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Population dynamics of copepods in the Southern Bight of the North Sea (1977-1979)

Use of a multicohort model to derive biological parameters

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Introduction

The aim of this study is the analysis and the interpretation of the population density fluctuations in time so that we can attempt an evaluation of dynamic parameters such as growth rate, mortality rate, fecundity and also of the net production.

Contrasting to our approach this problem has been studied *in vitro* in most cases (Gaudy, 1974; Heinle, 1970; Mc Laren, 1975; Paffenhöfer, 1970, 1976; Razouls, 1974).

However, it is often useful to assess values of such parameters for *in situ* natural conditions. But the situation is then much obscured since the zooplankton contains together different development stages and even different generations.

In order to solve this problem of sorting out and calculating population parameters and production values, a multicohort model simulating the life history of the copepods has been developed.

The first development stage is a tiny larva called nauplius (fig. 1). Nauplii grow in size and weight until a transformation occurs. Meanwhile, a number of them have died. The development stage that follows this transformation is called copepodite. Again copepodites grow and some of them die until the transformation to the adult stage occurs. Adults grow very little but females produce eggs so that the cycle can start again.

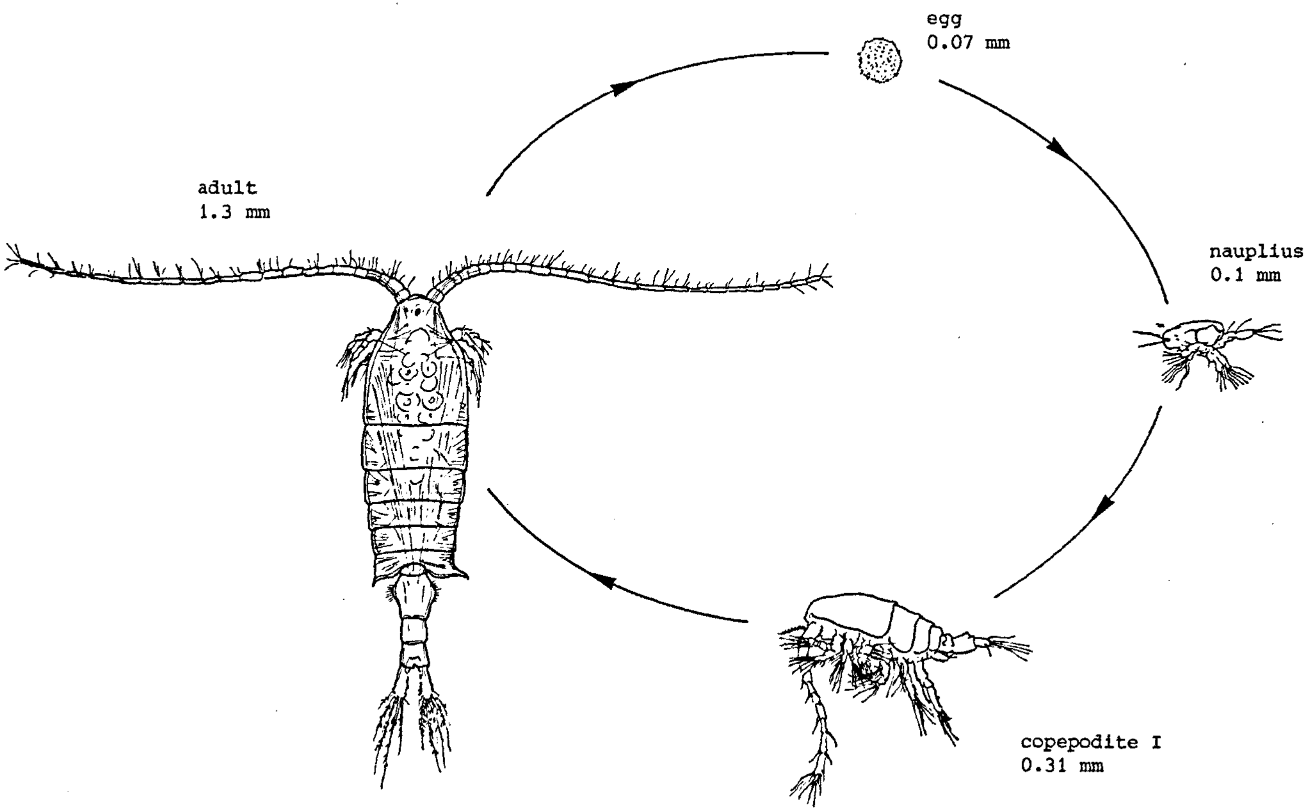


fig. 1.

Development stages of a copepod

In the North Sea three populations predominate : *Temora longicornis,* O.F. Müller; *Pseudocalanus elongatus,* Boeck and — to a lesser extent — *Acartia clausi,* Giesbrecht. The evolution of the two more abundant populations has been simulated with the model.

The simulation model

The numbers daily hatched during a given period are not constant : there is an increase at first and then a decrease.

This aspect is very important for the working of our simulation model. Indeed a special function describing this phenomenon, generates every day a new cohort, and thus serves as forcing function for the model.

A normal law has been chosen for the simulation of the hatching function in a simple way. Table 1 explains the different symbols.

Table 1

Nauplii	Copepodites	Adults	Populations parameters
N^j			Number of nauplii hatched on day j (= cohort j)
N_t^j			Numbers in cohort j , still alive on day t
N_t	C_t	A_t	Numbers (all cohorts) observable at time t
m_1	m_2	m_3	Specific mortality rate
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)
			Stocks and production parameters
B^N			Biomass of an individual
B_0^N			Initial biomass of an individual
k_1			Specific exponential growth rate
P_t^N			Net production (all cohorts) on day t
			Spawning and hatching
α			Coefficient giving the dispersion of the normal curve
β			Day with the highest hatched number
b			Number of nauplii hatched on day β

1.- THE HATCHING FUNCTION

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

2.- EQUATION FOR THE NAUPLIAR STAGES

For a cohort j the numbers of individuals decrease in function of the exponential mortality rate m_1 :

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

Hence, the number of living individuals at a time t between t_0 and t_f is

$$N_t = \int_0^{p_1} b\ e^{-a(t-\beta-i_1)^2 - m_1 i_1}\ di_1 \tag{3}$$

3.- EQUATIONS FOR THE OTHER DEVELOPMENT STAGES

Similar equations are developed for the copepodites and the adults :

$$C_t = \int_0^{p_2} b\ e^{-a(t-\beta-p_1-i_2)^2 - m_1 p_1 - m_2 i_2}\ di_2 \tag{4}$$

$$A_t = \int_0^{p_3} b\ e^{-a(t-\beta-p_1-p_2-i_3)^2 - m_1 p_1 - m_2 p_2 - m_3 i_3}\ di_3 \tag{5}$$

4.- EQUATIONS FOR THE NET PRODUCTION

Combining the equation for the net production of a single individual (*e.g.* a nauplius) during a given day (*e.g.* i_1) :

$$B_t^N = B_0^N\ e^{k_1 i_1}\ (e^{k_1} - 1) \tag{6}$$

with the equation for the numbers [*e.g.* equation (3)], one has

$$P_t^N = \int_0^{p_1} b\ e^{-a(t-\beta-i_1)^2 - m_1 i_1}\ B_0^N\ e^{k_1 i_1}\ (e^{k_1} - 1)\ di_1 \tag{7}$$

Application of this model

This model has been applied in the Southern Bight of the North Sea. Sampling was done daily from the lightship *West-Hinder* during the years 1977, 1978, 1979.

Two species predominate in this area : *Temora longicornis,* O.F. Müller and *Pseudocalanus elongatus,* Boeck. Figures 2(a,b), 3(a,b) and 4(a,b) show the seasonal evolution of numbers for the three categories of development stages in the predominating populations. The curves of 1977 are smoothed, using a floating-average technique. The seasonal evolution of the two species clearly shows a succession of three generations.

These population curves are synchronized for both species but with a marked opposition between the abundance patterns which is suggestive of interspecific competition.

We have no explanation for the higher numbers of nauplii observed in 1978 and for the low numbers observed in 1979.

The population curves generated by the model, after fitting, are given in figures 2(c,d), 3(c,d) and 4(c,d). The parameters of the model are adjusted so that an optimal fit is obtained with the field observations. The values for the growth rate, mortality rate and life span calculated thanks to the simulation are given in table 2.

LIFE-HISTORY PARAMETERS

1.- *Life span*

The life span computed for *Temora longicornis* varies between 23 and 39 days. Harris and Paffenhöfer (1976) have determined values in the range 21-30 for the same species grown *in vitro*. For *Pseudocalanus elongatus* the model gives a span of 19.5-25 days whereas Paffenhöfer and Harris (1976) find 24-29 days *in vitro*. Corkett and Urry (1968) give figures comprized between 14 and 116 days *in vitro*.

2.- *Growth rate*

According to the simulation, the growth rate tends to increase with the generation number. The rate computed for the nauplii of *Temora longicornis* varies between 0.09 and 0.24 day^{-1} . Harris and Paffenhöfer (1976) find a range of 0.12 - 0.21 *in vitro*. The copepodites exhibit growth rates between

Temora longicornis (O.F. Müller)

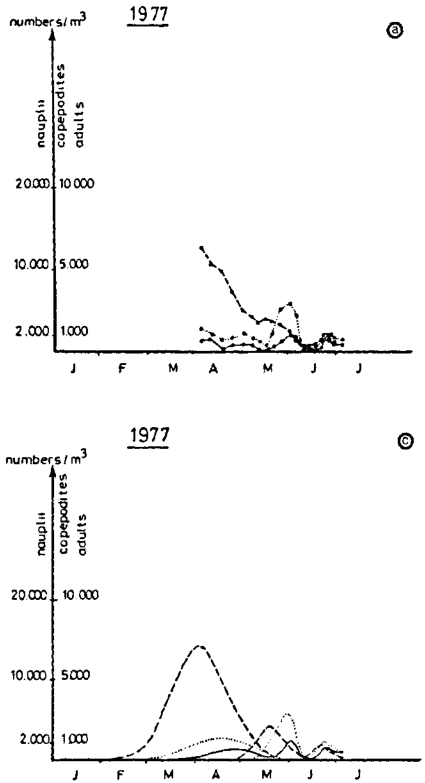


fig. 2.

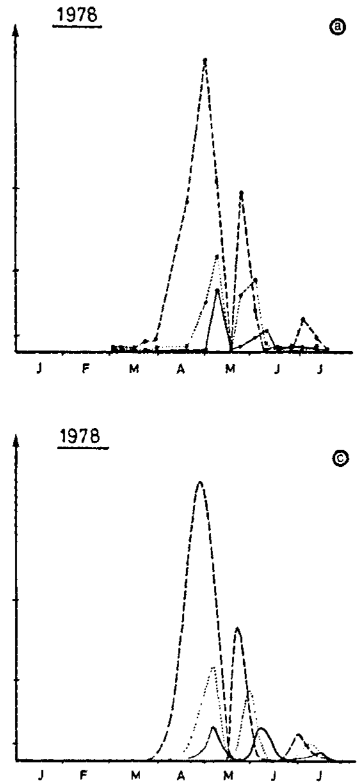


fig. 3.

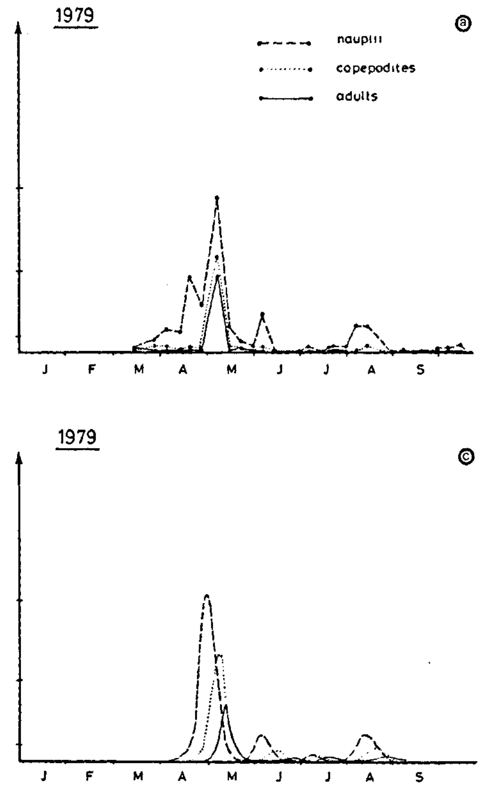


fig. 4.

Pseudocalanus elongatus (Boeck)

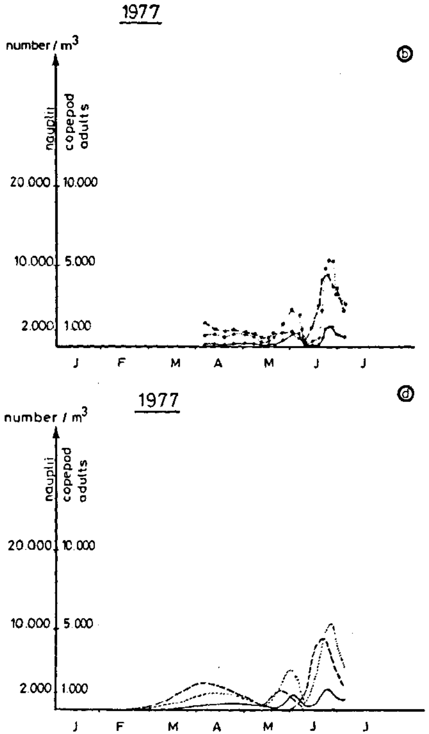


fig. 2.

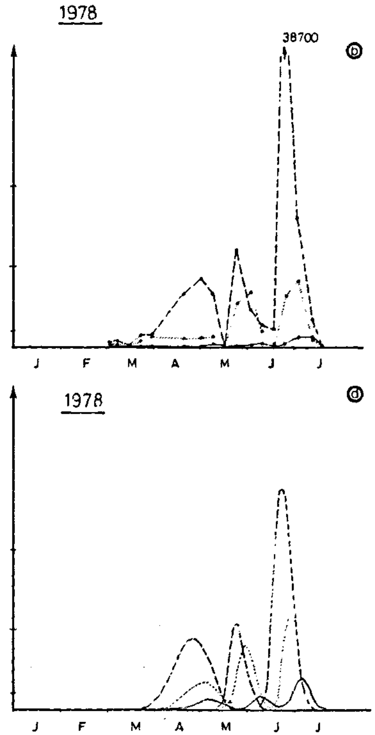


fig. 3.

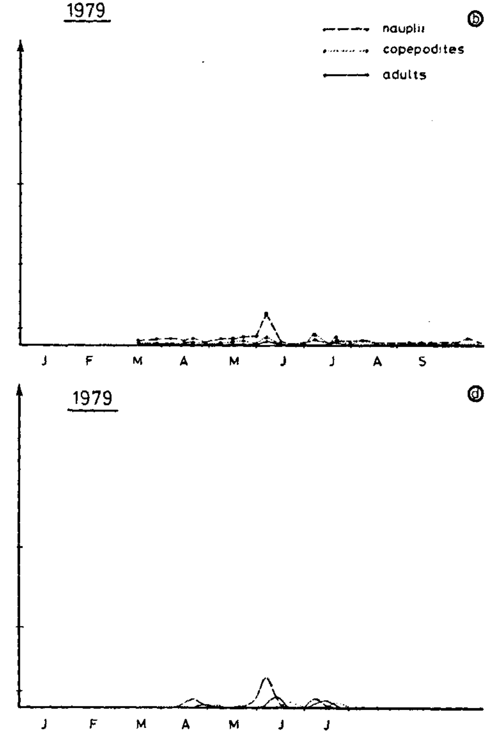


fig. 4.

Table 2

	Developing time (days)			Growth rate (day^{-1})			Viable eggs implied		Mortality rate (day^{-1})		
Generations	1	2	3	1	2	3	1	2	1	2	3
Temora longicornis											
Nauplii 77	13	10	5	0.09	0.12	0.24			0.22	0.10	0.15
78	9	9	8	0.13	0.13	0.15			0.22 → 0.35	0.10	0.10
79	8	9	5	0.15	0.13	0.24			0.15	0.18	0.13
Copepodites 77	13	13	5	0.13	0.13	0.33			0.1	0.001 → 0.3	0.001 → 0.15
78	8	9	6	0.21	0.18	0.27			0.07 → 0.27	0.17 → 0.22	
79	7	9	5	0.23	0.18	0.33			0.1 → 0.3	0.2	0.2
Adults 77	13	14	13	0	0	0	14	11	0.001	0.001 → 0.05	0.001 → 0.2
78	12	10	10	0	0	0	4	4	0.001	0.001 → 0.1	0.001 → 0.2
79	8	13	13	0	0	0	1	8	0.01 0.1	0.15	0.1
Total 77	39	37	23								
78	29	28	24								
79	23	31	23								
Pseudocalanus elongatus											
Nauplii 77	7	4	5.5	0.24	0.43	0.31			0.20	0.25	0.13
78	8	6	6	0.22	0.29	0.29			0.20	0.15	0.25
79	8	6	6	0.22	0.29	0.29			0.20	0.23	0.2
Copepodites 77	7	10	6	0.20	0.14	0.24			0.15	0.0005 → 0.4	0.10 → 0.25
78	7	7	6	0.20	0.20	0.24			0.20	0.15	0.20
79	7	7	6	0.20	0.20	0.24			0.20	0.25	0.15
Adults 77	9	11	8	0	0	0			0.20	0.0005 → 0.4	0.05 → 0.40
78	10	9	8	0	0	0			0.10	0.10	0.20
79	9	10	9	0	0	0			0.2	0.02	0.001
Total 77	23	25	19.5								
78	25	22	20								
79	24	23	21								

0.13 and 0.33 whereas Harris and Paffenhöfer (1976) find a range of 0.14 - 0.54 *in vitro*. As far as *Pseudocalanus elongatus* is concerned, the simulation gives rates in the range 0.22 - 0.43 for the nauplii and 0.14 - 0.24 for the copepodites whereas the above mentioned authors find respectively 0.14 - 0.18 and 0.04 - 0.38 *in vitro*.

3.- *Viable eggs*

The population curves simulated imply minimal numbers *i.e.* viable eggs. These numbers vary here between 1 and 14 for a female of *Temora longicornis* and 7 to 93 for a female of *Pseudocalanus elongatus*. Harris and Paffenhöfer (1976) find a range of 17 - 871 for *Temora longicornis in vitro* and Paffenhöfer and Harris (1976) find a range of 2 - 136 for *Pseudocalanus elongatus in vitro*.

4.- *Mortality rate*

According to the simulation, the mortality rate decreases as the development proceeds. Moreover, adaptations of the rate are generally not needed for the naupliar stages : for *Temora longicornis* the range is 0.10 to 0.22 and for *Pseudocalanus elongatus* it is 0.13 to 0.25.

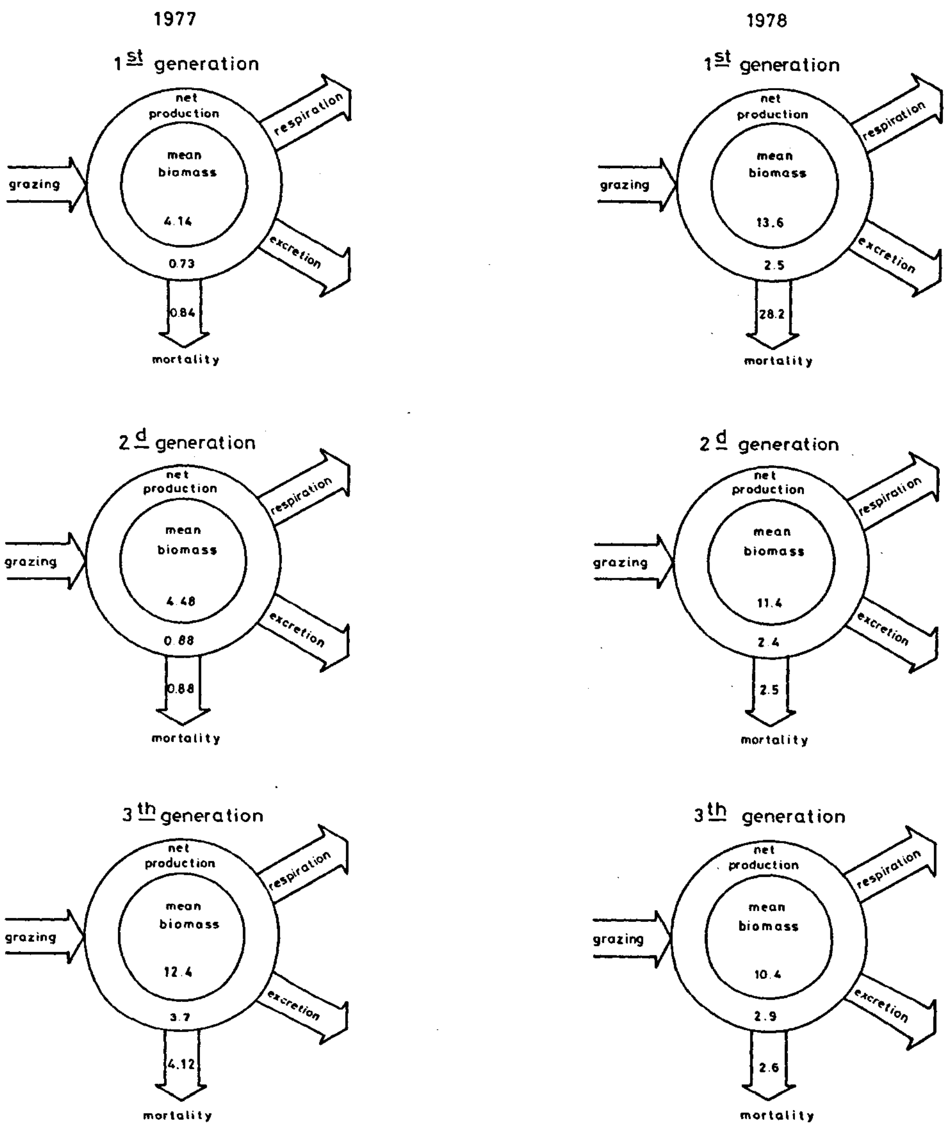
Harris and Paffenhöfer (1976) and Paffenhöfer and Harris (1976) find respectively 0.012 - 0.064 and 0.008 - 0.059 *in vitro* (recalculated figures). Where copepodites are concerned the ranges computed are 0.001 - 0.3 for *Temora longicornis* [0 - 0.0023 in Harris and Paffenhöfer (1976)] and 0.005 - 0.4 for *Pseudocalanus elongatus* [0 - 0.021 in Paffenhöfer and Harris (1976)]. There are no comparable data available for the adults.

Thus, there is generally a good agreement between the figures computed for an *in situ* situation and the figures determined *in vitro* where life span and growth rate are concerned. Discrepancies of one or two orders of magnitude are however observed for the mortality rate figures. This can be explained by the differences existing between the natural environment and the aquarium : none seems to be food-limiting but the natural environment is much more hazardous. The differences observed in the numbers of viable eggs could be explained by the lower probability for a female to reach maturity in nature.

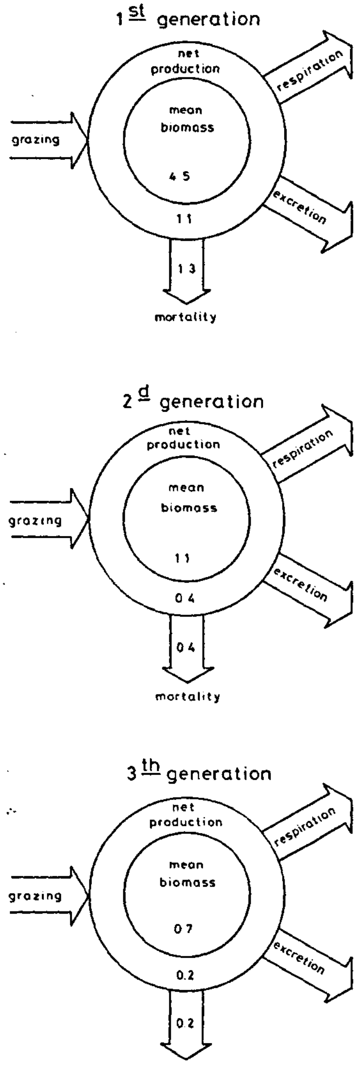
Thus, in order to achieve reasonably good predictive properties, an improved zooplankton model, regulated by the environmental conditions prevailing in the Southern Bight of the North Sea, should put the emphasis on the mortality and fertility functions.

Budget of metabolic activities

Pseudocalanus elongatus and *Temora longicornis* (mg C/m^3)



1979


1st generation
net production
respiration
mean biomass
grazing
4 5
excretion
1 1
1 3
mortality
2d generation
net production
respiration
mean biomass
grazing
1 1
excretion
0 4
0 4
mortality
3th generation
net production
respiration
mean biomass
grazing
0 7
excretion
0.2
0.2
mortality

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