

Regional and interannual variations in biomass and productivity of the marine copepod, *Calanus finmarchicus*, in subarctic environments

Calanus
Modelling
Biomass
Productivity
High-latitudes

Calanus
Modélisation
Biomasse
Productivité
Hautes latitudes

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Received 2/08/91, in revised form 18/03/92, accepted 2/04/92.

ABSTRACT

A model for estimating the productivity of *Calanus finmarchicus* in subarctic waters is developed based on data on individual growth, developmental rates, feeding, vertical behaviour and population parameters obtained from the same region. In fjords and coastal waters of Northern Norway and in the Barents Sea *C. finmarchicus* is considered to produce one generation every year. Population data obtained monthly from November 1976 to December 1977 in Balsfjorden, Northern Norway, show that *C. finmarchicus* reproduces during March and April, and has a quantitatively important growth and production period in May and June. A physiological model is developed to simulate the dynamics of population development and productivity from March to July, and details on individual production, energy expenditure and assimilation rates are compared with data from *C. pacificus*. Based on the abundance of the obtained populations, production is scaled for the following regions and time periods: 15 gC m⁻² in Atlantic waters in the Barents Sea in 1982 (scenario I), 3.1 gC m⁻² in Balsfjorden in 1977 (scenario II), and 0.1, 5.4 and 20.2 gC m⁻² in 1986 in Balsfjorden, Malangen and Grøtsund, respectively (scenario III). The results are discussed in relation to latitudinal and regional differences in productivity.

Oceanologica Acta, 1992. 15, 3, 309-321.

RÉSUMÉ

Études des variations régionales et inter-annuelles de la biomasse et de la productivité du copépode marin *Calanus finmarchicus* en environnement subarctique

Un modèle d'estimation de la production de *Calanus finmarchicus* en eaux subarctiques est développé. Ce modèle se fonde sur des données d'accroissement individuel, de taux de développement, d'alimentation, de comportement vertical et des paramètres de population obtenus dans la même région. Dans les fjords et eaux côtières du nord de la Norvège ainsi que dans la Mer de Barents, *C. finmarchicus* est supposé se reproduire d'une génération chaque année. Les données de population obtenues tous les mois, de novembre 1976 à décembre 1977, dans le Balsfjorden (nord de la Norvège), montrent que *C. finmarchicus* se reproduit de mars à avril, et connaît un accroissement et une production quantitativement importants entre mai et juin. Le modèle physiologique est documenté, et des

détails sur la production individuelle, la dépense d'énergie et les taux d'assimilation sont comparés aux données relatives à *C. pacificus*. Le modèle est conçu pour simuler la productivité et le développement de la population d'un point de vue dynamique entre mars et juin. Du fait de l'abondante population obtenue, la production s'étalonne sur les régions et périodes suivantes : 15 gCm⁻² dans les eaux atlantiques et en Mer de Barents en 1982 (scénario I), 3,1 gCm⁻² dans le Balsfjorden en 1977 (scénario II), 0,1 ; 5,4 et 20,2 gCm⁻² en 1986, respectivement dans le Balsfjorden, le Malangen et à Grøtsund (scénario III). Les résultats sont discutés en relation avec les différences de productivité régionales et de latitude.

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INTRODUCTION

Ecological studies of zooplankton have often been conducted in order to obtain quantitative information on economically important species. High latitude environments are characterized by few dominant species (Krebs, 1985) and in the pelagic marine copepod community, *Calanus finmarchicus* is considered a key species in the transformation of energy from primary producers to planktivorous fish (Tande *et al.*, 1985). Most of the considerable information on this species refers to temperate waters, but is nevertheless considered relevant from a quantitative point of view for higher latitudes. During the past decade *C. finmarchicus* has been studied in fjords in Northern Norway and in adjacent oceanic waters, both under field and experimental conditions (*see* Tande, *in press*, with references). The ultimate objective of this research has been to estimate the productivity of species in these waters.

Of the several methods available for estimating secondary production of aquatic invertebrates at the species level (*see* Winberg, 1971), all are subject to potential error because natural populations seldom conform with restrictions and assumptions implicit in any particular method (*see* Omori and Ikeda, 1984). This is to be expected in populations with complicated life histories and complex growth patterns (Waters, 1969). However, even for populations with simple and clear life histories, no two methods applied to the same data appear to give the same result (Waters and Crawford, 1973; Cushman *et al.*, 1978).

Among copepods, the cohort method, where information on weight increments and population densities is essential, is widely accepted, especially where the population consists of well distinguished age classes. If the life cycles of the species overlap and recruitment is continuous, so that it is difficult to separate cohorts of individuals, then various indirect methods based on population data, developmental and egg production rates are applied (*see* Corkett and McLaren, 1978). The so-called physiological method, which is based on the principle of energy balance, calculates instantaneous productivity in copepods from the difference between anabolism and catabolism (*see* Conover, 1978). However, as the predictive value of laboratory-derived feeding models (Huntley, 1988) is limited, calculations of the anabolic component based on available

laboratory data give only crude estimates of the actual growth rates in the field.

Model principles, combining information from the different methods outlined above, have been proposed in order to estimate productivity among lower trophic animals (*i. e.* Steele, 1974; Steele and Frost, 1977). Recently, a model to estimate productivity in the Arctic copepod *Calanus glacialis* was presented (Slagstad and Tande, 1990). A description of how this species functions, in quantitative terms, in the Arctic environment is based on available information of life history, behaviour, growth and developmental rates, fecundity, feeding and vertical behaviour.

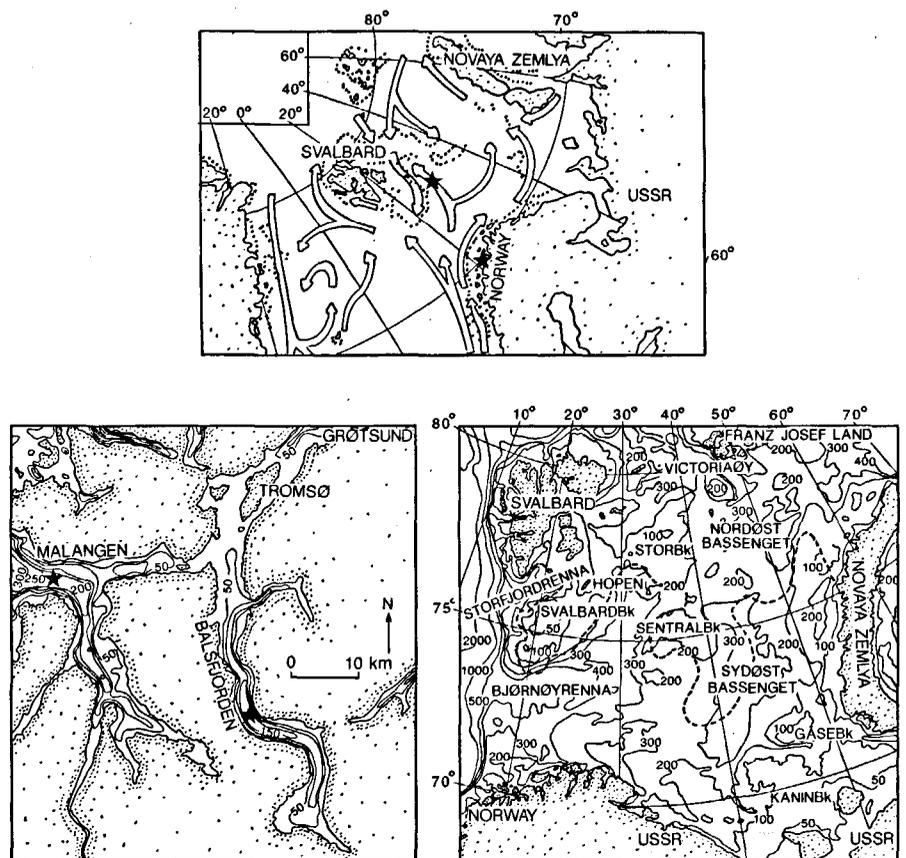
In the present paper a model for estimating productivity of *Calanus finmarchicus* in subarctic waters is presented. The model contains basically the same components as described for *C. glacialis* in Slagstad and Tande (1990), but has been changed according to data for *C. finmarchicus* on individual growth, developmental rates, feeding, vertical behaviour and population parameters. The changes are detailed later in the paper. In the fjords and coastal waters of Northern Norway and in the Barents Sea *C. finmarchicus* is considered to produce one generation per year (*see* Tande, 1982; Tande *et al.*, 1985). Population data obtained monthly from November 1976 to December 1977 in Balsfjorden, Northern Norway, shows that *C. finmarchicus* reproduces during March and April, and has a quantitatively important growth and production period in May and June. Thus the model is designed to simulate the dynamics in population development and productivity from March to July. Based on the abundance of the populations, productivity is scaled for the following regions and time periods: Atlantic waters in the Barents Sea in 1982 (scenario I); Balsfjorden in 1977 (scenario II); and Balsfjorden, Malangen and Grøtsund in 1986 (scenario III). The results are discussed in relation to latitudinal and regional differences in productivity.

BACKGROUND AND METHODS

The present quantitative model has been built on data which mainly stem from various studies conducted in the fjords in North Norway and in the Barents Sea (Fig. 1). The information concerning phytoplankton in the Barents Sea in 1982 is obtained from Rey *et al.* (1987) and Loeng (1989). For the

Figure 1

Map showing the Barents Sea and fjord areas around Tromsø, Northern Norway.



present purpose the phytoplankton data from Balsfjorden is considered representative for North Norwegian fjords and has been described in detail for the years 1976, 1977 and 1978 in Eilertsen *et al.* (1981 *a*) and Eilertsen and Taasen (1984). Information on the phytoplankton with regard to composition, abundance, and vertical distribution in Balsfjorden, Malangen, and Grøtsund during May and June 1986 has been published in Tande (1988 *a*).

Dry weight of the copepodite stages I-IV, was measured on the population in the Barents Sea, in the beginning of June 1987, in the region to the south east of Bear Island, from 72 to 74°N. Groups of 50, 30 and 20 individuals of CI, CII and CIII were sorted into beakers, concentrated on plankton gauze, and rinsed by adding a droplet of distilled water, which was immediately removed by placing the gauze on blotting paper. The animals were then transferred under a binocular microscope to small plates of aluminium foil and dried in a desiccator for minimum two days before being weighed. Dry weight measurements were performed on a Cahn microforce balance with an accuracy of 0.1 µg. For copepodite stages IV, V, and adult female the dry weights in the model are based on data on the population in Balsfjorden in 1976 and 1977 (Tande, 1982), and on the population in Atlantic waters of the Barents Sea during May and June in 1987 (*see* Tab. 1). The methods adopted for sampling, storing, and weighing the individual specimens, and for measuring the C/N-ratio are described in Tande (1982).

The developmental rates of the various copepodite stages of *Calanus finmarchicus* have been measured at 3° and 6°C at superabundant food concentrations in the laboratory in 1980 and 1981 (Tande, 1988 *b*). Based on the data obtai-

ned, a linear relationship between developmental time (days) and temperature was constructed in the temperature range of 3 to 7°C. These data have been combined with stage-specific dry weights to construct a functional relationship between weight and development stage (*see* section on the physiological model, below).

Data on population abundance of *Calanus finmarchicus* in the Barents Sea during the summer period in 1982, and details about the sampling methods are given in Skjoldal *et al.* (1987). The population data presented in scenario II were obtained in Balsfjorden from November 1976 to December 1977. The zooplankton population was sampled by use of double oblique hauls of the entire water column

Table 1

Calanus finmarchicus. The areas and time periods of investigations and references from where some of the background information have been obtained for the simulations of the scenarios presented in the paper.

Scenario	Time	Area	Source
I Barents Sea	1982	76°N 30°E	Rey <i>et al.</i> (1987) Skjoldal <i>et al.</i> , (1987) Loeng (1989) Unstad and Tande (in press)
II Balsfjorden	1977	69° 23'N; 19° 05' E	Eilertsen <i>et al.</i> (1981) Hopkins and Tande (1981)
III Balsfjorden	1986		
Malangen	1986	69° 30'N; 18° 21'E	Eilertsen and Taasen (1984)
Grøtsund	1986	69° 47'N; 19° 20'E	Tande (1988 <i>a</i>)

with a double sided Bongo net (200 μm mesh), as described in Tande (1982). Population data adopted in scenario III stem from a field study in spring and early summer 1986, in Grøtsund, Malangen, and Balsfjorden (see Tande, 1988 a). The recruitment generation in 1986 was collected during May and June using a plankton net (180 μm mesh) mounted on a plankton pump system. Separate zooplankton samples were taken at every 15 m from the surface to the bottom (200 m depth). The sampling period was set to 5 mn, which was the equivalent of filtering ca. 30 m^3 of water. The water flow was measured at each sampling level by a TSK flow meter, which was monitored at the outlet of the pump. Further details of the system are given in Tande (1988 a). During 1988 the spawning populations of *C. finmarchicus* in the three localities were collected by vertical hauls from bottom to surface using a WP-2 (180 μm mesh). In the laboratory, each zooplankton sample was split a number of times using either a piston pipette or a Lea Wiborg splitter (Wiborg, 1951). The plankton samples from Balsfjorden in 1977 were subsampled with a piston pipette so that more than 1/10 of the total sample was counted. The subsampling procedure for the zooplankton samples from May and June 1986 in the three fjords in Northern Norway was designed so that the variance due to subsampling was kept within 20 % of the real sample size.

MODEL FORMULATION

The plankton model presented contains submodels for zooplankton, phytoplankton, nutrients, and a 1-dimensional (1-D) model of vertical physical transport and mixing. The model illustrates the basic structure which has recently been described for *Calanus glacialis* in Arctic waters of the Barents Sea (Slagstad and Tande, 1990).

Physical environment

There are three main water masses in the Barents Sea which are related to different current systems. The Arctic water which occupies the northern part is characterized by temperatures below -1°C . The Atlantic water which enters the Barents Sea between Bear Island and Norway initially has a temperature of more than 4°C , which gradually decreases towards the east. Coastal water has almost the same temperature as Atlantic water, but the salinity is lower (Loeng, 1989). Large variations of temperature in Atlantic waters have been observed, which indicates variability in the inflow and/or cooling of these water masses (Loeng, in press). The temperature and salinity data for 1982 from the simulation area (72°N , 30°E) in the Barents Sea are used as input values in the simulation run.

The physical environment in the fjords around Tromsø is best described in Balsfjorden (Eilertsen *et al.*, 1981 b), although Malangen is more closely connected to the coastal current by the absence of a definite sill, and Grøtsund is best considered as an enlarged basin, coupled to more oceanic waters through Ullsfjorden to the north and Kvalsund in the west. For the present purpose, the physical

environment in Balsfjorden is considered as representative of the whole area. The general topography, seasonal variation in temperature, salinity and stability are described in Eilertsen *et al.* (1981 b). The fjord has from one to several basins with a maximum depth of ca. 200 m. The temperature varies from ca. 1° to 7°C and the salinity ranges from ca. 32.80 to 34.00 during most of the year. The development of a halocline, due to freshwater run-off from melting snow on land, is distinct from late May onwards. Nutrients such as nitrate and phosphate decrease from the high winter values of 5 and 6 $\mu\text{g-at l}^{-1}$ to the minimum levels of 1.2 and 0.5 respectively, at the end of April.

Vertical transport and mixing

If we assume that the horizontal gradients of the biological and physical variables are small, the important physical mechanisms for primary production are vertical turbulent mixing, and vertical transport. This is described by a 1-D model of the water column,

$$\frac{\partial \theta}{\partial t} + w \frac{\partial \theta}{\partial z} - \frac{\partial}{\partial z} (Dz \frac{\partial \theta}{\partial z}) = f_{\text{biol}} \quad (1)$$

where $\theta(t, z)$ is the concentration of a constituent (phytoplankton, nutrients) or temperature which is distributed in the water column, w is vertical velocity (usually sinking velocity), Dz is the vertical turbulence mixing coefficient and f_{biol} is a function that determines the generation of a constituent, usually as a consequence of biological activity.

This model contains one parameter that is determined by the hydrodynamics alone (Dz), and one that is derived from biological and hydrodynamics together (w). In this paper the vertical velocity of phytoplankton is taken to be a function of the ambient concentration of limiting nutrient (see also Slagstad, 1982, and Jamart *et al.*, 1977). By definition, the concentration of a constituent is in the middle of a layer, whereas vertical turbulent mixing is at the borders of the layers. The thickness of the layers (Δz) is 5 m. There is not sufficient hydrographical data from the Barents Sea to specify the variation in time and space of Dz for a specific year. However, the overall picture of vertical mixing of Atlantic water during spring is known through numerous spring and summer cruises during Pro Mare (see for instance Skjoldal and Rey, 1989).

The only available time series data of the hydrographical conditions in the Barents Sea are to be found in the surface temperature maps obtained by satellite through the Norwegian Meteorological Institute. When running the model we have assumed that the depth of the mixed layer is 75 m until a pronounced increase in surface temperature occurs. When this takes place we assume that a thermocline is formed and the depth of the mixed layer is reduced to 30 m. When using this data, the date of thermocline formation varies from year to year (from the second half of May to the second half of June). The numerical value of Dz is taken to equal to $150 \text{ cm}^2 \text{ s}^{-1}$ in the mixed layer and $0.1 \text{ cm}^2 \text{ s}^{-1}$ in the thermocline. The measured surface temperatures are allowed to mix downwards into the water column, thus creating a vertical distribution of temperature.

Irradiance

The seasonal variation in light climate in Northern Norway and in the Barents Sea is presented and discussed in relation to primary productivity in Eilertsen and Taasen (1984). In the present model irradiance is calculated with reference to the theoretical height of the sun. Measurements of irradiance from the Bear Island obtained through the Norwegian Meteorological Institute (MI) allow us to assume an average loss of 40 % through the atmosphere due to clouds. The Balsfjorden area is generally less clouded and we assume a 30 % loss through the atmosphere. Although the atmospheric light is considered to be similar in the whole region, the attenuation of light in the water column is quite different. In the Barents Sea, the attenuation coefficient for pure sea water is assumed equal to 0.04 m^{-1} (Morel, 1988; F. Rey, pers. comm.), whereas in Balsfjorden this coefficient is about 0.10 m^{-1} (Eilertsen, 1979).

The biological environment

The 1-D model (equation 1) which simulates the primary production produces a vertical, dynamic distribution of phytoplankton. Net change of phytoplankton is calculated on the basis of irradiance, temperature, concentration of nitrate and ammonium, respiration, sinking and grazing. A detailed description of the model and parameter values used for simulation in this region of the Barents Sea can be found in Rey *et al.* (1987), and Slagstad and Støle-Hansen (in press). The depth in this area is 250 m. The spring phytoplankton bloom is caused by diatoms (mainly *Chaetoceros socialis* and the haptophycean *Phaeocystis pouchetii*). The decline of nutrients during spring indicates that of the two, *P. pouchetii* tends to occur with the culmination period when silicate levels are low. Exceptions to this pattern, where *P. pouchetii* prevails during the entire bloom period, have also been found (Loeng, 1989). In the phytoplankton model, vertical stability is considered important for the development of the spring phytoplankton bloom. The timing of the bloom in Atlantic waters of the Barents Sea is defined to coincide with the formation of a thermocline. This means that the culmination of the spring bloom is coupled to the annual variation in the thermocline development in the Barents Sea.

In fjord areas around Tromsø, Northern Norway, the diatoms *Chaetoceros socialis*, *Nitzschia grunowii*, and the haptophycean *Phaeocystis pouchetii* are the three most important phytoplankters during the spring bloom (see Tande, in press with references). There was a relatively short autumn bloom (August-September) of *P. pouchetii*, coccolithophorids, and diatom nanoplankters. The winter season (November-February) was characterized by virtually negligible phytoplankton populations. Primary production in Balsfjorden during 1977 increased from *ca.* $6 \text{ mg C m}^{-2} \text{ day}^{-1}$ in the middle of February to a maximum of $650 \text{ mg C m}^{-2} \text{ day}^{-1}$ in the third week of April. The annual primary production is estimated to be *ca.* 110 gC m^{-2} . During the period of culmination of the bloom in May the production rate decreased to *ca.* 20 % of its maximum, at peak

production in April. However, in fjord areas in Northern Norway, the spring bloom starts in March and continues during April, prior to the formation of a thermocline (Eilertsen and Taasen, 1984).

Simulating the primary production in fjords

The development of vertical stability is quite different in fjords than in the oceanic parts of the Barents Sea. Based on the data presented in Eilertsen (1979) we assume the depth variation of the vertical eddy diffusion coefficient, D_z , is as follows: the water column is well mixed all the way to the bottom during the winter. From March 1 to April 20 there is a linear decrease in the depth of the mixed layer, from 50 to 5 m. The numerical value of D_z is taken to equal $5 \text{ cm}^2 \text{ s}^{-1}$ in the mixed layer, $0.1 \text{ cm}^2 \text{ s}^{-1}$ in the pycnocline and $0.5 \text{ cm}^2 \text{ s}^{-1}$ below the pycnocline. The temperature in the water column was measured monthly during the simulation period in 1986 by a Neil Brown CTD.

The copepod model

The model is designed to mirror the population dynamics of *Calanus finmarchicus* which is seen in Balsfjorden from November 1976 to December 1977 (Fig. 2). Here the sexual differentiation and ovary maturation takes place in January and February (Tande and Hopkins, 1981; Tande, 1982). This is accompanied by a decrease in the size of the population of copepodite stage V and adults in March and April. The recruiting generation enters the population as copepodite stage I at the end of April, and around 20 June the population consists of approximately 20 and 80 % of copepodite stages IV and V, respectively. Thus the intensive growth and production period of *C. finmarchicus* in Balsfjorden and adjacent waters takes place in the second part of May and in June. This pattern is also considered

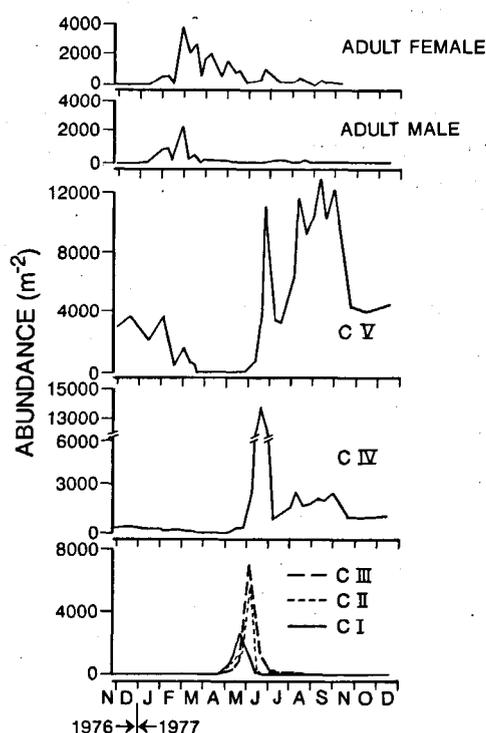


Figure 2
Calanus finmarchicus. Population abundance and seasonal progression of instars from November 1976 to December 1977 in Balsfjorden, Northern Norway. See text for further details.

representative for coastal waters and fjords in Northern Norway and in the Atlantic part of the Barents Sea. The main structure and the changes which have been made, from the model for *C. glacialis* (Slagstad and Tande, 1990) are as follows:

The physiological model

The physiological sub-model of an individual copepod is based on the principle of energy balance. The model contains two energy state variables (satiation and body weight). The total individual weight determines the potential capacity to feed, grow, and reproduce. The actual rates of growth and reproduction will depend on food availability. The level of satiation is a state variable which determines activities which can be related to hunger. These activities are ingestion, reproduction, growth and vertical migration behaviour. The level of satiation is associated with an energy storage which is about 5 % of the total weight of an animal. If ingestion exceeds the energy demand of the animal, the level of satiation will increase. A feedback mechanism will then reduce the filtering rate and thus adjust the ingestion to match the energy demands.

Ingestion

The maximum filtering rate for an animal, FR_m depends on its weight and the temperature given by the following equation:

$$FR_m = FR_o W^{0.75} \exp(0.17T) \quad (2)$$

where FR_o is the maximum filtering rate at 0°C of an individual of unit weight (1 μgC), T is temperature, and w is weight. The actual filtering rate depends on the satiation level which again depends on the energy demands and the concentration of phytoplankton.

Grazing of copepodite stage I to V *Calanus finmarchicus* on the diatoms *Thalassiosira nordenskiöldii* (ca. 20 μm ESD), *Porosira glacialis* (40 μm ESD) and two size categories (30-100 μm and > 100 μm ESD) of the gelatinous algae *Phaeocystis pouchetii* have been measured under laboratory conditions (Hansen *et al.*, 1990). In unialgal situations, diatoms were more readily consumed by copepodite stages I to III than the larger colonies of *P. pouchetii*. Given a proper prey size *C. finmarchicus* grazed both on diatoms and on colonies of gelatinous algae at equal rates. The data indicated that the ingestion rate was directly proportional to the ambient food concentration below 10 μg chlorophyll l^{-1} . The weight specific filtering rate describes the obtained grazing rates for copepodite stages I to

V with a weight exponent equal to 0.75, and the parameter FR_o equals 0.1 $\text{ml h}^{-1} \mu\text{gC}^{-1}$ (see also Conover and Huntley, 1980; Slagstad and Tande, 1990).

Assimilation and respiration

On the basis of data from copepodite stage V *Calanus hyperboreus*, the assimilation efficiency for *C. finmarchicus* has been set 80 % (see Slagstad and Tande, 1985; but see also Slagstad and Tande, 1981). Respiration in the present model has been separated into standard metabolism and energy cost of feeding and digestion (see Slagstad, 1981). These sub-processes have been summed so as to be in accordance with the respiration rates given for stage V and adult females of *C. finmarchicus* during the summer in the Barents Sea (Ikeda and Skjoldal, 1989). In the present model weight specific carbon consumption (R_w), is negatively related to weight (see Vidal, 1980 c), and calculated according to the equation:

$$R_w = R_{wo} w^{0.81} e^{0.07T} \quad (3)$$

where R_{wo} is the standard metabolic rate of an animal of unit weight ($\mu\text{gC h}^{-1}$) and w is weight (μgC).

Development, individual growth and production

The time spent in the naupliar stages depends on the temperature. Although possible food limitations are included in the model, there is always a surplus of food for the nauplii during the simulation run described in this paper. The development rate from egg to copepodite stage I is assumed to be proportional to $\exp(0.14T)$, where T is temperature.

Growth in copepods is a continuous process lacking immediate stage increments. In the present model the five copepodite developmental stages are given a continuous "age" scale called level of development, which is related to the weight of copepodite stages (see also Slagstad and Tande, 1990). The level of development ranges from 1 to 7 covering 29 grids in the model, where copepodite stages I to V occupies a time period equal to ca. 70 % of the total period (Tab. 2). Based on the obtained mean dry weight and carbon content, a "continuous" weight-developmental relationship is established for *C. finmarchicus*. The centre of the part of the continuous line representing each of the various copepodite stages corresponds to the mean dry weight of the specified copepodite stage.

In the present model the sensitivity of growth to food availability in *Calanus finmarchicus* demonstrates that the critical food concentration (*i. e.* 90 % of maximum growth) is obtained at ca. 75 and 125 $\mu\text{g C l}^{-1}$ in CI and CIV, respecti-

Table 2

Calanus finmarchicus. Relationship between copepodite stage, level of development, and dry weight used in the growth model.

Experimental stage	CI		CII		CIII		CIV		CV		CVI																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Grid	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Dry weight (μg)	1.0	1.12	1.4	1.7	2.2	2.7	3.3	4.1	5.1	6.4	7.9	9.9	12.3	15.3	19.0	23.6	29.3	36.5	45.3	56.4	70.1	87	108	134	167	208	258	321	400

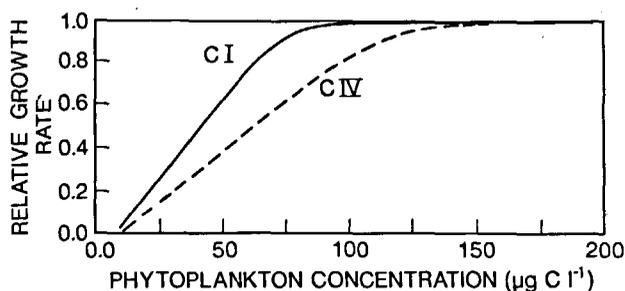


Figure 3

Calanus finmarchicus. Relative growth rate as a function of food concentrations for copepodite stages I and IV at a temperature of 3°C.

vely (Fig. 3). For copepodite stage IV *C. pacificus* and *C. finmarchicus* dry weight ranges between 45 and 62 µg and 45 and 87 µg, respectively, (Vidal, 1980 a: Fig. 1, Tab. 2 of this paper). The parameter P_c in the growth model for copepodite stage IV *C. pacificus* was inversely related to temperature, decreasing from 229 to 103 µg in the temperature range of 15.5° to 8.0°C. The above estimated parameter for copepodite stage IV is obtained in the present model in the scenario from the Barents Sea in 1982 with a dynamic temperature regime, where the sea surface temperature increased from 4° to 6°C during a two month period from the end of April. Growth sensitivity to food availability found for *C. finmarchicus* in the model tends to be in the same range as that found for *C. pacificus* in the lower normal temperature range for the latter species (Vidal, 1980 a).

The weight-specific rate of individual production of *Calanus finmarchicus* is defined as increase of body carbon. Production rates (defined as % body C day⁻¹) computed for the copepodite growth period at selected values of body weight, various food concentrations, and three different temperatures, decrease with increasing levels of development (Fig. 4). The relationship between the rate of total metabolic expenditure (defined as the energy loss through total respiration) and body size was allometric, and increased with food concentration. The rate of assimilation can be defined as the difference between the rates of ingestion and egestion. The latter rates was calculated as 80 % of ingestion (see above).

Simulation at 2, 5 and 8°C shows that the physiological model of *Calanus finmarchicus* mirrors the general weight-specific rates of individual production, metabolic expenditure and assimilation, which has been obtained in laboratory growth experiments at 8, 12 and 15.5°C with *C. pacificus* (Vidal, 1980 b). However, there are differences as to the manner in which individual production is related to temperature, body size and food concentrations between the two models. The overall individual productivity of *C. finmarchicus* amounts to half the productivity of *C. pacificus*. This is also reflected in the differences in stage durations found between these two species (see Vidal, 1980 b). The effect of size on individual production is more pronounced in *C. finmarchicus*, especially at the lower temperatures. At the highest individual weights a tem-

perature increase favours an increased individual production of *C. finmarchicus*, more so at lower food concentrations, while the opposite is true for *C. pacificus*.

The relationships presented in this model are to a large extent governed by the ingestion model, where the functional relationship between the maximum filtering rate, FR_m , and food concentration is determined by the weight exponent (w) and FR_0 . Temperature affects the growth rate with a factor which is proportional to the exponent (0.11T), where T is the temperature. This implies that the present individual production model is driven by the physiological submodels, and is considered to give a realistic overall picture of how individual production of *C. finmarchicus* is affected by environmental factors.

Reproduction

The rate of egg production is assumed to be a function of the satiation levels (Slagstad, 1981), which means that reproduction will be closely related to food consumption. A total spawning period of two months (from March 15 to May 15) is found in fjords around Tromsø, Northern Norway (Marshall and Orr, 1955; Diel and Tande, in press). The mean clutch size increased from ca. 20 eggs female⁻¹ in March, reached a maximum of 70 eggs

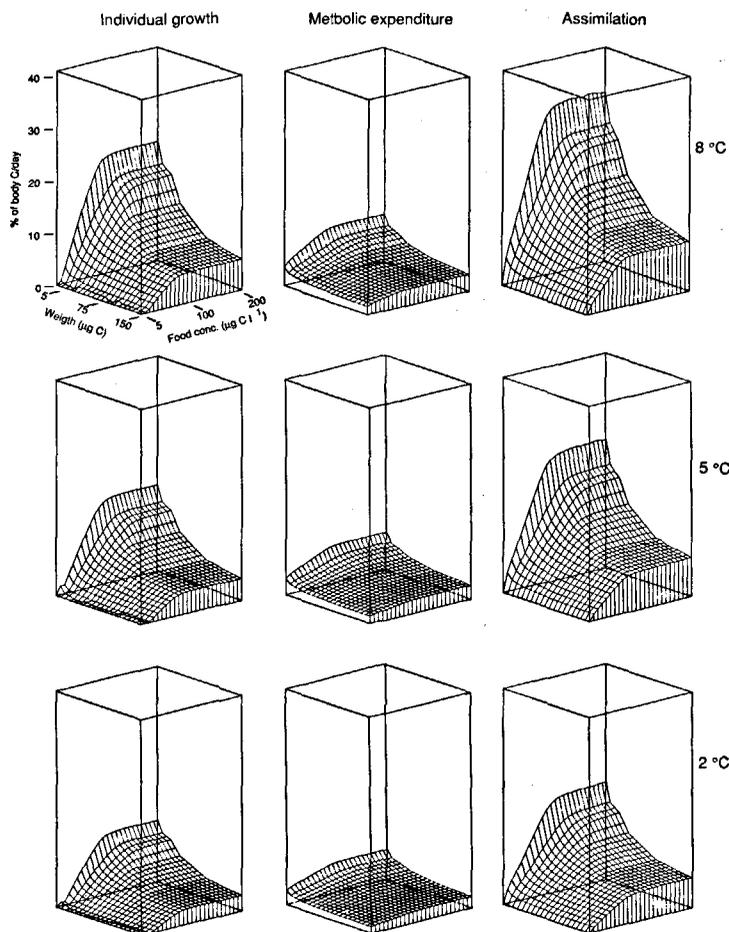


Figure 4

Calanus finmarchicus. Rate of individual production, metabolic expenditure and assimilation, as a function of body size and food concentration at three different temperatures.

around April 15, and decreased to *ca.* 20 eggs female⁻¹ at the end of June (Diel and Tande, in press). It has been found that the total spawning period in fjords around Tromsø lasts for a period of two months during which an average individual *Calanus finmarchicus* would produce approximately 600 eggs. The model is devised to mirror the fecundity of *C. finmarchicus* during an egg production period of one month, with a production rate of 20 eggs day⁻¹. The model does not simulate the continuous mortality among females during March and April seen in the data from Balsfjorden 1977 (Fig. 2), but in order to have a similar pattern of egg production, we have assumed zero mortality amongst females during the period when the first 400 eggs are laid, after which the mortality is made to equal 0.01 h⁻¹. This means that ovigerous females are not presented in the population after May 1 in the simulations.

The migration model

The vertical distribution of *Calanus finmarchicus* in the Atlantic part of the Barents Sea depends on the stage composition and the vertical structure of phytoplankton. In spring and autumn diurnal light variations cause a classical vertical migration pattern with upward movements at dusk and downward movements at sunrise. The vertical distribution of the copepodite stages of *C. finmarchicus* in high-latitude environments during the annual recruitment period in May and June have been studied in fjords in Northern Norway (Tande, 1988 *a*) and in Atlantic waters of the Barents Sea (Unstad and Tande, in press). Ontogenetic vertical migration, where the migration range becomes progressively wider with advancing stage, was seen in both investigations. In the fjords in Northern Norway, frequent sampling during a 24 hours period indicated that none of the copepodite stages could be classified as vertically static in May and June.

The model uses information about hunger state, daily light variations, and the vertical gradient of phytoplankton to produce a vertical distribution at different stages which is in accordance with field data (see Fig. 6; Tande, 1988 *b*; Unstad and Tande, in press). In the euphotic layer, individuals in the model have been made to seek out the layer containing the maximum amount of chlorophyll. Both hunger state and light level influence the duration of the grazing period and the residence time in the layer containing the maximum amount of chlorophyll. The model describes the vertical behaviour of the various copepodite stages of *Calanus finmarchicus* most accurately, when each individual avoids light beyond an upper limit, which varies depending on age and hunger state (see Slagstad and Tande, 1990).

The population model

The general structure of the population model has been simplified for *Calanus finmarchicus* in comparison with that given for *Calanus* in Slagstad (1981). The version adopted in the present paper is described in Slagstad and Tande (1990) for *C. glacialis*, where the population is des-

cribed by use of a density function $\mu(t, w)$ which satisfies the partial differential equation

$$\frac{\partial \eta}{\partial t} + \frac{\partial}{\partial w} (g\eta) = -D\eta \quad (4)$$

where $g(t, w)$ and $D(t, w)$ are the growth and mortality rates, respectively, for individuals of weight w at time t . The growth rate (g), is calculated by the physiological model.

The mortality rates of nauplii, and each individual copepodite stage are kept constant in the simulation. In the various scenarios mortality rate parameters have been used to scale the population abundance, according to the different sets of data (see Tab. 3). In the present study natural mortality and predation are not treated separately, but scaled in order to correspond to the observed maximum of spawning females and recruiting cohorts found during spring and early summer at high latitudes. This is done at the time when the proportion of the copepodite stages in the model coincides with the population data obtained from the field. Since mortality in the present model is dependent only on time, the temperature will have considerable effect on survival throughout the various stages of the copepodite growth period.

Table 3

Calanus finmarchicus. Instantaneous mortality constants adopted in the simulations.

SIMULATION	Nauplii	MORTALITY (h ⁻¹)			
		CI	CII	CIII	CIV
Scenario I	0.0	0.0045	0.0032	0.0032	0.0023
Scenario II	0.00168	0.0038	0.0028	0.0028	0.0019
Scenario III					
Balsfjorden	0.0022	0.004	0.003	0.003	0.002
Malangen	0.0022	0.004	0.003	0.003	0.002
Grøtsund	0.0	0.004	0.003	0.003	0.002

RESULTS

Scenario I: the Barents Sea

The surface temperature in spring 1982 at 72°N 30°E in the Barents Sea (Fig. 5), was characterized by low temperatures, around 2°C in March and April. The annual temperature increase started around June 10, and the sea temperature reached approximately 7°C in July. Primary production, here defined as the total of new and regenerated thus peaks in the middle of June, coinciding with the onset of the temperature increase. The overall production during the period from March 1 to July 30 is estimated to be 60 gC m⁻². In the present scenario grazing increases with time, and is thus dynamically coupled to the phytoplankton model. Abundance data from the Barents Sea, for the year 1982, is only available from early June. The abundance that year was unusually high in the area, compared with other years (Skjoldal *et al.*, 1987). In order to obtain similar abundance

during the simulation as that reported by Skjoldal (*op. cit.*), we could either choose a sufficient high number of females as an initial value or change the mortality of the nauplii to zero (see Tab. 3). Based on the population size obtained (Fig. 5) and the general model description given above, the production of *Calanus finmarchicus* is estimated to be 15 gC⁻² from March 1 till the end of July. If we increase the initial value of females from 2 000 to 4 000 individuals m⁻², the total production will only increase to 18 gC m⁻², due to food limitation. The population dynamics of *Calanus finmarchicus* during the simulation mirrors the annual generation pattern found for the species in Balsfjorden during 1977. Since the abundance of ovigerous females was not determined from the area in 1982, the population is set, at 2 000 individuals m⁻² at the onset of simulation in March. The subsequent development of the recruiting generation is scaled through mortality in order to meet the abundance in the area reported by Skjoldal *et al.* (1987).

The vertical distribution of phytoplankton carbon from surface down to 100 m depth shows, generally speaking, a high standing crop (> 200 µg C l⁻¹) in the uppermost 80 m on May 15 (Fig. 6). Maxima of carbon are found in the upper layers of water, on June 15 and July 15. The vertical distribution of biomass of *Calanus finmarchicus* (in terms of carbon) shows a unimodal vertical distribution at the beginning and end of June, while a bimodal pattern was found in the middle of June. Throughout June 30 a low proportion of the population is found at depths >100 m. Both high and low phytoplankton standing crops

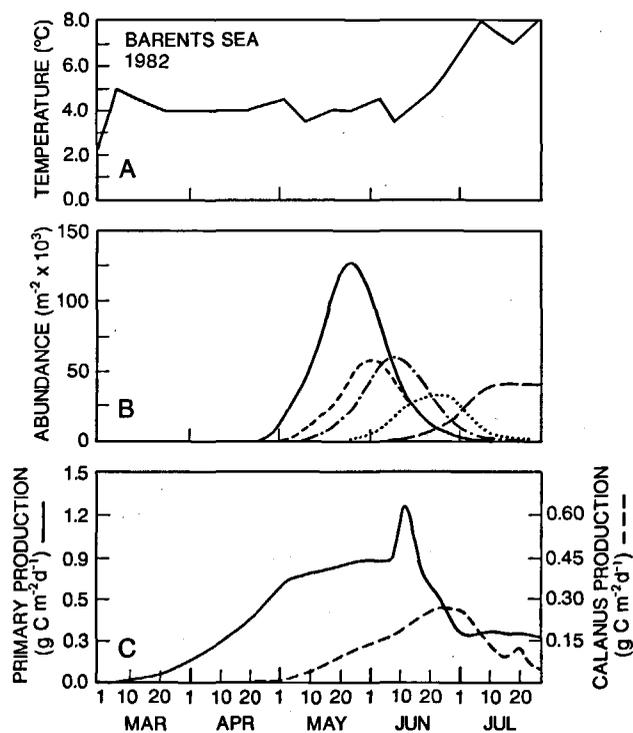
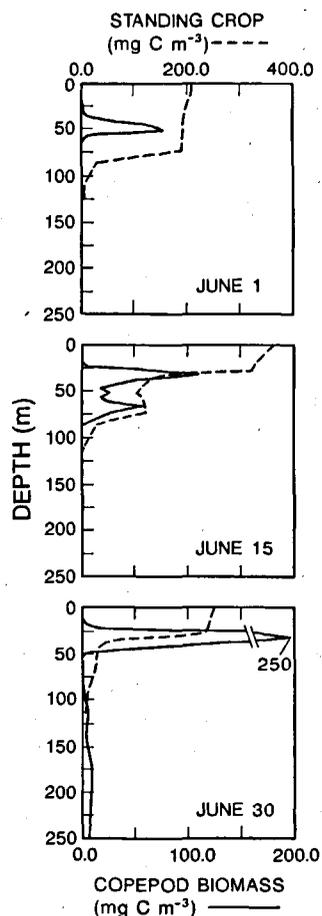


Figure 5

Calanus finmarchicus. Scenario I: sea temperature, and model simulation of the stage distribution and abundance of adult females and copepodite stages CI-V, primary production and *Calanus* production from March to July 1982 in the Barents Sea. See text for further details. Symbols: —, CI; ---, CII; ----, CIII;, CIV, and - - - - , CV.

Figure 6

Calanus finmarchicus. Simulated vertical distribution of phytoplankton and *Calanus* biomass at three selected dates from scenario I in the Barents Sea. The vertical distribution patterns are daily (24 h) average at the three time periods in June.



appear to increase vertical separation among *C. finmarchicus* during this period in the Barents Sea (Unstad and Tande, in press). In the model vertical distribution is determined by search for maximum food in surface waters, and hunger state, modified by age dependent avoidance of light. Although the model predicts a vertical distribution which to a large extent is in accordance with available information, it oversimplifies the observed vertical behaviour in *C. finmarchicus* found in high latitudes during this period. (*i. e.* Tande, 1988 a; Unstad and Tande, in press).

Senario II: Balsfjorden 1977

The winter minimum in sea temperature at Svartnes in Balsfjorden lasted until the end of April when thermal stratification started in surface waters. At 15 m depth the temperature increased from approx. 1.5° to 6°C during the period April to July. The phytoplankton model simulates the primary production as described with a production of 66 gC m⁻² from March 1 to July 30 (Fig. 7). The version adopted in scenario II and III does not specify productivity in relation to diatoms and *Phaeocystis pouchetii*, and gives the phytoplankton production as a time series, without feedback from grazing.

The simulation mimics the population dynamics seen in the data obtained for *Calanus finmarchicus* at Svartnes in Balsfjorden 1977 (Fig. 2). The timing of the spawning period is basically identical with that described for the species in Malangen during the spring of 1989 (Diel and

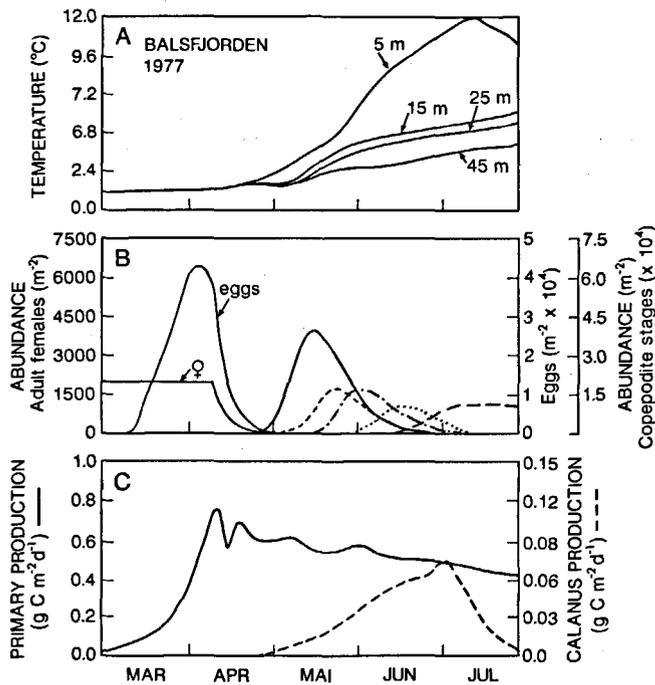


Figure 7

Calanus finmarchicus. Scenario II: sea temperature, and model simulation of the stage distribution and abundance of adult females and copepodite stages I-V, primary production and *Calanus* production from March to July 1977 in Balsfjorden. See text for further details. Symbols as in Figure 5.

Tande, in press). Starting with the observed abundance of overwintering females at Svartnes at the end of March, the abundance of copepodite stages IV and V are met through changes in the mortality rate constants (see Tab. 3) among nauplii and copepodite stages. Since the Bongo net obviously obscured CI-CIII, probably due to clogging in surface waters, the abundance of the recruiting generation was scaled at the end of June. The *Calanus* production at Svartnes in Balsfjorden from March 1 to July 30 is estimated at 3.1 gC m^{-2} in 1977.

Scenario III: North Norwegian fjords 1986

In May 1986 the zooplankton communities in three different localities (Balsfjorden, Malangen and Grøtsund) near Tromsø were sampled three times at different depths (every 15 m), from the surface to the bottom, with a plankton pump (see Tande, 1988 a). The population information obtained for *Calanus finmarchicus* is adopted to verify the production model for these areas. Temperature data from March to July for the three different fjords has been used as the physical settings for the simulations. Temperatures selected at 15 m are shown in Figure 8. The phytoplankton model defined for Balsfjorden 1977 has been adopted as a background for the *Calanus* simulations in Scenario III.

Although not shown in Figure 8, the spawning behaviour of the overwintering females, and the timing of the egg production has the same characteristics as those given for Balsfjorden 1977. The observed differences with regard to

the progression of recruits is mainly caused by the different temperature regimes in each locality. Information on the amount of females during the spring of 1986 is lacking. From 1988, the stock of overwintering females found at the beginning of April in Balsfjorden, Malangen and Grøtsund were 104, 3 630 and 2 240 individuals m^{-2} , respectively.

In the model simulations for Balsfjorden 1986, the spawning stock of *Calanus finmarchicus* was set at 100. Recent unpublished data indicates that this is a realistic figure for the stock at the beginning of the 1990-s (Falkenhaus and Tande, unpublished data). As for simulations of productivity in Malangen and Grøtsund, the spawning stock in April was set at 3 000 females m^{-2} . The abundance of the copepodite stages in May was scaled by a change of mortality constants for the different areas (see Tab. 3). The same mortality constants for the simulation of Balsfjorden and Malangen gave the abundances observed in the two localities in May, resulting in a production estimate of *Calanus* of 0.1 and 5.4 gC m^{-2} , respectively for the period March 1 to July 30 (Fig. 8). In order to meet the abundances recorded in Grøtsund in May 1986, mortality had to be neglected during the nauplii developmental period. This resulted in an estimated *Calanus* production of 20.2 gC m^{-2} during the simulation period. Comparing the population data obtained during April and May this year, the decline of *C. finmarchicus* in Balsfjorden during the nine-year period from 1977 to 1986 is a recurring feature.

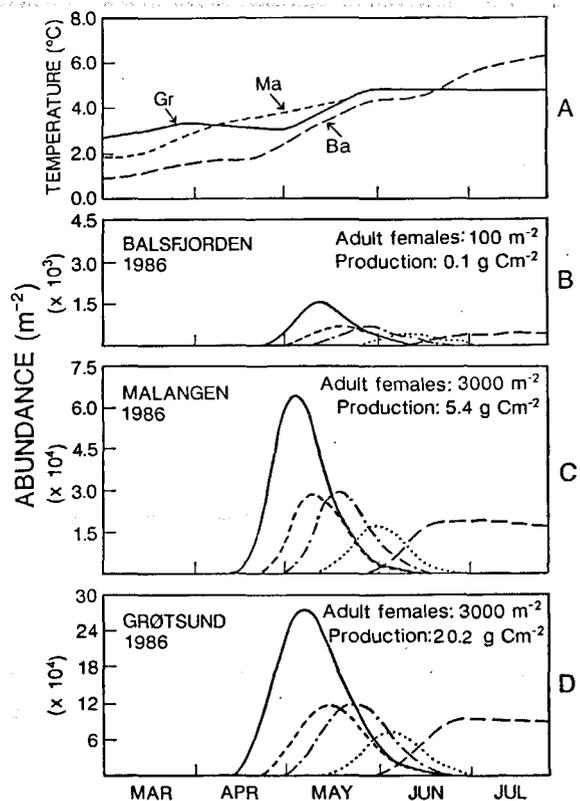


Figure 8

Calanus finmarchicus. Scenario III: sea temperature, and model simulation of the stage distribution and abundance of copepodite stage I-V during the period from March to July 1986 based on the observed population abundances in Balsfjorden, Malangen and Grøtsund in April and May. Symbols as in Figure 5.

DISCUSSION

In the present study, productivity estimates of *Calanus finmarchicus* in Atlantic waters of the Barents Sea and in North Norwegian fjords demonstrate the heterogeneous nature of the flow of energy through this component in the area investigated. A range of 0.1 to 20.2 gC m⁻² during the main annual productive period highlights different aspects well known in quantitative plankton ecology. The estimated production of *C. finmarchicus* of the Barents Sea (15 gC m⁻²) appears, at least in 1982, to exceed that of species in other copepod communities over vast geographical areas in temperate waters (see Aksnes and Magnesen, 1983; Tremblay and Roff, 1983; Middelbrook and Roff, 1986; McLaren *et al.*, 1989). However, based on the abundance data from 1983-1985 in the same region and at approximately the same time (Skjoldal *et al.*, 1987), large interannual variations in the productivity of *C. finmarchicus* are likely to be found in the Barents Sea.

In order to compare existing data with the simulations in the present study, conversion factors of 6 kcal or 25 kJ g dw⁻¹ (Tremblay and Roff, 1983; McLaren *et al.*, 1989) and a factor of 0.6 from dry weight to carbon have been adopted. In Canadian waters at the Scotian shelf where *Calanus finmarchicus* was found to produce essentially one generation per year, the main productive period was found to be from March to July on the Emerald Bank (McLaren *et al.*, 1989). This correlates well with the period of simulation in the present study. For the year 1979-1980 production estimates for *C. finmarchicus* amounted to approx. 6.5 gC m⁻² yr⁻¹, 28 % of the total production of 23.4 gC m⁻² yr⁻¹ calculated for nine copepod species (McLaren *et al.*, 1989). Although a considerably lower overall copepod production (12.6 gC m⁻² yr⁻¹) was estimated by Tremblay and Roff (1983) for the same period and area, the production of *C. finmarchicus* amounted to 5.6 gC m⁻² yr⁻¹, which agrees fairly well with the estimate in McLaren *et al.* (1989). An even lower figure for herbivorous zooplankton on the Scotian shelf (2.1 gC m⁻² yr⁻¹) is given by Mills and Fournier (1979). Middelbrook and Roff (1986) estimated a copepod production of 19-20 gC m⁻² yr⁻¹ in Passamaquoddy Bay, New Brunswick, only slightly less than that of Emerald bank. In the report by McLaren *et al.* (1989), the assessed annual copepod production on Georges bank is approximately 27 gC m⁻² yr⁻¹, *i. e.* considerably greater than that of Emerald bank.

In parts of the North Sea such as the area of Northumberland, where *Calanus finmarchicus* is of minor importance, the annual production of smaller organisms (*i. e.* *Acartia* spp., *Oithona similis*, *Pseudocalanus* spp., and *Temora longicornis*) adds up to 18.2 gC m⁻² yr⁻¹ (recalculated from Evans (1977) by Roff *et al.* (1988)). Similarly, during a 15-year period (from 1969 to 1983) the mean annual production of the same four copepod species was estimated to be 21.6 gC m⁻² yr⁻¹ (Roff *et al.*, 1988). In the central North Sea, where *C. finmarchicus* plays a quantitatively more important role, estimated copepod production, extrapolated for the entire growing season, is 18 gC m⁻² yr⁻¹ (Franz *et al.*, 1984). In a study from the

Fladen Ground in the North Sea, Williams and Lindley (1980) estimated that production of *C. finmarchicus* might be in the range of 14.5-27.5 gC m⁻² during a 30 d exponential growth phase in May 1976. Considering the species' polycyclic generation pattern in the Flex area in the northern North Sea, these figures are high, which the authors emphasize by suggesting that the lower production value of 0.49 gC m⁻² d⁻¹ is considered to be their best estimate (Williams and Lindley, 1980). Although McLaren *et al.* (1989) caution that many earlier production estimates are suspect, they suggest that it may well be that copepod production is similar over the whole temperate shelf of eastern North America or even over broader geographic areas.

Production estimates of planktonic copepods in Norwegian waters are sparse. In Lindåspollene, a landlocked fjord in Western Norway where *Calanus finmarchicus* has one yearly generation, the annual production in 1980-1982 was estimated to be 2.2 gC m⁻² in the central area at Spjeldnesosen (Aksnes and Magnesen, 1983). Although the production in the Barents Sea in 1982 and in Malangen and Grøtsund 1986 is higher than the rates obtained from Western Norway, the data in this paper document very well the regional variability in *Calanus* production in coastal and offshore waters in Norway. The abundance of *C. finmarchicus* in Grøtsund in May 1986 exceeded that of Malangen by a factor of 10. The abundance of spawning females in the simulations for Malangen and Grøtsund is not available from the spring of 1986, and the production was therefore obtained by adjusting mortality of the recruits during May and June (see Tab. 3). The error introduced by scaling the model simulations according to population abundance through mortality is of minor quantitative importance, since the main growth and production takes place among CIV and CV in *C. finmarchicus* (see also Tande, in press). On the other hand, the highly different mortality rates in the two simulations are unlikely to reflect real differences of the *in situ* predation loss in the two areas. Although detailed physical and biological data from the areas around Tromsø are lacking, the large difference in abundance between the recruiting populations during 1986 in the two areas suggest that topography and current patterns most likely create the large differences seen in these fjord systems.

Provided with data on sets of growth characteristics and population parameters, the present model concept estimates productivity (*i. e.* potential production) of *Calanus finmarchicus* for the annual cohort produced in spring and early summer. The model therefore furnishes scenarios for one species during a single time sequence of 3-4 months. In order to increase its trophodynamic significance, the model requires a substantial input especially of population data from various time periods and areas.

The scenarios considered in the present paper, range from fjords to the continental shelf in the Barents Sea and cover different years. In central parts of the Barents Sea, the abundance of copepodite stages of *C. finmarchicus* monitored yearly in June from 1979 to 1984 varied from 10 x 10³ to 54 x 10⁴ number m⁻² at 74 and 75°N (Skjoldal *et al.*, 1987). The minimum in copepodite

abundance in 1983 and 1984 coincided with the time period of the collapse in the stock of capelin, which suggests that the decrease in *C. finmarchicus* was not mediated by predation. Large seasonal and interannual variation of inflowing water is considered likely in the Barents Sea. Skjoldal and Rey (1989) have argued that the seasonal descent of *C. finmarchicus* below the continental shelf during autumn and winter in the North Atlantic prevent copepods from being advected to the Barents Sea, and that these mechanisms should be considered important in order to explain interannual variations in plankton biomass and productivity. The environmental conditions responsible for interannual variation in the abundance of copepodite stages and productivity of *Calanus finmarchicus* in the Barents Sea has also recently been addressed by Tande (in press). The model predicted lowered productivity during cold periods, which basically supports the contention that climatic events play a major role in interannual variability of copepod populations in the Bering Sea (see also Vidal and Smith, 1986).

The above scenarios, demonstrate that mechanisms related to mortality and physical transport are key questions for future implementation of the model concept. Mortality ope-

rates through the entire life cycle, but it is most relevant for productivity estimates to measure it during the recruitment period in spring and early summer. Advective processes should be used as a guideline for defining areas for studying plankton production. This would improve the relevance of the productivity model as a quantitative instrument in future trophodynamic studies. Although some of the scenarios in this paper highlight elements of interannual variation and long-term shifts in the copepod community, it should be stressed that the model has not been designed to mirror these events or explain the underlying mechanisms.

Acknowledgements

This work was financially supported, in part, by the Norwegian Fishery Research Council (NFFR) through the Norwegian Research Programme for Marine Arctic Ecology (PRO MARE). The authors wish to thank L. Raste and B. Vaaja for technical assistance. Thanks are also due to H. Falkseth for drawing the figures and to O. Breimo for photographic expertise. Constructive criticism from anonymous referees is also appreciated.

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