International Council for
the Exploration of the Sea

C.M. 1978/L:43
Biological Oceanography Committee

Modelling the dynamics of the zooplanctonic copepods in the Southern Bight of the North Sea. (1)

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(1) This investigation was carried as a part of the National R & D Prograama on the Environment. Project Sea. Programmation of Scientific Policy. 8, rue de la Science - 1040 Brussels.

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ABSTRACT.

It is difficult to interpret the fluctuations of observed numbers of the differents stages of copepods in terms of dynamics of the populations

Several phenomenons enter into account : the life history of each individual, a continuous recruitment of the nauplii, the growth, the mortality in each stage.

The mathematical model proposed here is based on the life characteristics of the copepods. It permits us to understand and calculate the parameters difficult to be measured.

I. INTRODUCTION.

Calanoïd copepods are a major component of the zooplankton in temperate seas of the european continental shelf. As they are herbivorous and/or omnivorous, they play an important role in the biogeochemical cycle of matter by making a link between photosynthetizing microalgae of the first trophic level, and higher trophic levels (especially fishes).

Their life cycle is relatively complicated as several development stages occur before the individuals reach maturity: after hatching, there is a succession of six naupliar stages followed by five copepodite stages (fig. 1.).

The individuals of a given stage can be considered to belong to a population with its specific characteristics (food ratio, growth rate, mortality ...)

As hatching is not synchronous (the hatching period actually extends up to 70 days), populations of different development stages are mixed in natural samples.

Contrary to what resulting seasonal curves (with their well marked maxima for each stage) suggest, the interpretation of such observable data interms of populations dynamics is difficult without a mathematical model.

II. GENERAL DESCRIPTION OF THE MODEL.

Rates are assumed to remain constant during the development of a given stage. This of course implies that nutrition, competition, predation ... are supposed not to vary during all this time. A numerical integration taking such regulations into account is an alternative approach, presently on hand. The eclosion function is parametrized. Therefore a normal law gives a reasonably good approximation. For each of the cohorts generated (one a day), a growth and a mortality rate are included in the development function. As these rates are constant, the surviving individuals remain grouped in the developmental stage considered. At selected times, cohorts switch from their actual stage to the next one. Each development stage is characterized by different rates. At the adult stage, a partition occurs between males and females. The female copepods release eggs before dying.

III. EVOLUTION EQUATIONS OF THE PRINCIPAL STAGES.

1. Eclosion equations (1)

This curve is still paramatrized.

A normal law describes the phenomenon :

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

2. Equations for the cohorts of the naupliar stages.

For a cohort j, the number of individuals decrease in function of the exponential mortality rate .

$$N_t^j = b\ e^{-a(t-c)^2 - m_1 i_1}$$

Hence, the numbers of living individuals at a time t is :

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

and the numbers of living individuals observed during the generation is :

$$N = \int_{t=to}^{t=t_f} \int_{i_1=0}^{i_1=p_1} b\ e^{-a(t-d-i_1)^2 - m_1 i_1} di_1 dt \qquad (3)$$

In a complementary way the number of dead individuals during the generation is :

$$n = \int_{t=t0}^{t=t_f} \int_{i_1=0}^{i_1=p_1} b\ e^{-a(t-d-i_1)^2 - m_1 i_1} (1-e^{-m_1}) di_1 dt \qquad (4)$$

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(1) For the explanation of the symbols see table 1.

3. Equations for the cohorts of the copepodite and adult stages.

In a similar way the numbers of living individuals observed during the whole generation can be calculated :

a) copepodites

$$C = \int_{t=t0}^{t=t_f} \int_{i_2=0}^{i_2=p_2} b\ e^{-a(t-d-p_1-i_2)^2-m_1p_1-m_2i_2}{}_{2}di_2dt \qquad (5)$$

b) adults

$$A = \int_{t=t0}^{t=t_f} \int_{i_3=0}^{i_3=p_3} b\ e^{-a(t-d-p_1-p_2-i_3)^2-m_1p_1-m_2p_2-m_3i_3}{}_{3}di_3dt \qquad (6)$$

In a complementary way the number of dead individuals during the generation is :

a) copepodites

$$c = \int_{t=t0}^{t=t_f} \int_{i_2=0}^{i_2=p_2} b\ e^{-a(t-d-p_1-i_2)^2-m_1p_1-m_2i_2(1-e^{-m_2})}di_2dt \qquad (7)$$

b) adults

$$a = \int_{t=t0}^{t=t_f} \int_{i_3=0}^{i_3=p_3} b\ e^{-a(t-d-p_1-p_2-i_3)^2-m_1p_1-m_2p_2-m_3i_3(1-e^{-m_3})}di_3dt_t \qquad (8)$$

4. Numbers of eggs produced for the next generation.

The total number of adults during the generation being (ref.eq.(6))

$$A^{*} = \int_{t=t0}^{t=t_f} b\ e^{-a(t-d)^2-m_1p_1-m_2p_2}dt \qquad (9)$$

The number of produced eggs - if each ♀ releases eggs before dying - will be :

$$E = \int_{t=t0}^{t=t_f} o\ \alpha\ b\ e^{-a(t-d)^2-m_1p_1-m_2p_2}dt \qquad (10)$$

IV. CALCULATION OF NET PRODUCTION.

1. Nauplii.

1.1. Growth.

The growth equation for a given individual can be written :

$$B^N_{i_1} = B^N_0 e^{k_1 i_1} \qquad (11)$$

1.2. Net production.

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

$$B^N_{i_1+1} - B^N_{i_1} = B^N_0 e^{k_1 i_1}(e^{k_1}-1) \qquad (12)$$

and combining eq.(3) with eq. (12), the global net production during the whole generation becomes :

$$P^N = \int_{t=t0}^{t=t_f} \int_{i_1=0}^{i_1=p_1} b\ e^{-a(t-d-i_1)^2-m_1 i_1} B^N_0 e^{k_1 i_1}(e^{k_1}-1)\,di_1\,dt \qquad (13)$$

2. Copepodites.

Similar considerations as those developed for the nauplii lead to the calculation of the net production of the copepodites :

$$p^{C} = \int_{t=to}^{t=t_f} \int_{i_2=o}^{i_2=p_2} b\ e^{-a(t-d-p_1-i_2)^2-m_1p_1-m_2i_2}B_o e^{k_2i_2}(e^{k_2}-1)\,di_2\,dt \qquad (14)$$

3. Adults.

There is no significant weight increase at that stage but a production of eggs (eq. (10))

$$p^{E} = \int_{t=to}^{t=t_f} B^{E}_{o}\ \alpha\ b\ e^{-a(t-d)^2-m_1p_1-m_2p_2}dt \qquad (15)$$

V. APPLICATION OF THE MODEL TO THE SOUTHERN BIGHT OF THE NORTH SEA.

The sampling frequency in the Southern Bight of the North Sea in 1974 allows us to follow reasonably well the fluctuations of the copepods numbers. Several species of copepods, among which *Temora longicornis*, were observed in this area. The records are similar to those made by Fransz (1976) in the same area and those of Digby(1950) off Plymouth.
The copepodites and the adults have been identified to the species level. The nauplii have been counted together.

The fitting of our model to this populations assemblage taken as a whole allows us to calculate parameters for the equations governing the several development stages.

1. Development time.

We found a development time of 7, 6 and 6 days respectively for the naupliar, the copepodite and the adult stages.

2. Growth rate.

The daily exponential growth rate k is determined from the general expression

$$B_t = B_o e^{kt}$$

where B_o is the biomass at time to

where B_t is the biomass at time t_t

where t is the time t_t - to

According to literature data the individual weight at the beginning of each stage is :

- naupliar I stage	0,19 µg C
- copepodite I stage	0,62 µg C
- adult	3,2 µg C

Thus the growth coefficient k_1 calculated for the nauplii is 0,17 d^{-1} and for the copepodites o,27 d^{-1};

3. Sex-ratio

As can be seen in table 2 the sex-ratio of *Temora longicornis* is 0,5 on an average. For *Paracalanus parvus* and *Acartia clausi* there seems to be more ♀ than ♂.

4. Mortality.

The model allows us to calculate a mortality rate of :

$0{,}18\ d^{-1}$ for the nauplii
$0{,}2\ d^{-1}$ for the copepodites
$0{,}18\ d^{-1}$ for the adults.

VI. RESULTS OF THE SIMULATION

The figures of the optimized coefficients are :

$b = 15000$ individuals m^{-3}
$a = 0{,}0035$
$d = 127^{th}$ day in the year
$t_o = 90^{th}$ day in the year
$t_f = 160^{th}$ day in the year

$p_1 = 7$ days
$p_2 = 6$ days
$p_3 = 6$ days
$m_1 = 0{,}18\ d^{-1}$
$m_2 = 0{,}2\ d^{-1}$
$m_3 = 0{,}18\ d^{-1}$

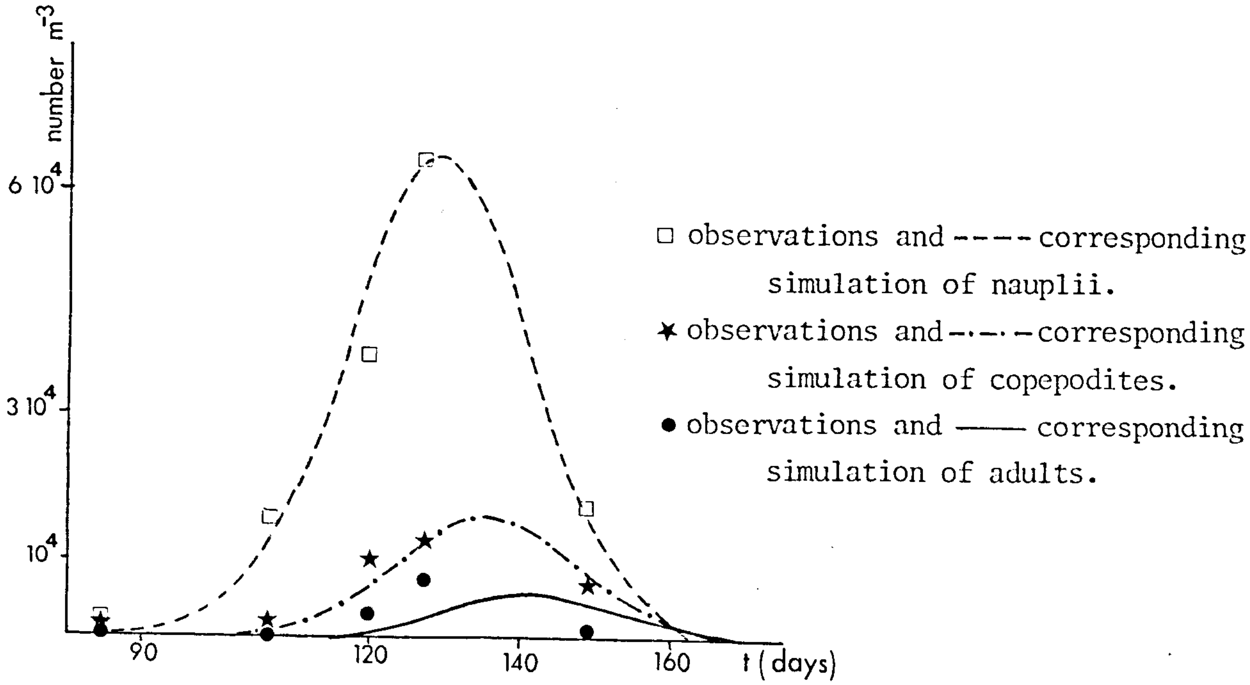
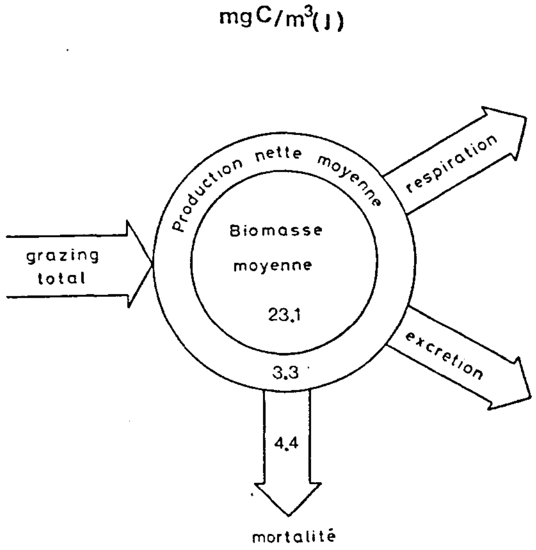


Fig. 2. Fluctuations of the number of the three development stages observed in the Southern Bight of the North Sea in 1974 and the corresponding mathematical simulation.

VII. BUDGET



From the day 90 to the day 160.

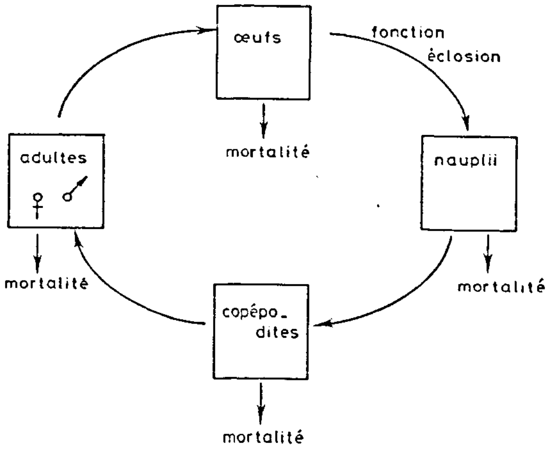


Fig. 1. Life history of a copepod.

VIII. CONCLUSION.

At the present stage, this model, however considering only a global population, gives reasonably good results. It is well suited for the simulation of several species taken independently. Very encouraging results were obtained with the 1977 observations serie (paper in preparation). Keeping the coefficients constant implies that the environmental conditions are not changing during the development of the population.

In the future it will also be interresting to include a forcing effect of temperature as well as several other regulation mechanisms (food, competition, predation, etc....).

TABLE 1. MATHEMATICAL SYMBOLS.

Nauplii	Copepodites.	Adults	Populations parameters.
N_t^j			numbers in cohort j, still alive on day t
N_t^T			numbers (all cohorts) still alive on day t
N	C	A	numbers (all cohorts) observable during the whole generation.
		A^*	total number of adults during the whole generation.
n	c	a	total number of dead during the whole generation.
i_1	i_2	i_3	age of a given individual (days)
p_1	p_2	p_3	maximum age of a given individual (days)
m_1	m_2	m_3	specific mortality rate.

Nauplii	Copepodites	Adults	Stocks and production parameters
B_o^N			Initial biomass of an individual
$B_{i_1}^N$			Biomass of an individual of age i_1
k_1	k_2		Specific exponential growth rate.
P^N	P^C		Net production for the whole generation.
			Hatching.
P^E			Egg production for the whole generation.
B^E			Biomass of an egg.
α			Proportion of ♀ in the population.
o			Average number of eggs / ♀
E			Number of eggs during the whole generation.
a			Coefficient giving the dispersion of the normal curve.
b			Maximum number of nauplii hatched on day d.
d			Day with the highest hatched number.
N^d			Number of nauplii hatched on day j.

	25-3-74		17-4-74			30-4-74			7-5-74			29-5-74		
	Copepodites	Adults	Copepodites	Adults		Copepodites	Adults		Copepodites	Adults		Copepodites	adults	
				♀	♂		♀	♂		♀	♂		♀	♂
Temora longicornis	120	0	360	80	0	6340	1000	1	9460	2600	3120	1520	280	300
Acartia clausi	0	0	340	20	0	1340		100	1660	680	160	320	0	0
Paracalanus parvus	0	0	0	20	0	120	420	100	20	780	120	0	80	0
Indetermined	0	0	1180	0	0	2400	0	0	1780	0	0	1180	0	0
Rest	0	0	40	0	0	200	460		160	620		4060	480	
Nauplii	880		16420			38560			64600			17980		

Table 2. Fluctuations of the numbers m^{-3} of the nauplii, copepodites and adults in the Southern Bight of the North Sea, 1974.

REFERENCE.

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