Population growth parameters and production of *Calanus finmarchicus* in the Fladen Ground as calculated with a simulation model*

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Abstract

A mathematical model taking the life history of copepods into account has been developed. Thus, parameters that are difficult to measure *in situ* can be calculated. These are growth and mortality rates, development times, reproductive efficiency for the several stages, as well as net production and mortality for the total population.

This model has been applied to the situation observed in the Fladen Ground with the experimental data of Dr. Krause (Universität Hamburg, F.R.G.).

1.- Introduction

Copepods are a prominent fraction in the zooplankton. They are small swimming crustacea generally not exceeding a length of 2 mm. Being herbivorous and/or omnivorous, they play an essential role in the cycle of organic matter since they make a link between the first trophic level (synthesis of organic matter by the phytoplanktonic micro-algae) and the higher trophic levels (carnivorous zooplankton, fish ...) .The life history of the copepods is rather complex as there are many development stages (nauplii I to VI and copepodites I to V) from the egg to the fertile adult.

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Each of these stages can be fully considered as a population with its specific functional characteristics (Fig. 1). Since hatching is spread in time , the populations of the different stages occur together in the natural samples. The resulting seasonal curves can possibly show a succession of maxima for the various development stages. The correct interpretation of the observable data in terms of population dynamics is much more complex and requires the development of an adequate mathematical model (Mommaerts and Bossicart, 1975; Mommaerts, 1978).

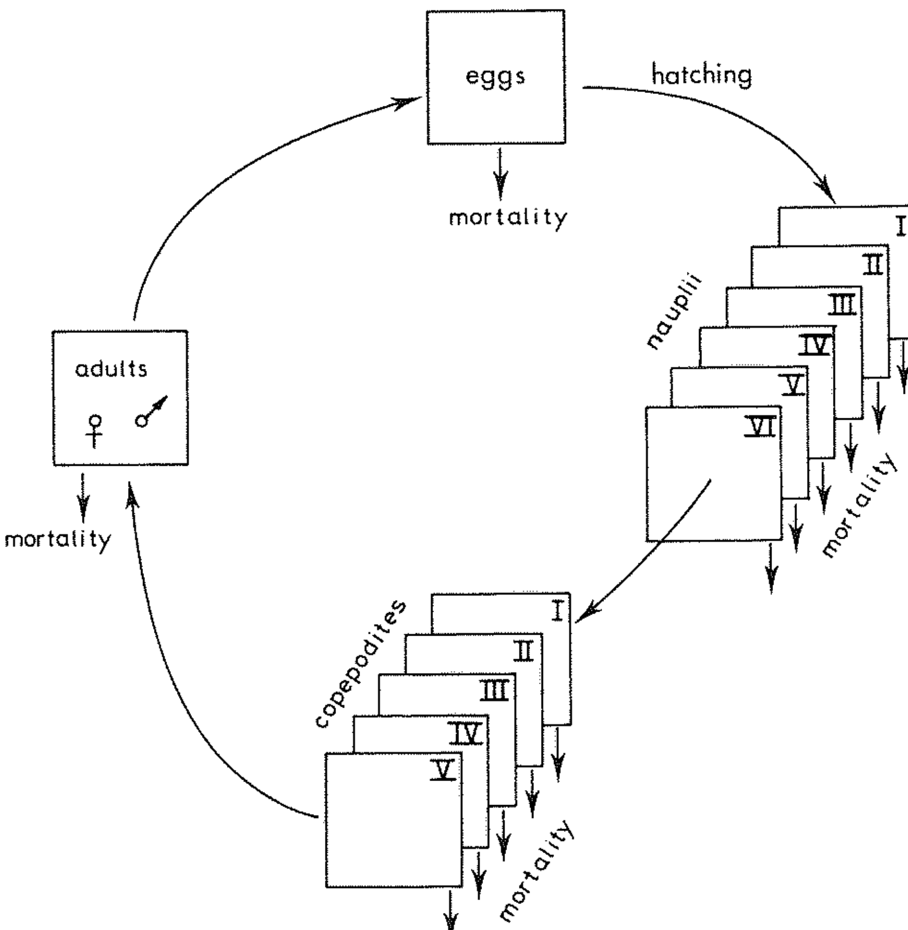

fig. 1.

Parameters that are particularly relevant to the population dynamics of marine copepods (*i.e.* growth, mortality rate) and their production can be calculated.

2.- General description of the model

At the present stage of development, the model is able to describe the dynamics of a full generation in the case of a homogeneous waterbody. For the needs of the model, the occurence of nauplii has been discretized in time, considering there are as much cohorts generated as there are days in the hatching period. The hatching curve is parametrized. The six naupliar stages are globalized but the next five copepodite stages are described. One has considered that growth is exponential. At the adult stage, the model makes a distinction between males and females, using a sex-ratio as observed in nature.

One is also considering that just before dying, each female will have produced a given average number of eggs that will be the input to the next generation.

3.- Biological functions and evolution equations*

3.1.- THE HATCHING CURVE

At the present time this curve is still parametrized. A normal law describes the phenomenon in a acceptable way :

$$N^j = b\ e^{-\alpha(t-\beta)^2} \qquad (1)$$

3.2.- EQUATIONS FOR THE NAUPLIAR STAGES

Mortality causes an exponential decrease of the number of individuals in a cohort.

Living population observable at a time t for the globalized naupliar stages :

* For the explanation of the symbols see table 1.

$$N_t^T = \int_{i_1=0}^{i_1=p_1} b\ e^{-\alpha(t-\beta-i_1)^2 - m_1 i_1}\, di_1 \qquad (2)$$

Table 1

Legends of the symbols

Nauplii	Copepodites	Adults	
			Populations parameters :
N_t^T	$C_{It}^T \ldots C_{Vt}^T$	A_t^T	Numbers (all cohorts)still alive on day t
i_1	$i_I \ldots i_V$	i_3	Age of a given individual (days)
p_1	$p_I \ldots p_V$	p_3	Maximum age of a given individual (days)
m_1	$m_I \ldots m_V$	m_3	Specific mortality rate
			Stocks and production parameters :
B_o^N			Initial biomass of an individual
$B_{i_1}^N$			Actual biomass of an individual of age $i_{(1)}$
k_1			Specific exponential growth rate
P_t^N			Net production (all cohorts) on day t
			Spawning and hatching :
E			Numbers (all cohorts) of eggs observable during the whole generation.
γ			Average number of eggs/female.
δ			Proportion of females in the totale population.
α			Coefficient giving the dispersion of the normal curve.
β			Day with the highest hatched number.
b			Number of nauplii hatched on day β

3.3.- EQUATIONS FOR THE COPEPODITE STAGES

Similar considerations as those developed for the nauplii lead to the various equations.

Living population observable at a time t for each copepodite stage :

$$C^{T}_{It} = \int_{i_I=0}^{i_I=p_I} b\, e^{-\alpha(t-\beta-p_1-i_I)^2-m_1p_1-m_Ii_I}\, di_I \qquad (3)$$

$$C^{T}_{IIt} = \int_{i_{II}=0}^{i_{II}=p_{II}} b\, e^{-\alpha(t-\beta-p_1-p_I-i_{II})^2-m_1p_1-m_Ip_I-m_{II}i_{II}}\, di_{II} \qquad (4)$$

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$$C^{T}_{Vt} = \int_{i_V=0}^{i_V=p_V} be^{-\alpha(t-\beta-p_1-p_I-\ldots-p_{IV}-i_V)^2-m_1p_1-m_Ip_I-\ldots-m_{IV}p_{IV}-m_Vi_V}\, di_V \qquad (5)$$

3.4.- EQUATIONS FOR THE ADULT STAGES

$$A^{T}_{t} = \int_{i_3=0}^{i_3=p_3} be^{-\alpha(t-\beta-p_1-p_I-\ldots-p_V-i_3)^2-m_1p_1-m_Ip_I-\ldots-m_Vp_V-m_3i_3}\, di_3 \qquad (6)$$

3.5.- PRODUCTION OF THE EGGS FOR THE NEXT GENERATION

The total number of individuals (all cohorts) that will have reached the adult stage within a generation cycle is :

$$A = \int_{t=t_o}^{t=t_f} b\, e^{-\alpha(t-\beta)^2-m_1p_1-m_Ip_I-\ldots-m_Vp_V}\, dt \qquad (7)$$

and hence the number E of produced eggs is :

$$E = \int_{t=t_o}^{t=t_f} \gamma\delta \; b \; e^{-\alpha(t-\beta)^2 - m_1 p_1 - m_I p_I - \ldots m_V p_V} \, dt \tag{8}$$

4.- Calculation of net production*

4.1.- NAUPLII

4.1.1.- *Growth*

The growth equation for a given individual can be written :

$$B^N_{i_1} = B^N_0 \; e^{k_1 i_1} \tag{9}$$

4.1.2.- *Net production*

Furthermore, the net production of a given individual during the day i_1 being :

$$B^N_{i_1+1} - B^N_{i_1} = B^N_o e^{k_1 i_1} (e^{k_1} - 1) \tag{10}$$

and combinating with eq. (2), it follows that the global net production at time t is :

$$P^N_t = \int_{i_1=o}^{i_1=p_1} b \; e^{-\alpha(t-\beta-i_1)^2 - m_1 i_1} B^N_o e^{k_1 i_1} (e^{k_1} - 1) \; di_1 \tag{11}$$

4.2.- COPEPODITES

In a similar way, equations are written for the growth and the production of the copepodites.

* The loss of exuviae during the transformations has not been taken into account.

4.3.- ADULTS

There is no significant weight increase at that stage but a production of eggs.

5.- Application to the Fladen Ground data

We have attempted to apply this model to the experimental data from the Fladenground acquired by Dr. Krause(Universität Hamburg, F.R.G.) Samples were taken from the research vessel "Meteor" at the central station 4 times a day and from 9 sampling depths. At this time, only adults and copepodites had been sorted. The information concerning the nauplii is presently available so that the same simulation work will also be possible for the naupliar stage in the future.

Fig.2 gives the time series of numbers for each of the 5 copepodite stages and the female and male adult stages.

A moving average technique (5 points) has been used for the smoothing of the curves. This data set is limited in time, however we were able to fit our model to the experimental curves and thus evolve the values of the various rates implied (table 2).

Table 2

	Developing time (days)	Growth rate (day^{-1})	Mortality rate (day^{-1})
Copepodites I	5	0.15	0.04
II	5	0.25	0.04
III	6	0.12	0.05
IV	7	0.18	0.05
V	7	0.04	0.05
Total ($C_I - C_V$)	37		
Adults			0.06

$\alpha = 0.0015$

$\beta = 145$ day

$b = 45$ individuals

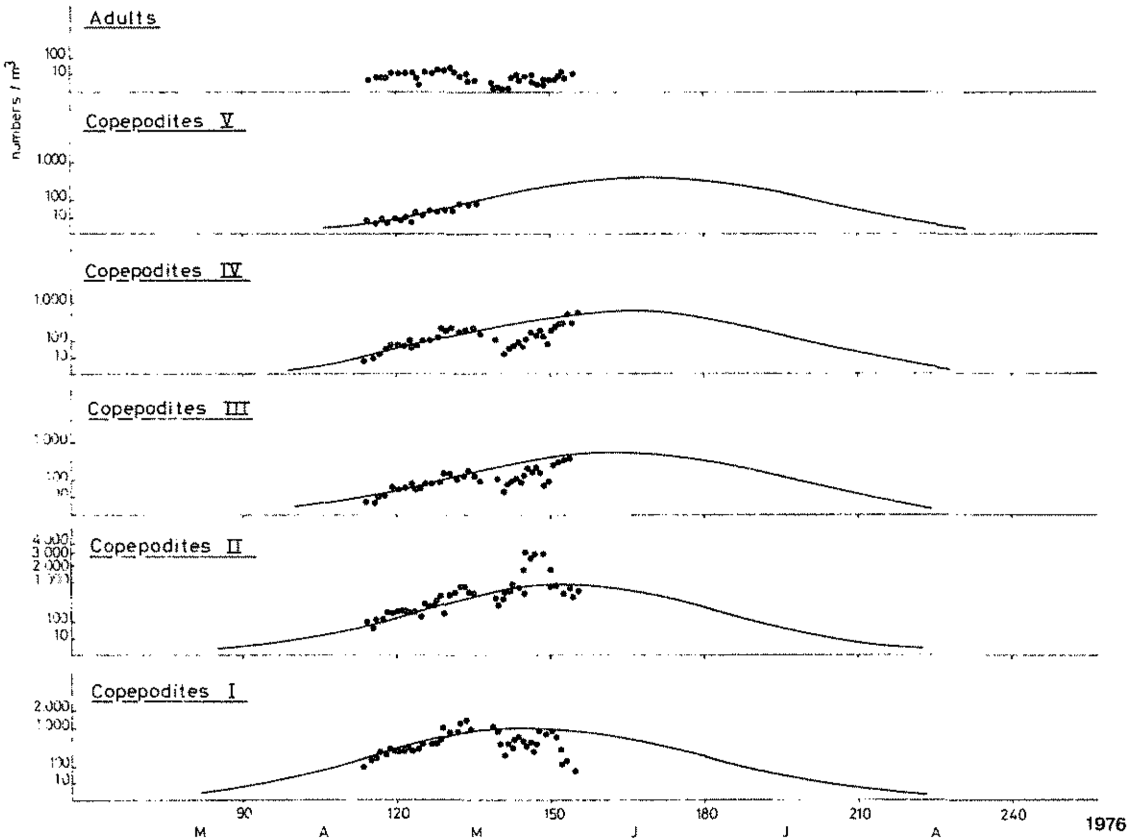

fig. 2.

FLEX : Season evolution of the numbers of Calanus finmarchicus (copepodites and adults)
Experimental values of M. Krauze.

5.1.- DEVELOPING TIME

The developing times for the copepodite stages are 5 , 5 , 6 , 7 and 7 days. The life span for a copepodite from stages I to VI is consequently of 37 days.

Marshall and Orr (1972) find in laboratory culture a life span of 60 - 70 days. It amounts to 3 months in Norwegian coastal water (Ruud, 1929), 71 - 79 days in the Gulf of Maine (Fish, 1936), 70 - 80 days in the North Sea (Rees, 1949) (in Marshall and Orr, 1972).

5.2.- GROWTH RATE

The individual weights at the beginning of each development stage have been measured by B. Williams (Plymouth; personal communication) and are respectively for C_I to C_{VI} 2.7, 5.2, 20.1, 145.2, 191.6 µg dry weight.

Knowing the development time for each stage and the weights, the exponential growth rates can be calculated.

They are respectively for C_I to C_V 0.15, 0.25, 0.12, 0.18, 0.04 per day.

Mullin and Brooks (1970) find a coefficient of exponential growth of 0.17 per day for C_I to C_{IV} for Calanus feeding on Thalassiosira at 10° C and 0.08 per day for C_{IV} to Adult.

At 15°C this coefficient is higher: 0.27 per day for C_I to C_{IV} and 0.22 per day for C_{IV} to Adult.

5.3.- MORTALITY

The mortality rates calculated for the 5 copepodites stages are respectively 0.04 , 0.04 , 0.05 , 0.05 , 0.05 per day and 0.06 per day for the adults.

5.4.- OTHERS PARAMETERS.

45 individuals (b in the model) are the highest hatched number on day 145 (β in the model). The constant α giving the dispersion of the normal curve is 0.0015 .

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