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A MATHEMATICAL MODEL OF THE POPULATION DYNAMICS OF THE DOMINANT COPEPOD SPECIES IN THE SOUTHERN BIGHT OF THE NORTH SEA, 1977-1978.

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ABSTRACT

Growth rates, mortality rates and net production values were calculated for two populations of planktonic copepods dominant in the Southern Bight of the North Sea, by fitting a simulation model to the observed population curves. This model is of the multicohort type and takes the life history of the two species into account. It is driven by hatching frequency functions which have been parametrized. The results are compared with values from the recent literature and discussed.

RESUME

Les taux de croissance et de mortalité ainsi que la production nette de deux populations de copépodes planctoniques dominants de la Baie Sud de la Mer du Nord ont été calculés en ajustant un modèle mathématique aux courbes de population observées. Ce modèle est du type "multicohortes" et tient compte du cycle de vie des deux espèces. Il est commandé par des fonctions décrivant les fréquences d'éclosion et qui ont été paramétrisées. Les résultats sont comparés avec des valeurs de la littérature récente et discutés.

I. INTRODUCTION

Parametres that are particularly relevant to the population dynamics of marine copepods (i.e. growth rate, mortality rate) and their production have mostly been studied in vitro.

However, it is often desirable to assess values of such parametres for in situ natural conditions. 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 parametres and production values , a multicohort model simulating the life history of the copepods has been developed.

Three populations predominate in the study area : 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.

II. METHODS

Sampling was done daily at 4 P.M. from the lightship "West Hinder" (2°26'20"E 51°23'00"N) from January to July , during the years 1977 and 1978. Fifty litres of seawater were pumped from a depth of 3 metres and filtered on a 50 micrometres mesh net . The choice of a single depth was possible because of the good vertical homogeneization of the water in this part of the North Sea . The collected material was preserved with neutralized 4 % formalin . When counting , a particular attention was given to proper identification of the various development stages , including the nauplii .

III. RESULTS OF THE ENUMERATIONS

Figs. 1(a,b) and 2(a,b) show the seasonal evolution of numbers for the three categories of development stages in the predominating populations. These curves are smoothed , using a floating-average technique. The seasonal evolution of Pseudocalanus and Temora 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 so far no explanation for the higher numbers of nauplii observed in 1978 .

IV. THE SIMULATION MODEL

1. Short description

This model reduces the life history of the copepods to their three basic development stages : nauplii , copepodites and adults and makes the difference between males and females . Rates are assumed to remain constant for each development stage . However , better results are obtained if the mortality rate is increased when the numbers are maximal (in agreement with the observation of numerous empty carapaces at such times).

For each generation , the evolution of the number daily hatched is parametrized . These functions give their pace to the whole system.

2. Equations (symbols are explained in table 1)

2.1. the hatching function

A normal law describes the phenomenon :

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

2.2. equation for the naupliar stages

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

$$N_t^{j} = b\, e^{-\alpha (t - \beta)^{2} - m_1 i_1} \qquad (2)$$

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

$$N_t = \int_{i_1 = 0}^{i_1 = p_1} b\, e^{-\alpha (t - \beta - i_1)^{2} - m_1 i_1}\, di_1 \qquad (3)$$

2.3. equations for the other development stages

Similar equations are developed for the copepodites and the adults :

$$C_t = \int_{i_2 = 0}^{i_2 = p_2} b\, e^{-\alpha (t - \beta - p_1 - i_2)^{2} - m_1 p_1 - m_2 i_2}\, di_2 \qquad (4)$$

$$A_t = \int_{i_3=0}^{i_3=p_3} b\, e^{-\alpha(t-\beta-p_1-p_2-i_3)^2 - m_1p_1 - m_2p_2 - m_3i_3}\, di_3 \quad (5)$$

2.4. 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) :

$$\frac{\Delta B^N}{\Delta t} = B_0^N\, e^{k_1 i_1} (e^{k_1} - 1) \quad (6)$$

with the equation for the numbers (e.g. equation (3)) ; one has :

$$P_t^N = \int_{i_1=0}^{i_1=p_1} b\, e^{-\alpha(t-\beta-i_1)^2 - m_1 i_1}\, B_0^N\, e^{k_1 i_1} (e^{k_1} - 1)\, di_1 \quad (7)$$

V. RESULTS OF THE FITTING OPERATIONS AND DISCUSSION

The population curves generated by the model , after fitting , are given in figs. 1(c,d) and 2(c,d) . As can be seen , the agreement with the observed curves is good. The values of the various parametres calculated in this way are given in table 2 .

1. Life span : according to the simulation , the life span of an individual tends to decrease with the generation number in both species . The life span computed for Temora varies between 23 and 39 days . Harris and Paffenhöffer (1976) have determined values in the range 21-30 for the same species growed in vitro . For Pseudocalanus the model gives a span of 19.5-25 days whereas Paffenhöffer 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 varies between 0.09 and 0.24 day^{-1} . Harris and Paffenhöffer (1976) find a range of 0.12-0.21 in vitro . The copepodites exhibit growth rates comprized between 0.13 and 0.33 whereas Harris and Paffenhöffer (1976) find a range of 0.14-0.54 in vitro . As far as Pseudocalanus 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 4 and 14 for a female of Temora and 7 and 33 for a female of Pseudocalanus. Harris and Paffenhöffer (1976) find a range of 17-871 for Temora in vitro and Paffenhöffer and Harris (1976) find a range of 2-136 for Pseudocalanus 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 the range is 0.10 to 0.22 and for Pseudocalanus it is 0.13 to 0.25 . Harris and Paffenhöffer (1976) and Paffenhöffer 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 (0-0.0023 in Harris and Paffenhöffer,1976) and 0.005-0.4 for Pseudocalanus (0-0.021 in Paffenhöffer 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 .

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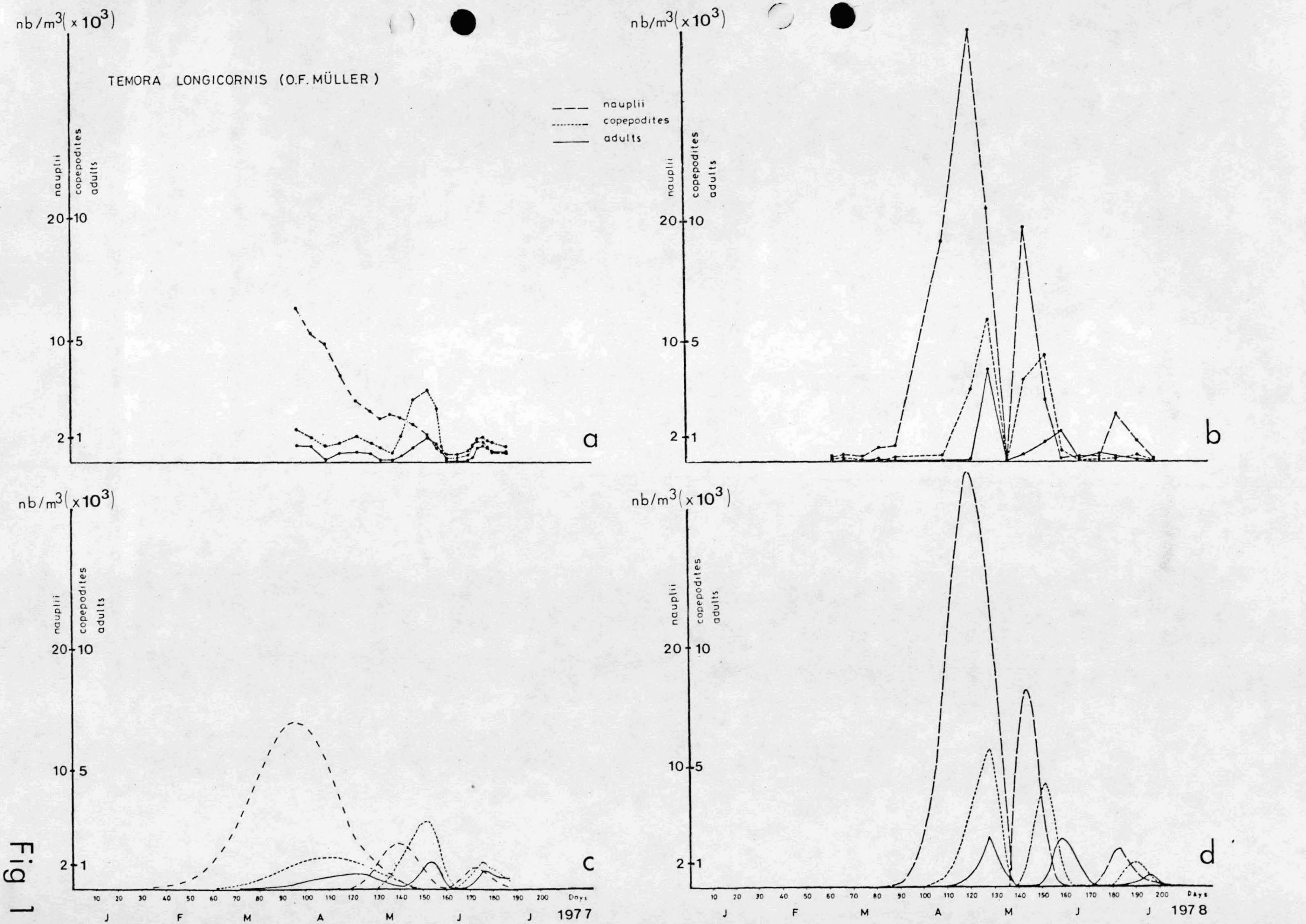
TABLE 1. LEGENDS OF THE SYMBOLS.

Nauplii	Copepodites	Adults	
			Populations parameters :
Nj			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).
			Stoks 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.

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 : 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
copepo-	77	13	13	5	0.13	0.13	0.33			0.1	0.001→0.3	0.001→0.15
dites	78	8	9	6	0.21	0.18	0.27			0.07→0.27	0.17→0.22	0.001→0.25
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
total	77	39	37	23								
	78	29	28	24								
Pseudocalanus : 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
copepo-	77	7	10	6	0.20	0.14	0.24			0.15	0.005→0.40	0.10→0.25
dites	78	7	7	6	0.20	0.20	0.24			0.20	0.15	0.20
adults	77	9	11	8	0	0	0	7	20	0.20	0.0005→0.40	0.05→0.40
	78	10	9	8	0	0	0	33	29	0.10	0.10	0.20
total	77	23	25	19.5								
	78	25	22	20								



TEMORA LONGICORNIS (O.F. MÜLLER)
nauplii
copepodites
adults
nb/m3(x 10³)
a
b
c
d
Days
J
F
M
A
M
J
J
1977
1978

Fig 1

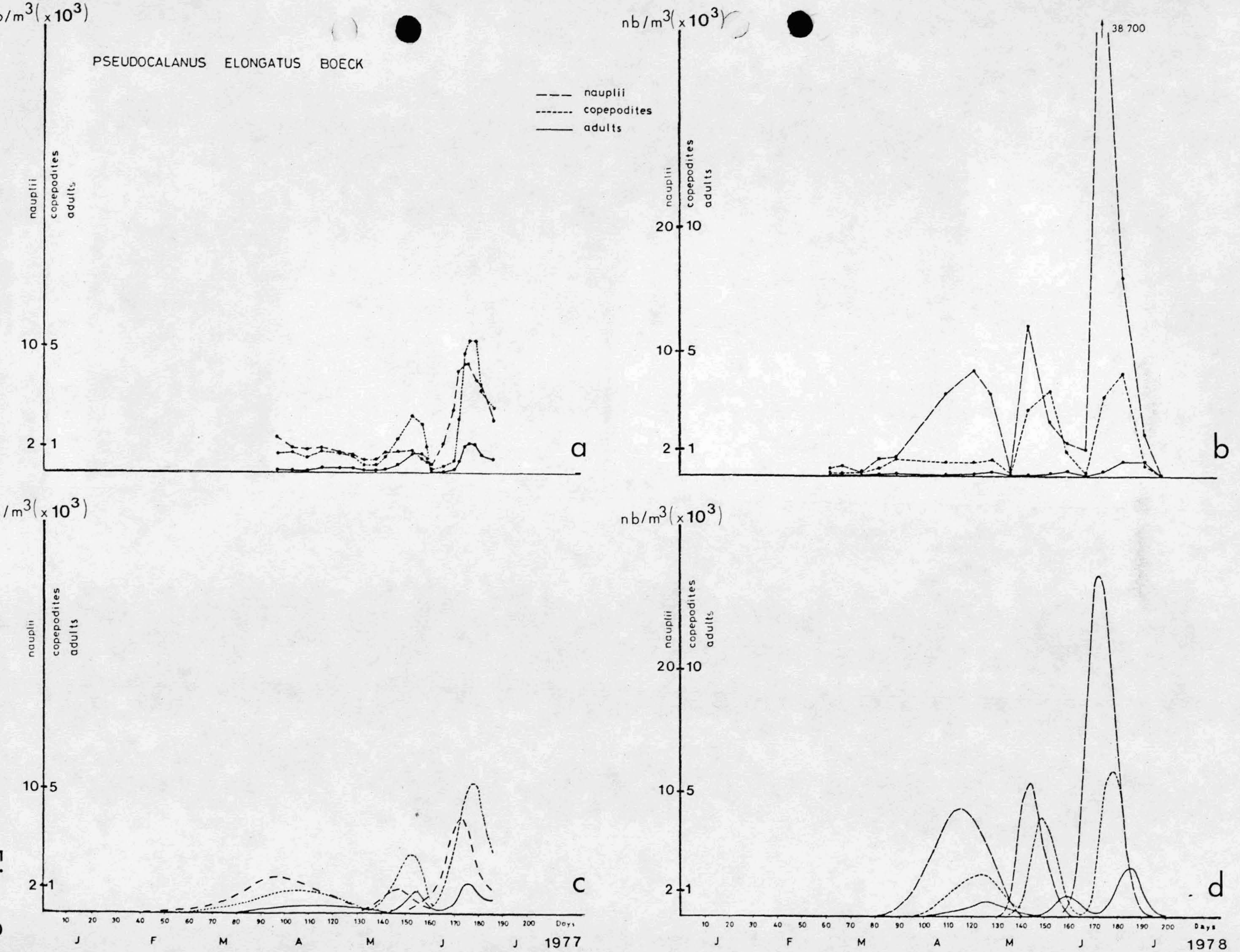

PSEUDOCALANUS ELONGATUS BOECK
nauplii
copepodites
adults
nb/m3 (x 10^3)
38 700
a
b
c
d
Days
J F M A M J J
1977
1978

Fig 2