning in relation to the phytoplankton spring bloom have been essential (Melle *et al.* 1987). Due to low temperatures and slow development of eggs and nauplii, species identification of these young stages are important for the accuracy of the results. Species identification by size differences seem to be the only practical method for processing a large number of samples. Therefore typical size ranges of the eggs and nauplius stages of the commonest copepods of the Barents Sea (Figure 4), will hopefully be of help in future studies. Size measurements of eggs and nauplii of these species from the Barents Sea are not reported earlier, and due to big variations in size both geographically and between investigations, comparison with investigations from other areas (Sømme 1934, Wiborg 1948, Ogilvie 1953) are difficult.

Numeric classification of the water masses of the Barents Sea (Figure 2) confirmed the traditional subjective classification. The major environmental features of the Barents Sea, as described by Rey and Loeng (1985), Skjoldal and Rey (1989), Loeng (in press) were reproduced by the classification. Figure 3 relates typical values of environmental variables to the classes of stations. Again the fluctuations in the environmental variables between water masses and stages in the phytoplankton bloom development coincide with descriptions given of the Barents Sea (Rey & Loeng 1985, Skjoldal & Rey 1989, Loeng in press).

The classes of stations were assumed to represent regions of different spawning populations and/or different environmental conditions for growth of *Calanus finmarchicus*. By applying RDA on nominal environmental classes an overall difference in size of eggs and nauplii of *C. finmarchicus* between four selected environmental classes was found. This supports the assumption that the classes of stations represent ecological regions. The four classes (Atlantic and Coastal

pre-bloom water from the southwestern part of the Barents Sea, Atlantic post-bloom water from the central and eastern parts, and Melt water post-bloom and Atlantic bloom near the polar front) represents different geographical locations, as well as different biological seasons as characterized by phytoplankton bloom development. Size differences possibly related both to geographical location (water types) and season (stages in bloom development) are found between the classes. Often seasonal differences are related to differences between succeeding generations (Wiborg 1954, Deevey 1960, McLaren 1965). In the Barents Sea *C. finmarchicus* generally have only one generation a year (Tande *et al.* 1985), although in the southwestern parts a second generation seem to start in late July in waters warmer than 6^0C (Manteufel 1938). However, this investigation did not cover those parts at that time. Therefore, in the area and time period covered by this study, the size differences, both geographically and seasonally, were probably related to between water mass differences in the parental populations, and/or growth in different environmental regimes.

The three variables that showed the closest relationship with overall size pattern of eggs and nauplii were food supply (LNCHLM), temperature during growth (TEGG), and influence of the water masses of the Norwegian Sea (LNATLA) (Figure 7). In other investigations food supply and temperature are proved to be the most important environmental factors governing growth (see Introduction), and the influence of Atlantic water from the Norwegian Sea may be a good indicator of the place of origin of the parental population. Thus, these variables seem to represent both spatial and environmental differences in size as discussed above.

That size of the youngest stages, eggs and the nauplius stages 1 to 3, were positively correlated with distance from the Norwegian Sea, strengthened the impression of a causal relationship between the origin of the parental population and size of the next generation. From the general tendency that the specimens of a species get larger towards colder regions (e.g. Wiborg 1954, Grainger 1961), it was assumed that females of *C. finmarchicus* are smaller in the Norwegian Sea than in the Barents Sea. The positive relationship between female size and distance from the Norwegian Sea, that was found here, are interpreted as the effect of gradually mixing of Norwegian Sea water with Barents Sea water, creating a mixed population of *C. finmarchicus* with increasing dominance of the Barents Sea component towards east. The rule of

increased size towards colder regimes is not absolute, however, and towards the northernmost range of a species size may even decrease (e.g. Grainger 1961). In *C. finmarchicus* the size of specimens in the Barents Sea have been found to be both smaller and larger than specimens from the Norwegian Sea (Wiborg 1954, Jashnov 1972). Jashnov (1972) interpreted increased size of *C. finmarchicus* towards colder regions as an increasing tendency of hybridization with *C. glacialis*. Nevertheless, the positive correlations between female size and distance from the Norwegian Sea, and between female size and egg size, may explain the positive correlation between egg size and distance from the Norwegian Sea. Egg size in turn was correlated with the size of N1, and N1 with N2, and N2 with N3.

A strong inverse relationship was found between egg size and temperature (Figure 8). Egg size in *Pseudocalanus* was significantly related to both temperature and females size, but only between generations (McLaren 1965). In this study only one generation was considered, therefore, the negative correlation between egg size and temperature could not be due to differences between generations. A probable explanation to the egg-temperature correlation, is that females spawn bigger eggs in low temperatures. As shown in the results female size was not significantly correlated with temperature near the surface where the eggs were found, but with temperature below the pycnocline. (possibly due to an effect of over-wintering temperature on female size). Therefore, the egg-temperature and egg-female correlations seem to be the results of two independent mechanisms governing egg size, which both, however, are maternal effects: either directly by bigger females spawning bigger eggs, or indirectly by females spawning bigger eggs at low temperatures. Altogether; significant correlations are established between egg size and both female size and temperature within the same generation, and the results of the RDA and the correlation analyses showed that egg size and size of N1-N3 are related to distance from the Norwegian Sea and temperature.

The size of N4 and N6 were positively related to chlorophyll content and negatively related to temperature. Since the two variables were negatively inter-correlated, the separate effect of the two could not be estimated. However, the fact that the effect first appears after the nauplii start feeding indicates that either chlorophyll or temperature (or both) govern growth. It is concluded that chlorophyll and temperature together explain 52 % of the variation in both N4 and N6.

This is the same problem that Corkett & Mclaren (1978) claims hamper the investigations done by Deevey (1960), where temperature and chlorophyll were found to be related to the size of copepodites.

Growth in length of copepods is mainly limited to the molting, except some stretching between segments (Sømme 1934). Therefore, growth in the first feeding stage, N3, could not be measured. Growth in this stage, however, are presumably reflected in the size of stage 4.

The size of N5 was not significantly related to any of the environmental variables included in the analyses. The two closest related variables were temperature and chlorophyll, as in N4 and N6. It is not probable that size of N5 is governed by other variables than N4 and N6. The sizes used to distinguish between the species may have been less correctly chosen for N5 than the other stages, although there was no indication of this during the processing of the data. Probably the lack of significant relationships with stage 5 can be explained by the low number of stations involved in the analysis.

The lack of relationship between distance from the Norwegian Sea and size of N4 indicate a strong and immediate effect of food supply/temperature ruling out the maternal effect. In this investigation the environmental factors seem to govern final size at the end of the nauplius stage. This indicates that the difference in adult size of *C. finmarchicus* between the different areas of the Barents Sea, and perhaps within its range of distribution, may be largely governed by environmental factors and less by maternal effects between the generations.

The size range in N6, by applying an intermediate growth rate as estimated by assuming exponential growth from mean size of N6 to mean size of adult females, could explain the size range observed in the females. This shows that growth differences in the nauplius stage may be important for size differences trough out the life cycle. In other words, the influence of environmental factors on size at the nauplius stage that was found here, may govern body size of the whole population of *C. finmarchicus*, the most important link between primary production and pelagic fish stock of the Barents Sea.

Time was included in the analyses as the variable DATE, number of days since 1 January. In most field investigations of size of copepods several generations a year have been considered, and size have changed from

generation to generation and therefore with time (e.g. Deevey 1960). In this study only one generation was analysed. Far less is known about change in size within a single generation, and a change in size with time is not necessarily to be expected. Any change in size with time was expected to be caused by environmental factors, and Figure 3 shows a weak tendency of increased temperature with time while chlorophyll content decreased. From this a negative correlation between time and the size of the developmental stages arised (Figure 7). The relationship was not significant, however. As described in the Introduction, time is not expected to be correlated with phytoplankton bloom development when stations from different water types of the Barents Sea are included in the analyses. The weak correlation between DATE and LNDSIG and LNCHLM demonstrated this, and a strong relationship between time and size of eggs and nauplii was not expected.

In the analyses a generally low percent of the variation in size was explained by the environmental variables, and there are many possible reasons for this. First, the number of stations included in the analyses were low. In the cold environment of the Barents Sea rate of development in eggs and nauplii is low causing problems with mixing of different cohorts of the new generation. The size of a nauplius stage may be determined by environmental factors, e.g. food supply, several days before capture and be less related to the environmental conditions at the time of sampling. There was no possibility in this data set to relate size to environmental conditions some time before sampling. Concentration of chlorophyll is only an index of food supply and may introduce extra variance in the analyses. At last, the length distributions of the different species may have been confounded by other species, this problem, however, was minimized as well as possible as described in Material and Methods.

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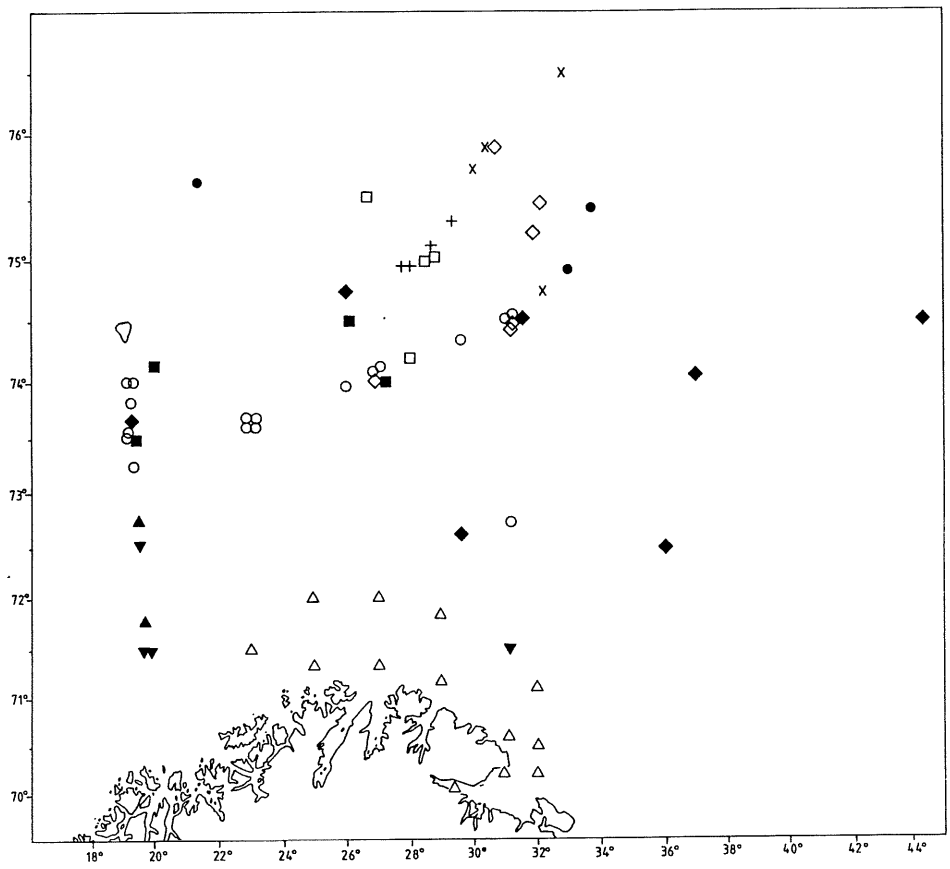

Figure 1. Map showing sampling stations. Symbols: filled circle;Arctic early bloom, empty circle; Atlantic pre-bloom, filled square; Atlantic early bloom, empty square; Atlantic bloom, filled diamond; Atlantic post-bloom, empty diamond; melt-water pre- and early- bloom, + shape; melt-water bloom, X shape; melt water post-bloom, down-triangle; coastal pre-bloom, filled up-triangle; coastal early bloom, empty up-triangle; coastal post bloom.

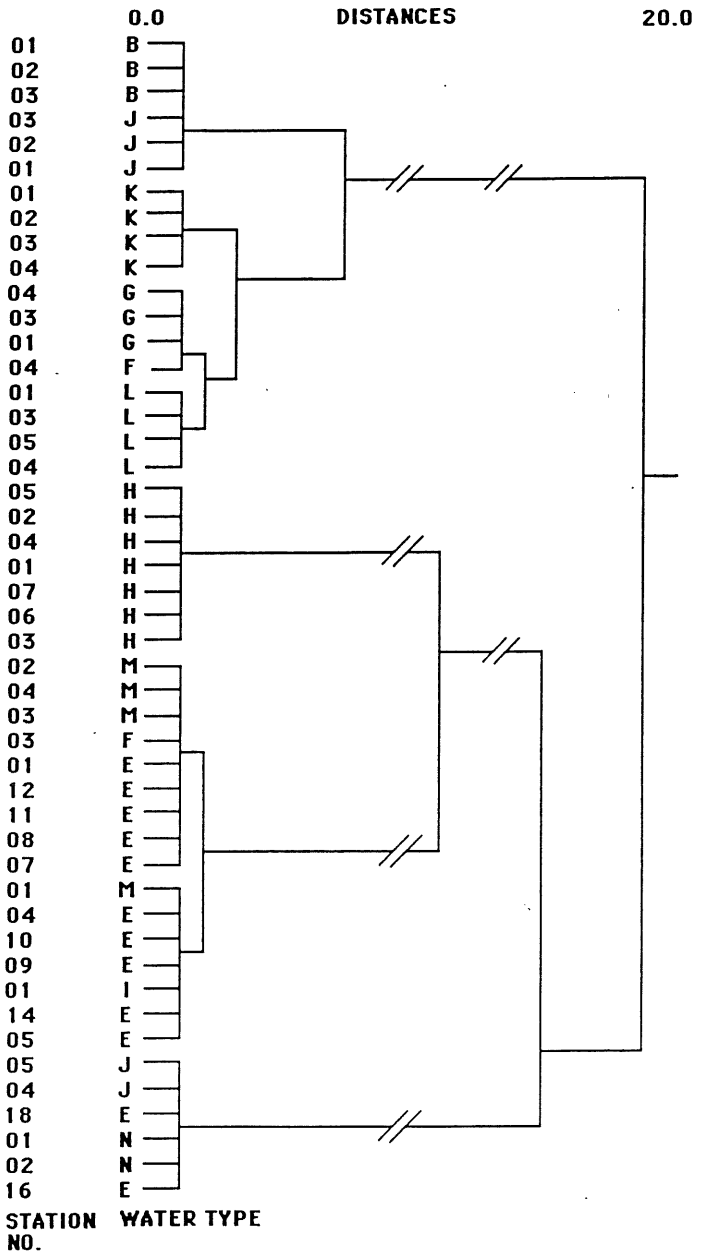

Figure 2. Dendogram of 47 sampling stations based on cluster analysis of environmental variables (see text). **B**; Arctic early bloom, **E**; Atlantic pre-bloom, **F**; Atlantic early bloom, **G**; Atlantic bloom, **H**; Atlantic post-bloom, **I**; Melt water pre-bloom, **J**; Melt water early bloom, **K**; Melt water bloom, **L**; Melt water post-bloom, **M**; Coastal pre-bloom, **N**; Coastal early bloom.

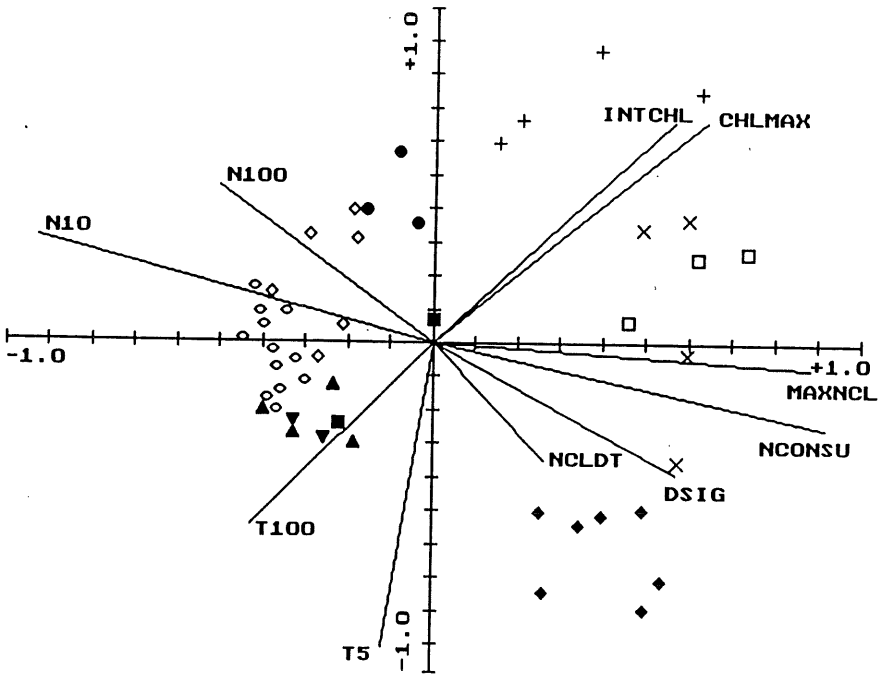

Figure 3. Principal Component Analysis ordination diagram of derived environmental variables (Table 2) at 47 stations. Environmental variables represented by arrows. Groups of stations belonging to the same water types are represented by different symbols (see Figure 1).

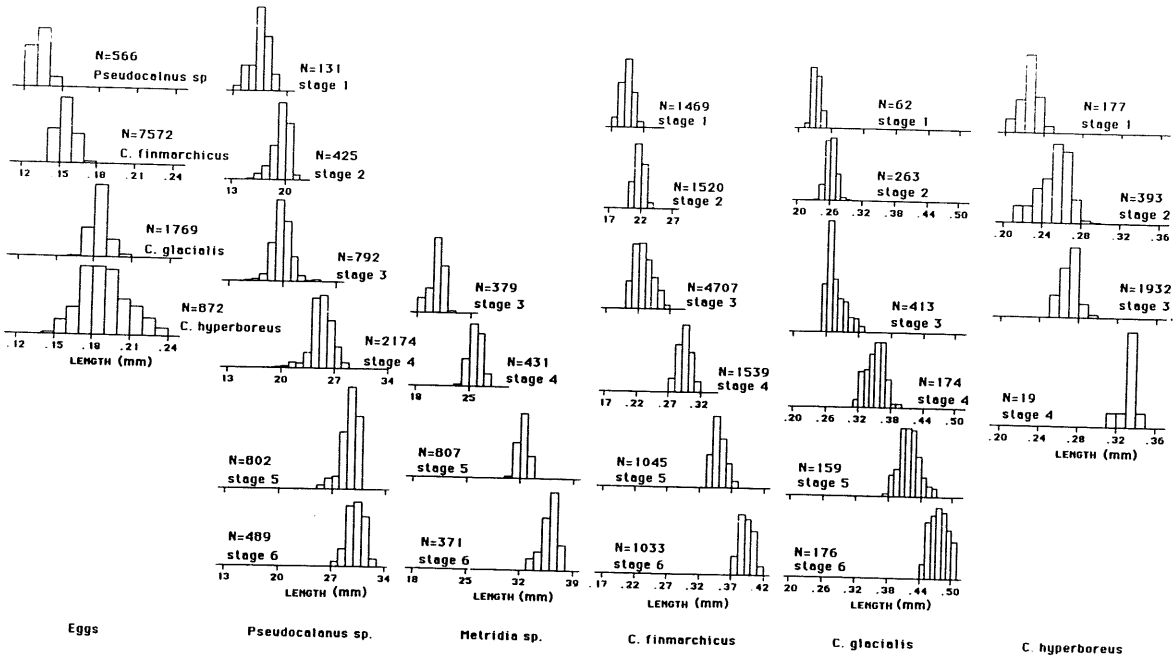

Figure 4. Length frequency distributions of *Calanus finmarchicus, C. glacialis, C. hyperboreus, Pseudocalanus sp.,* and *Metridia sp.*. Measures given are: egg diameter, nauplius stages 1 and 2 total length, stages 3-6 carapax length.

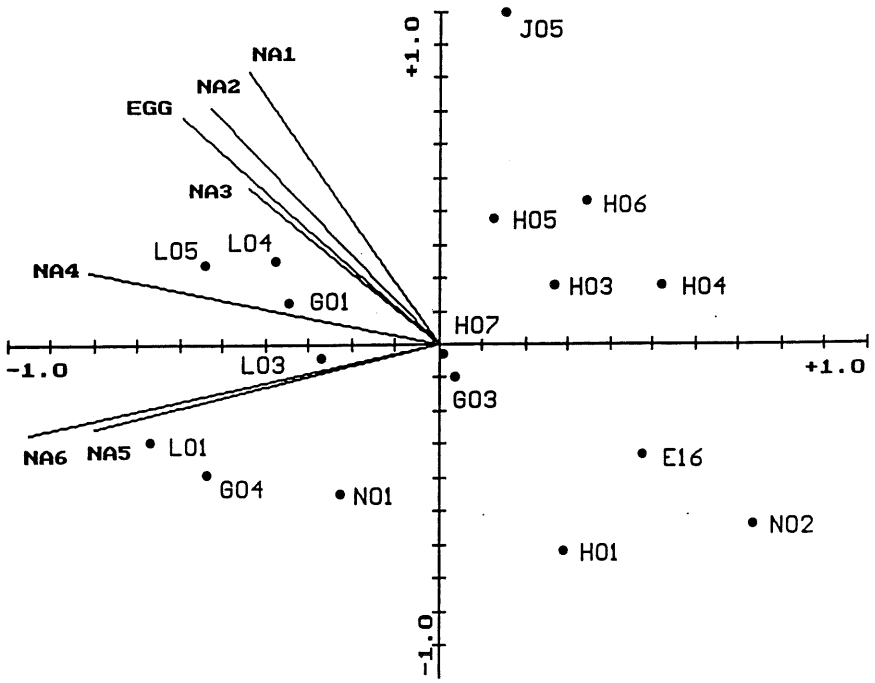

Figure 5. Principal Component Analysis ordination diagram of size of eggs and nauplius stages, 17 stations. Size of stages represented by arrows (EGG, NA1-NA6), stations by dots (station names as in Figure 2).

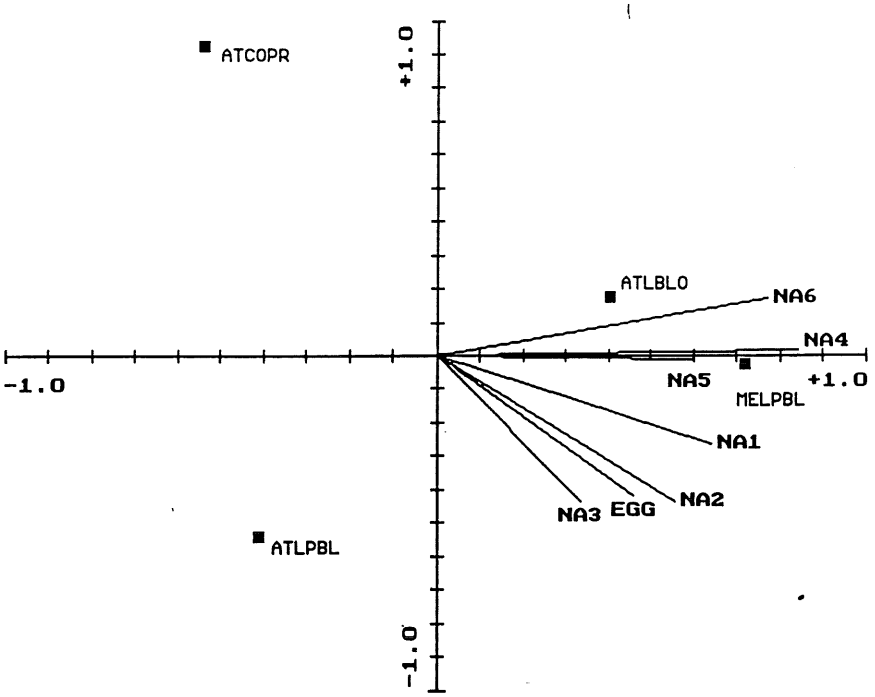

Figure 6. Redundancy analysis ordination diagram of size of eggs and nauplius stages. Groups of stations from cluster analysis represented as 4 nominal dummy environmental variables. Size of stages represented by arrows, see text for explanation of shortening of station groups.

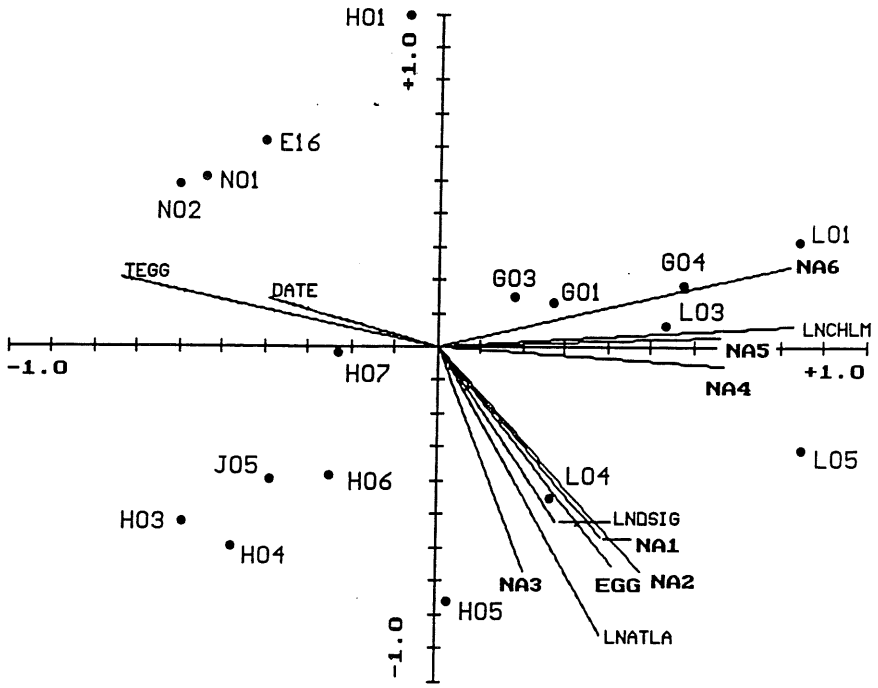

Figure 7. Redundancy analysis ordination diagram of size of eggs and nauplius stages. Size of stages and derived environmental variables (Table 2) represented by arrows, stations by dots. Otherwise as Figure 5.

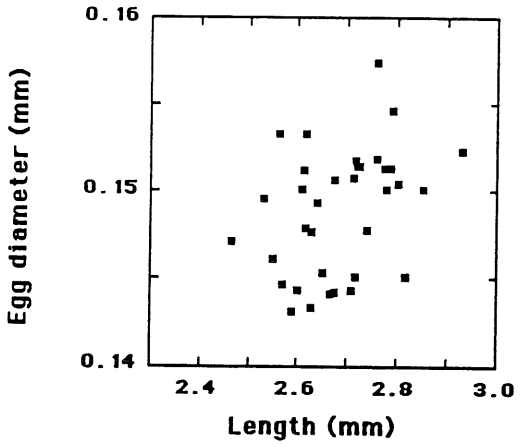

Figure 8. Scatter plot of *Calanus finmarchicus* egg diameter vs. index of female size.

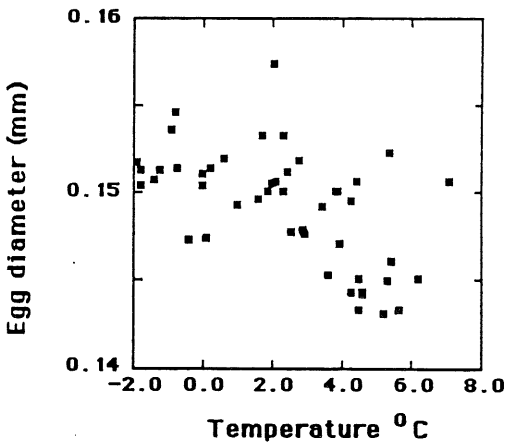

Figure 9. Scatter plot of *Calanus finmarchicus* egg diameter vs. temperature at depth of maximum concentration of eggs (TEGG).