

## Brage IMR – Havforskningsinstituttets institusjonelle arkiv

Dette er forfatters siste versjon av den fagfelleurderte artikkelen, vanligvis omtalt som postprint. I Brage IMR er denne artikkelen ikke publisert med forlagets layout fordi forlaget ikke tillater dette. Du finner lenke til forlagets versjon i Brage-posten. Det anbefales at referanser til artikkelen hentes fra forlagets side.

*Ved lenking til artikkelen skal det lenkes til post i Brage IMR, ikke direkte til pdf-fil.*

## Brage IMR – Institutional repository of the Institute of Marine Research

This is the author's last version of the article after peer review and is not the publisher's version, usually referred to as postprint. You will find a link to the publisher's version in Brage IMR. It is recommended that you obtain the references from the publisher's site.

*Linking to the article should be to the Brage-record, not directly to the pdf-file.*

# Growth of Barents Sea capelin (*Mallotus villosus*) in relation to zooplankton abundance

Harald Gjøsæter, Padmini Dalpadado, and Arne Hassel

Gjøsæter, H., Dalpadado, P., and Hassel, A. 2002. Growth of Barents Sea capelin (*Mallotus villosus*) in relation to zooplankton abundance. – ICES Journal of Marine Science, 59: 000–000.

Because capelin feed on zooplankton, the availability of the latter may be a limiting factor for capelin growth in at least some areas and at certain times. It was therefore hypothesized that a relationship exists between capelin growth and zooplankton biomass either in the same year or in the previous autumn. Capelin growth in a given year was more closely correlated with the estimate of zooplankton abundance in the previous autumn than with that in the present autumn. Growth of the youngest capelin was well correlated with abundance of the smallest zooplankton, whereas growth of older capelin was more closely correlated with abundance of the larger zooplankton forms. Various water masses were defined on the basis of hydrographic conditions, and significant differences in the zooplankton content among the water masses were detected. An inverse relationship between zooplankton abundance and capelin biomass was found, indicating that grazing by capelin has a negative effect on zooplankton abundance.

Keywords: Barents Sea, capelin, growth, zooplankton.

H. Gjøsæter, P. Dalpadado, and A. Hassel: Institute of Marine Research, PO Box 1870, N-5817 Bergen, Norway; tel: +47 55 238500; fax: +47 55 238555; e-mail: [harald@imr.no](mailto:harald@imr.no).

## Introduction

Capelin, *Mallotus villosus* (Müller), the dominant planktivore in the Barents Sea ecosystem, utilizes the zooplankton production in the central and northern areas of the Barents Sea. Copepods, krill, and amphipods are major prey, their relative importance varying with season, year, and capelin size (Lund, 1981; Panasenکو, 1981, 1984; Gjøsæter, 1998). *Calanus finmarchicus* was the main prey of juvenile capelin whereas two species of krill, *Thysanoessa inermis* and *T. raschii*, and the amphipods, *Themisto abyssorum*, *T. compressa*, and *T. libellula*, dominated the diet of adults.

Capelin in the Barents Sea have been studied by Norwegian and Russian biologists since the turn of the last century. Around 1960, the species became the target of an industrial fishery, and the monitoring of stock size, structure, and geographical distribution was intensified. From 1972, annual surveys to monitor stock size acoustically have been carried out (Gjøsæter, 1998; Gjøsæter *et al.*, 1998). These studies include an intensive biological sampling programme, which facilitated studies of the life history of the capelin, in particular studies of growth. Analysis of the data has revealed growth varying considerably among sexes, maturity groups, years, and geographical areas (Gjøsæter, 1999a). Growth is also influenced by ambient temperature (Gjøsæter, 1999b). In the present paper, spatial and temporal variations in growth are compared with variations in zooplankton abundance, to seek possible relationships between these variables.

## Material and methods

The study is based on capelin sampled for biological studies during annual scientific cruises to the Barents Sea in September and October of the years 1972–2000. Sampling methods for capelin are described in detail by Gjøsæter *et al.* (1998). The data were limited to these surveys

because a relatively large number of samples of age-determined fish were available. In addition, they included a synoptic bio-acoustic measurement of total stock size, which allows the samples to be weighted by fish abundance to be as representative as possible of the whole stock (Gjøsæter, 1999c). Additionally, the surveys were conducted just prior to the winter cessation of growth and the corresponding annulus formation in otoliths of capelin, making the data well suited for back-calculation of growth (Gjøsæter, 1999d).

The measurements used here are total length, weight, and age of capelin, and the radius of each growth ring in the otoliths. Two methods were used to describe the growth history of capelin. First, length- and weight-at-age were used to describe changes actually taking place in the distribution of length and weight in the stock. This method does not, however, describe the individual growth of a fish, because maturation is length-dependent and spawning mortality is substantial. To describe growth in length during the last growth season, back-calculated length at the previous winter (deposition of the last winter zone in the otolith) was subtracted from the measured length at sampling in autumn. The back-calculation method, a modified Frazer–Lee equation (Francis, 1990) with a “biological intercept” (Campana, 1990) at 35 mm fish length and 0.08 mm otolith radius as starting point, is fully described by Gjøsæter (1999a).

Sampling of zooplankton on a regular basis began in the Barents Sea during 1979 and, since 1987, zooplankton abundance has been monitored in annual surveys during the period August–October. Plankton samples were obtained using WP2 (Anon., 1968) and MOCNESS (Multiple Opening Closing Net and Environmental Sensing System) plankton nets (Wiebe *et al.*, 1976, 1985). The WP2 was equipped with a single net of mesh size 180  $\mu\text{m}$ . Sampling depths at each station were from the seabed to the surface and from 100 m to the surface. The MOCNESS was equipped with eight nets of mesh size 180  $\mu\text{m}$  (333  $\mu\text{m}$  before 1992). At most stations the nets were towed in oblique hauls from 200 to 175, 175 to 150, 150 to 125, 125 to 100, 100 to 75, 75 to 50, 50 to 25, and 25 m to the surface. The number of nets varied from five to eight according to water depth. The volume of water filtered in each stratum varied from 100 to 600  $\text{m}^3$ . In addition to combined WP2 and MOCNESS sampling stations, the WP2 was regularly used alone.

Zooplankton samples were usually separated into two halves using a Motoda plankton splitter (Motoda, 1959). One half was preserved in 4% formaldehyde and the second was size-sorted through sieves of three mesh sizes: 180, 1000, and 2000  $\mu\text{m}$ . Before 1984, the volume of plankton in each of the three size fractions was estimated and converted to dry weight using conversion factors. From 1984 onwards, the samples were dried at 70°C for 24 h before weighing. Large organisms (e.g. euphausiids, shrimps, fish) were treated separately. In this investigation, the density ( $\text{g m}^{-2}$ ) of the three size fractions and the total density from the bottom to surface from the biomass fraction have been used.

Despite their difference in size and mode of operation, MOCNESS and WP2 have been considered as supplementing each other, both contributing commensurate estimates of plankton abundance (Hassel *et al.*, 1991). A comparison of the performance of the two gears (Gjøsæter *et al.*, 2000) showed that the WP2 was more efficient in catching small zooplankton and that the MOCNESS was better at catching larger forms. However, the overall performance on the plankton composition of the Barents Sea during autumn was not statistically different for the two gears. Consequently, for density calculations, samples from the two gears were combined.

Plankton sampling was initially conducted during summer. In 1987, an extensive zooplankton sampling programme was introduced during the international 0-group survey in August–September (ICES, 1996) and the Norwegian–Russian acoustic survey for pelagic fish in September–October (Gjøsæter *et al.*, 1998). Table 1 lists the number of samples of plankton and capelin.

The smallest size fraction was dominated by small copepods, the median fraction by large copepods and small euphausiids, and the largest by euphausiids and amphipods (Table 2).

A CTD drop sonde was used to obtain salinity and temperature data at all WP2 and MOCNESS stations. Salinity and temperature values at depths of 10, 50, 100, 200, and 500 m were used to classify sampling stations into different water masses. Classification was based on the description of water masses given by Loeng (1991; Table 3). Three main water masses are defined: Coastal, Atlantic, and Arctic. We classify stations that were in the transition zone between Atlantic and Coastal Water masses as mixed Atlantic/Coastal and between Atlantic and Arctic Water masses as mixed Atlantic/Arctic. The mixed Atlantic/Arctic waters are defined in Loeng (1991) as Polar Front Water and Barents Sea Water in the western and eastern Barents Sea respectively. In addition to the main water masses is the locally formed Melt Water, which has similar temperature and salinity characteristics to Coastal Water, but lies north of 74°N and is restricted to the upper 50 m.

Plankton and capelin samples and CTD casts were categorized according to sampling position inside a 2° (longitude) × 1° (latitude) grid, to allow results from the various samples to be compared. In cases where there was more than one sample of each type inside a grid cell, mean values of all variables were calculated. In the comparisons, cells that did not contain all three types of samples were omitted from the analyses. The tables and figures giving information on zooplankton and capelin (Tables 4 and 5, Figure 1) contain individual station data. When comparisons were made between capelin and zooplankton parameters (Table 6), mean values within a grid cell were used.

## Analytical methods

To investigate whether there was any relationship between zooplankton density one year and capelin growth the next, linear regression analyses were undertaken. For these analyses, mean values of zooplankton density in year Y were compared with mean growth in length of capelin during year Y+1. As serial correlation could invalidate regression on these time-series data, regression with correction for autocorrelation (AUTOREG procedure; SAS Institute Inc., 1993) was applied. For comparison, capelin growth data were also regressed against total zooplankton abundance measured after the growth season.

An analysis of variance (GLM procedure; SAS Institute Inc., 1990) was used to analyse differences in capelin growth among the five different water masses. A principal component analysis (PRINCOMP procedure; SAS Institute, 1990) was conducted to investigate the relationship between environmental variables (temperature, salinity), zooplankton density, and capelin growth.

## Results

The variation from year to year is not totally synchronous for the zooplankton size fractions (Figure 1). Among the years 1987–2000, where data on all size fractions exist, the medium and smallest size fractions of zooplankton as well as the total were most abundant in 1994, whereas zooplankton larger than 2000 µm were most abundant in 1989. The years 1990–1991 scored low for all size fractions. Although 1987 was the year with the second greatest abundance of medium-sized plankton, both smaller and larger zooplankton were scarce.

Large zooplankton was found in highest quantities in Arctic Water, which is often rich in amphipods, especially *Themisto libellula* (Table 4). Medium-sized and small zooplankton were dominant in North Atlantic Water, and zooplankton belonging to these size fractions constituted the bulk of the total zooplankton density. Analysis of zooplankton data from individual years and water masses showed that, in 11 of the years and overall, there were significant (ANOVA,  $p < 0.05$ ) differences between mean density in the various water masses. North Atlantic Water was the most plankton-rich water mass. The mixtures of Coastal Water and North Atlantic Water and of Arctic Water and Polar Front Water ranged next with more-or-

less equal quantities of plankton. Plankton density was lowest in the Melt Water. For the period 1984–2000 there is apparently an inverse relationship between plankton density and capelin biomass (Figure 1).

There appears to be a relationship between zooplankton abundance and capelin growth, both at high levels (Figure 2). However, when these variables were compared in a linear correlation analysis (Table 5), the relationship is not so obvious. Mean growth in length during the last growth season shows positive relationships with total zooplankton density for all age-classes. The correlation coefficients are generally low, but they are statistically significant for one-, two-, and four-year-olds. Three-year-old capelin growth rates during the last season do not correlate well with estimated total zooplankton density.

One-year-old length, weight, and growth were all significantly correlated with zooplankton density. For age-classes 3 and 4, none of the first two variables was significantly correlated with plankton density.

All but one of the regressions with AUTOREG between capelin growth and zooplankton density gave positive slopes. When comparing growth in year Y with zooplankton abundance in year Y–1 (Table 6, left panel), the coefficients of determination ( $r^2$ ) varied from 0.03 to 0.66, and the regression coefficients for the two youngest age-classes were significant at the 5% level. However, when comparing growth in year Y with zooplankton abundance in year Y,  $r^2$  ranged from 0.02 to 0.49 and no regressions were significant (Table 6, right panel).

Highly significant differences among growth in length-at-age in the five different water masses were found (Figure 3). With few exceptions, growth was fastest in North Atlantic Water. Normally, capelin growth was slowest in Arctic Water and in Polar Front Water.

A multivariate analysis revealed that various hydrographic variables were highly interrelated as one dimension in each of the first two principal components. Zooplankton dominated the third principal component. However, these principal components explained only a small amount of the total variation in capelin growth. Hence, the use of multivariate analysis did not add much to our understanding of the relationship between environmental variables and capelin growth.

Growth of one- and two-year-old capelin was negatively related with total capelin biomass (Figure 4).

## Discussion

When trying to determine a relationship between plankton density and capelin growth, several questions and problems need to be discussed. First, what do the variables in question – estimated density of zooplankton, and estimated capelin growth in length during the current growth season – represent? Second, under the most likely hypothesis that there is a positive relationship between the quantity of food and the growth rate of capelin, what is the expected relationship between these variables? Estimates of both these variables are based on observations taken simultaneously, near the end of the main feeding season of capelin. Whereas the growth estimates sum up the growth process during months or a whole year, the estimates of plankton density are snapshots of the situation during the survey. Such snapshots represent what is left on the table when the meal is nearly ended. The interesting variable when it comes to plankton abundance, however, is not this snapshot, but the zooplankton abundance during the previous months. Two factors, the initial stock of plankton, and the plankton production during the season, determine that abundance. Both factors are unknown.

The production of zooplankton is partly determined by the quantity of overwintering zooplankton from the previous year, which makes up the parent generation. Variations in zooplankton stocks may also be due to varying degrees of advective transport into the Barents Sea (Skjoldal and Rey, 1989). Giske *et al.* (1998) suggested that advective transport of *Calanus* into the Barents Sea had a major effect on abundance. Little is known of the magnitude and

timing of outflow and inflow, but large interannual variation is likely (Midttun and Loeng, 1987).

The observations referred to in the present paper may, therefore, be interpreted in different ways. Is a large zooplankton density at the end of the capelin growth season a sign of great abundance and availability during the season, and should it be hypothesized to relate to rapid capelin growth? Several studies have indicated that grazing by capelin has a significant impact on zooplankton abundance (Skjoldal and Rey, 1989; Hassel *et al.*, 1991). An inverse relationship between the annual abundance of zooplankton and capelin abundance is supported by the current analysis (Figure 1). If this is an important mechanism on a large scale, one would expect to find relative scarcity of zooplankton at the end of the capelin growth season in areas where capelin were feeding, and to find no relationship between zooplankton abundance and the capelin growth attained.

Various hypotheses may, therefore, be suggested:

- 0-hypothesis – there is no linear relationship among measured zooplankton abundance in autumn and capelin growth during the growth season.
- Alternative hypothesis  $A_1$  – zooplankton abundance measured in autumn reflects the production in this water mass during the year and, consequently, a positive relationship is found between zooplankton abundance in year Y and capelin growth in year Y.
- Alternative hypothesis  $A_2$  – zooplankton abundance measured in autumn reflects the zooplankton production during the succeeding year from great abundance of overwintering survivors and, accordingly, a positive relationship exists between zooplankton abundance in year Y and capelin growth in year Y+1.

Hypotheses  $A_1$  and  $A_2$  are not mutually exclusive because the quantity of zooplankton measured in autumn may well contain information both about what has happened in the previous season and, at the same time, about what will happen during the next.

The present results indicate positive relationships between zooplankton abundance and capelin growth in most analyses. Some of the relationships are highly significant (Table 5) when the analysis is made on spatially distributed data. It is, however, difficult to explain why four-year-olds show significant relationships between growth and plankton abundance while three-year-olds do not. The possibility of spurious correlations, e.g. through hidden variables such as temperature, which is probably positively related to both zooplankton abundance and capelin growth, cannot be ruled out. Consequently, due caution should be exercised when interpreting these analyses of capelin growth and zooplankton abundance.

When the analyses were performed on spatially aggregated data (Table 6), no linear relationships were evident. In those cases, however, there was much better correspondence between the present year's capelin growth and zooplankton density measured in autumn the previous year. This analysis was not feasible using the spatially resolved data, only on averaged values per year.

The alternative hypothesis ( $A_2$ ) that autumn zooplankton abundance is an indicator of abundance the next year, and that zooplankton abundance in autumn is related to capelin growth the next year, is supported by our results. It is difficult to compare the results of the analysis reported in Table 5 and the analysis on mean values by year (Table 6), and to evaluate hypothesis  $A_1$  (measured zooplankton abundance in autumn reflects the production in this water mass during the year). Considering the problems and possible pitfalls in interpreting the results of the analysis shown in Table 5, and the supporting evidence for hypothesis  $A_2$  in the regression analyses shown in Table 6, hypothesis  $A_2$  is favourable. A relationship between zooplankton abundance measured in autumn and capelin growth the next year could prove useful for prognostic purposes. However, as stated previously, hypothesis  $A_2$  does not rule out hypothesis  $A_1$ ; they could both be true.

In general, the correlation coefficients (Table 5) and the coefficients of determination (Table 6) decrease with increasing age of capelin. This is probably partly caused by the length range of

older age-classes being greater than that among younger age-classes. As growth tends to level off with increasing length, an increased range of lengths will entail increased growth variation attributable to a length effect among individuals in older age-classes, and consequently an increased variation not accounted for by the correlation or regression model. Another possible explanation is that, for maturing fish, the partitioning of surplus energy to growth and reproduction may be different from that among immature fish (Shin and Rochet, 1998). As most older capelin sampled during autumn are maturing, gonad growth and maturation would likely have higher priority than length increase in older fish.

Although there is considerable variation, there seems to be a decreasing trend in growth with increasing size of the capelin stock; such effects are frequently observed among populations where food is a limiting resource. When the number of consumers increases, there is less food for each. However, in the Barents Sea ecosystem, a large capelin stock has the potential of grazing down not only the zooplankton production but, at least locally, the standing stock of zooplankton as well (Skjoldal and Rey, 1989; Hassel *et al.*, 1991). If this mechanism is important on a larger scale, it would amplify the effect of capelin stock size on zooplankton production and on capelin growth. Density-dependent growth variation was thoroughly discussed in Gjørseter (1999a), where it was concluded that density-dependent effects, or rather, stock abundance effects, were evident for all age-classes during the study period 1973–1998.

As mentioned previously, there are differences in zooplankton abundance among the water masses during late autumn. If we assume that this difference in zooplankton content reflects the production of zooplankton in that water mass during the growth season, we may hypothesize that there is a positive relationship between capelin growth during the last season and the water mass type where it is sampled at the end of the season.

## Summary and conclusions

This study has confirmed some of the earlier findings of capelin–zooplankton interactions. Several investigations previously carried out in the Barents Sea show an inverse relationship between zooplankton density or abundance and capelin biomass (Skjoldal and Rey, 1989; Dalpadado and Skjoldal, 1996; Dalpadado *et al.*, 2001). Our study verifies earlier findings, with a longer data time-series. The observation of a relative scarcity of zooplankton when the capelin stock is large is not surprising because capelin are the most important predators of zooplankton in the Barents Sea ecosystem and probably exploit most of the secondary production during their feeding season. During periods when the capelin stock was very low, the predation pressure on zooplankton was minimal, so allowing zooplankton individuals to grow. This again probably led to faster individual growth rates and rapid recovery of the capelin stock.

In the current study, we found clear evidence that growth of capelin is related to zooplankton abundance. The growth of the youngest capelin was significantly correlated with the abundance of the smallest zooplankton, and the growth of older capelin was significantly correlated with the abundance of larger zooplankton forms, >2000  $\mu\text{m}$ . Unfortunately, most capelin and zooplankton data in the Barents Sea are from the months August–October. This leaves us with little option but to study the growth and feeding pattern of capelin in seasons other than autumn. However, relating the growth of capelin in a given year to zooplankton density during that year and the previous year, it was clear that the growth of capelin in one year was best correlated with zooplankton abundance estimated the previous autumn.

Future investigations on capelin growth should focus on collecting capelin and zooplankton samples throughout the year. Quantitative feeding studies of capelin are quite limited. A joint stomach database of capelin involving international partners including Russia, Iceland, and other countries is recommended. It will provide an opportunity not only to study diet and

feeding habits of capelin on a wider context, but also to investigate predator–prey interactions in detail. We should also aim to collect absolute abundance and production data for zooplankton as well as to estimate the consumption of zooplankton by capelin in the Barents Sea.

## Acknowledgements

We thank our colleagues and the crew members who helped us in collecting and analysing zooplankton and capelin samples, as well as the two anonymous referees whose comments added to the quality of the paper. This work was partly supported by the EU project (FAIR: PL 95 817) – Barents Sea Impact Study (BASIS).

## References

- Anon. 1968. Smaller mesozooplankton. Report of Working Party No. 2. *In* Zooplankton sampling (Monographs on oceanographic methodology, 2), pp. 153–159. Ed. by D. J. Tranter. UNESCO, Paris. 174 pp.
- Campana, S. 1990. How reliable are growth back-calculations based on otoliths? *Canadian Journal of Fisheries and Aquatic Sciences*, 47: 2219–2227.
- Dalpadado, P., and Skjoldal, H. R. 1996. Abundance, maturity and growth of krill species *Thysanoessa inermis* and *T. longicaudata* in the Barents Sea. *Marine Ecology Progress Series*, 144: 175–183.
- Dalpadado, P., Borkner N., Bogstad B., and Mehl, S 2001. Distribution of *Themisto* (Amphipoda) spp. in the Barents Sea and predator-prey interactions. *ICES Journal of Marine Science*, 56: 876–895
- Francis, R. I. C. C. 1990. Back-calculation of fish length: a critical review. *Journal of Fish Biology*, 36: 883–902.
- Giske, J., Skjoldal, H. R., and Slagstad, D. 1998. Ecological modelling for fisheries. *In* Models for Multispecies Management, pp 11–68. Ed. by T. Rødseth. Physica Verlag, Heidelberg.
- Gjøsæter, H. 1998. The population biology and exploitation of capelin (*Mallotus villosus*) in the Barents Sea. *Sarsia*, 83: 453–513.
- Gjøsæter, H. 1999a. Growth of the Barents Sea capelin (*Mallotus villosus* Müller). 1. Individual growth in relation to size, structure and spatial distribution of the stock. *In* Studies on the Barents Sea capelin (*Mallotus villosus* Müller), with emphasis on growth, pp. 65–102. Ph.D. thesis, University of Bergen, Norway.
- Gjøsæter, H. 1999b. Growth of the Barents Sea capelin (*Mallotus villosus* Müller). 2. Distribution and individual growth in relation to temperature. *In* Studies on the Barents Sea capelin (*Mallotus villosus* Müller), with emphasis on growth, pp. 105–136. Ph.D. thesis, University of Bergen, Norway.
- Gjøsæter, H. 1999c. A combined method for detailed acoustic stock size estimation and statistical weighting of capelin samples. *In* Studies on the Barents Sea capelin (*Mallotus villosus* Müller), with emphasis on growth, pp. 49–64. Ph.D. thesis, University of Bergen, Norway.
- Gjøsæter, H. 1999d. An evaluation of the IMR sampling of Barents Sea capelin (*Mallotus villosus* Müller). *In* Studies on the Barents Sea capelin (*Mallotus villosus* Müller), with emphasis on growth, pp. 31–46. Ph.D. thesis, University of Bergen, Norway.
- Gjøsæter, H., Dalpadado, P., Hassel, A., and Skjoldal, H. R. 2000. A comparison of performance of WP2 and MOCNESS. *Journal of Plankton Research*, 22: 1901–1908.
- Gjøsæter, H., Dommasnes, A., and Røttingen, B. 1998. The Barents Sea capelin stock 1972–1997. A synthesis of results from acoustic surveys. *Sarsia*, 83: 497–510.

- Hassel, A., Skjoldal, H. R., Gjøsæter, H., Loeng, H., and Omli, L. 1991. Impact of grazing from capelin (*Mallotus villosus*) on zooplankton: a case study in the northern Barents Sea in August 1985. *Polar Research*, 10: 371–388.
- ICES. 1996. Preliminary report of the International 0-group Fish Survey in the Barents Sea and adjacent waters in August–September 1996. ICES CM 1996/G:31. 37 pp.
- Loeng, H. 1991. Features of the physical oceanographic conditions of the Barents Sea. *Polar Research*, 10: 5–18.
- Lund, A. 1981. Ernæring hos lodde, *Mallotus villosus villosus* Müller, i Barentshavet. (Food and feeding of capelin in the Barents Sea). Cand. real. [in full please] thesis, Institute of Fisheries Biology, University of Bergen, Norway. 128 pp. (in Norwegian).
- Midttun, L., and Loeng, H. 1987. Climatic variations in the Barents Sea. *In* Effect of Oceanographic Conditions on Distribution and Population Dynamics of Commercial Fish Stocks in the Barents Sea. Proceedings of the 3<sup>rd</sup> Soviet-Norwegian symposium, Murmansk, May 1986, pp. 13–27. Ed. by H. Loeng. Institute of Marine Research, Bergen, Norway.
- Motoda, S. 1959. Devices of simple plankton apparatus. *Memoirs of the Faculty of Fisheries, Hokkaido University*, 7: 73–94.
- Panasenko, L. D. 1981. Diurnal rhythms and rations of capelin feeding in the Barents Sea. ICES CM 1981/H:26. 14 pp.
- Panasenko, L. D. 1984. Feeding of the Barents Sea capelin. ICES CM 1984/H:6. 16 pp.
- SAS Institute Inc. 1990. SAS/STAT User's guide, Version 6, 4. Edition, Vol. 2. Cary, North Carolina, SAS Institute Inc. 846 pp.
- SAS Institute Inc. 1993. SAS/ETS User's guide, Version 6, 2. Edition, Cary, North Carolina, SAS Institute Inc. 1022 pp.
- Shin, Y-J., and Rochet, M-J. 1998. A model for the phenotypic plasticity of North Sea herring growth in relation to trophic conditions. *Aquatic Living Resources*, 11: 315–324.
- Skjoldal, H. R., and Rey, F. 1989. Pelagic production and variability of the Barents Sea ecosystem. *In* Biomass Yields and Geography of Large Marine Ecosystems, pp. 241–286. Ed. by K. Sherman and L. M. Alexander. American Association for the Advancement of Science. Selected Symposia Series, 111.
- Wiebe, P. H., Burt, K. H., Boyd, S. H., and Morton, A. W. 1976. A multiple opening/closing net and environmental sensing system for sampling zooplankton. *Journal of Marine Research*, 34: 313–326.
- Wiebe, P. H., Morton, A. W., Bradley, A. M., Backus, R. H., Craddock, J. E., Barber, V., Cowles, T. J., and Flier, G. R. 1985. New developments in the MOCNESS, an apparatus for sampling zooplankton and micronekton. *Marine Biology*, 87: 313–323.

## Figure legends

- Figure 1. Time-series of zooplankton density and total biomass of capelin during autumn. The data from 1981 and 1984 are based on comparatively few stations. In 1985 and 1986 the data were size-sorted into two groups only: smaller and larger than 1000  $\mu\text{m}$ .
- Figure 2. Mean growth in length (cm) of capelin during the last growth season compared with density of plankton in three size fractions. Fractions are as keyed in Figure 1. Capelin ages are: 1, diamonds; 2, squares; 3, stars; 4, circles.
- Figure 3. Mean growth in length of capelin during the last growth season sampled in the five different water masses defined in Table 3. Capelin ages are: 1, diamonds; 2, squares; 3, stars; 4, circles.
- Figure 4. Growth (length increment during the last growth season) for one- (triangles) and two-year-old (squares) capelin compared with the total biomass of the capelin stock.

Table 1. Number of plankton and capelin samples taken during autumn of the years 1981–2000. For capelin, the number of fish from which biological measurements were taken is also given.

Year	Plankton net samples			
	MOCNESS	WP2	Number of capelin samples	Number of capelin measured
1981	–	36	74	6537
1982	–	–	72	3361
1983	–	–	94	7510
1984	–	64	66	6005
1985	–	129	72	6743
1986	–	42	44	2496
1987	29	18	32	1954
1988	13	52	43	3303
1989	15	84	28	1584
1990	28	107	64	2692
1991	30	137	108	6728
1992	28	125	81	5007
1993	31	115	47	3032
1994	33	148	37	1737
1995	47	130	29	1775
1996	57	117	36	1714
1997	49	162	63	3510
1998	45	210	76	5706
1999	42	184	83	6233
2000	58	147	95	7271

Table 2. Main composition of the various size fractions of zooplankton. The various groups are sorted by importance.

180–1000 $\mu\text{m}$	>1000–2000 $\mu\text{m}$	>2000 $\mu\text{m}$
Copepods	Copepods	Krill
Small copepods and stages I–III	<i>C. finmarchicus</i> stages III–VI	<i>T. inermis</i>
<i>Oithonia</i> spp.	<i>Metridia</i> spp.	<i>M. norvegica</i>
<i>Oncaea</i> spp.	Most copepods	<i>T. longicaudata</i>
<i>Metridia</i> spp.	Krill	Amphipods
<i>Microcalanus</i> spp.	Furcilia and calytopis stages	<i>T. abyssorum</i>
<i>Pseudocalanus</i> spp.	Arrow-worms	<i>T. compressa</i>
Nauplii and eggs	Appendicularians	<i>T. libellula</i>
Gastropods		Jellyfish
Juvenile <i>Limacina</i> spp.		<i>Aglantha</i> spp.
Krill		Arrow-worms
Nauplii and eggs		<i>Sagitta</i> spp.
Echinoderms and polychaetes		Copepods
Larval forms		<i>C. hyperboreus</i> stage VI
Appendicularians		<i>Euchaeta</i> spp. stages V–VI
<i>Fritillaria</i> spp.		Gastropods
Barnacles		<i>Limacina helicina</i>
Nauplius and cypris stages		<i>Clione limacina</i>

Table 3. Water masses in the Barents Sea (after Loeng, 1991).

Water masses	Characteristics	
	Temperature ( $^{\circ}\text{C}$ )	Salinity
Main water masses		
Coastal Water (CW)	>2.0	<34.7
North Atlantic Water (NAW)	>3.0	>35.0
Arctic Water (AW)	<0.0	34.3–34.8
Locally formed water masses		
Melt Water (MW)	>0.0	<34.2
Barents Sea Water (BSW)	–1.5–2.0	34.7–35.0
Polar Front Water (PFW)	–0.5–2.0	34.8–35.0
Mixed Atlantic/Coastal (CW–NAW)*	>3.0	34.7–35.0
Mixed Atlantic/Arctic (NAW–AW)*	0.0–2.0	34.3–34.7

\* Defined in the present study

Table 4. Average zooplankton dry weight density ( $\text{g m}^{-2}$ ) in the three size fractions and the total sample during autumn in different water masses (abbreviations and characteristics are listed in Table 3). n depicts the number of stations and s.d. the standard deviation.

Water mass	180 – 1000 $\mu\text{m}$			1000 – 2000 $\mu\text{m}$			> 2000 $\mu\text{m}$			Total		
	n	Mean	s.d.	n	Mean	s.d.	n	Mean	s.d.	n	Mean	s.d.
AW	363	1.91	1.29	353	4.03	4.13	285	2.28	2.52	402	7.38	5.90
CW	126	2.25	2.56	126	1.93	2.15	113	0.67	1.27	132	4.58	4.53
CW–NAW	190	2.59	2.73	188	3.74	3.38	175	1.46	1.87	195	7.52	5.85
MW	42	1.24	0.76	43	1.10	1.53	39	0.77	0.66	50	3.01	2.24
NAW	721	3.26	3.80	721	4.44	4.99	700	1.74	1.89	737	9.18	8.27
PFW	850	2.54	2.09	839	3.39	3.47	733	1.57	1.93	910	6.86	5.78

Table 5. Correlation coefficients between various capelin variables (MLGT, mean length; MWGT, mean weight; MGLS, mean growth of last season) and the size-fractionated zooplankton density. \* denotes significance at a level of 5%, \*\* significance at a level of 1%, and n the number of stations.

Capelin age	n	Variable	180–1000 $\mu\text{m}$	>1000–2000 $\mu\text{m}$	>2000 $\mu\text{m}$	Total
1 year	283	MLGT	0.175**	0.128*	0.055	0.152**
		MWGT	0.215**	0.152*	0.078	0.189**
		MGLS	0.219*	0.149*	-0.025	0.160**
2 year	305	MLGT	0.027	0.020	0.019	0.023
		MWGT	0.004	0.015	0.013	0.007
		MGLS	0.193**	0.151**	0.032	0.171**
3 year	198	MLGT	-0.055	-0.028	-0.019	-0.053
		MWGT	-0.084	-0.044	-0.004	-0.071
		MGLS	0.030	0.078	0.154*	0.089
4 year	54	MLGT	0.359**	-0.006	-0.105	-0.200
		MWGT	0.319*	-0.032	-0.101	-0.198
		MGLS	0.207	0.399**	0.442**	0.481**

Table 6. Time-series regression (regression with correction for autocorrelation) between annual mean capelin growth in length, and annual mean zooplankton density. Capelin growth in length = a + b (total zooplankton abundance).

Age	Capelin growth in year Y vs zooplankton density in year Y-1				Capelin growth in year Y vs zooplankton density in year Y			
	a	b	r <sup>2</sup>	p	a	b	r <sup>2</sup>	p
1	3.374	0.156	0.659	<0.001	3.634	0.107	0.372	0.058
2	2.664	0.143	0.425	0.014	3.082	0.076	0.176	0.302
3	2.373	-0.017	0.033	0.580	2.155	0.014	0.022	0.685
4	1.513	0.023	0.377	0.334	1.438	0.031	0.485	0.116







