Cah. Biol. Mar. (1993), **34** : 201-214
Roscoff

Estimating secondary production for the brackish Westerschelde copepod population *Eurytemora affinis* (Poppe) combining experimental data and field observations.

V. Escaravage and K. Soetaert
Netherlands Institute of Ecology
Centre for Estuarine and Coastal Ecology
Vierstraat 28, 4401 EA Yerseke - The Netherlands

Abstract : *Eurytemora affinis* (Poppe) (Copepoda : Calanoida) development is studied through cultures supplied with naturally occurring particulate matter (Western Schelde estuary) and kept at six constant temperatures in the range 2-20 °C. At 2 °C the copepods do not reach the copepodite stages and at 5 °C, do not develop further than the fourth copepodite stage.

A field production estimate is given combining the biomass present in the field and weight specific growth rates derived from the culture experiment. The P/B obtained are very close with those measured for the same species in other estuaries.

Résumé : Le développement du Copépode *Eurytemora affinis* (Poppe) a été étudié grâce à des cultures dans lesquelles la nourriture fournie était constituée de particules provenant du milieu naturel (estuaire de l'Escaut occidental) et maintenues à six températures constantes dans la gamme 2-20 °C. À 2 °C les Copépodes n'atteignent pas le stade copépodite 1 et à 5 ° C les individus ne dépassent pas le 4e stade copépodite.

Une estimation de la production naturelle a été faite en combinant la biomasse mesurée dans le milieu et les taux spécifiques de croissance pondérale calculés à partir des élevages expérimentaux. Les valeurs de P/B obtenues sont très proches de celles mesurées pour la même espèces dans d'autres estuaires.

INTRODUCTION

Calanoids copepods constitute a dominant group in estuarine planktonic communities. Among them, the species *Eurytemora affinis* (Poppe) is distributed world wide and particularly abundant in the brackish areas of the North Atlantic zone where it alone may represent more than 90 % of the planktonic copepods. With densities up to 100,000 individuals per m^3 (Bakker *et al.*, 1977), this species plays a significant role in the estuarine trophic food web such as a link to higher exploitable levels (Mauchline, 1970 ; Burkill & Kendall, 1982).

Such high densities make any quantitative approach of the estuarine productivity strongly relying on precise knowledge about the *in situ* dynamics of these populations. Unfortunately the existence of mixed cohorts resulting from a continuous reproduction makes it hard to elucidate the demographic dynamics of these populations, even through a high frequency field sampling. Thus, one has to turn to laboratory cultures.

The two main variables controlling population dynamics in the field are bemperature and food availability (quantity and quality) (Nassogne, 1970 ; Klein-Breteler & Gonzalez, 1988). In cultures devoted to a description of field processes, one has to keep a high simila-

rity between experimental and field conditions concerning temperature and food availability. If such conditions are reproduced within the cultures, one may expect the copepods to express a similar metabolism as in the field.

Most of the published data concerning the development rate of this species used cultures supplied with artificial food (Heinle, 1970 ; Katona, 1970 ; Heinle & Flemer, 1975 ; Burkill & Kendall, 1982 ; Vuorinen, 1982). However many papers dealing with zooplankton grazing gave evidence of the importance of suspended and sedimentary inert particles in the diet of many calanoid copepods including *E. affinis* (Heinle & Flemer, 1975 ; Heinle *et al.*, 1977 ; Lenz, 1977 ; Chervin, 1978 ; Boak & Goulder, 1983 ; Roddie, 1988 ; Powell & Berry, 1990). As far, only Poli (1982) and Poli & Castel (1983) produced results about the duration of *E. affinis* development in cultures supplied with naturally occurring particulate matter (Gironde estuary, France). However, according to the specificity of the estuarine particles in term of their nutritive potential, such experiments can not be generalized and have to be done for each estuary.

Firstly, cultures of *E. affinis* (Western Schelde estuary) have been performed in so called 'field simulated' conditions of temperature and food availability in order to obtain growth rates matching natural rates. These growth rates were then applied to the abundances measured in the field population over a year cycle to provide an estimate of the *in situ* secondary production.

This study is a part of a multi-disciplinary research of the Westerschelde, aiming at an ecosystem model of the entire estuary, and part of the Joint European Estuarine Program (Jeep I, MAST Program) of the Commission of the European Community.

METHODS

Sampling of the natural populations

Field sampling and samples processing have been performed by K. Soetaert and P. van Rijswijk ; the field data used here are part of Soetaert & Rijswijk (submitted). The sampling area was in the lower estuarine part of the Schelde, called the Westerschelde. Zooplankton and auxiliary environmental data were collected from October 1989 to October 1990 on thirty surveys with a mean time interval of twelve days between each. During each survey twelve stations were sampled along a longitudinal transect from the mouth of the Westerschelde (Vlissingen) to Antwerp (limit of the saline intrusion). At each sampling point hundred liters of water were collected (pump Pleuger type, n#64) beneath the surface, above the bottom and at mid depth. These samples were poured over a 55 µm mesh size net, pooled and fixed in buffered 4 % formaldehyde. The present study concerns only with the depth averaged results of the stations situated in the 10 ‰ salinity area (central part from the estuary). All development stages from the copepod *Eurytemora affinis* were enumerated and their biomass were directly measured or calculated by length-weight regression. Cephalothorax of copepods was measured using a digitizing tablet connected to a

microscop, weights measured using a CAHN electronic balance (precision 0.1 µg) after a 24 hours drying process at 60 °C.

Copepods culturing

The copepods used in the cultures (*Eurytemora affinis*) were isolated from the brackish part of the Western Schelde estuary (the Netherlands) in April 1990, June 1990 and March 1991 with a high speed sampler ("Nackthai" Hydrobios, towed at ≈ 3 knots) with a mesh size of 300 µm. Salinity was always around 10 ‰. The temperature ranges used in the cultures were chosen according to the corresponding field temperature (Table I).

TABLE I

Temperatures in the field at the sampling dates and corresponding ranges used in the cultures.

Date	April 1990	June 1990	March 1991
Temperature in the field (°C)	10	17	5
Temperature(s) in cultures (°C)	10	14 17 20	2 5 8

Culture medium characteristics

Each week about 40 l of water were collected from the same water mass as the copepods. This water was used as a culture medium stock after being filtered on a 55 µm mesh size sieve and maintained at field temperature. Settlement of particles was prevented by continuous pumping with an ordinary aquarium pump. The size spetrum of suspended particles, total particulate content (Coulter Counter) and chlorophyll pigment concentration (fluorimetry) were measured every two days in the culture medium stock to check the variations of these potential trophic indicators. In April 1990, these measurements have only been performed during the second half of the culture experiment.

Eggs incubation time

Paired copepods were incubated in 100 ml glass beakers filled with 40 ml culture medium and held at 2, 5, 8 and 14 °C (30 replicas per temperature). The beakers were checked twice a day in order to measure the incubation time counted between the egg sac appearance and the hatching of at least 50 % of the eggs.

Development rate

Copepods were cultured from adult to adult in 100 ml glass beakers filled with 40 ml of culture medium and held at the experienced temperatures (at least 30 copepods for each temperature). The density in these culture units was 10 and 2 individuals for nauplii and

copepodites respectively. The culture medium was renewed every two days in the beakers from the main stock. The copepods were checked every two days and their state of development was then noted.

Weight specific growth rates measurements

The molts released by copepods when accessing to a new stage were systematically collected, identified and measured. The molts lengths were converted into dry weights following a Log/Log weight length regression estimated in the course of this experiment. The mean development stage durations and dry weights being known, the weight specific growth rate was estimated following the 'instantaneous growth rate method' given in Rigler & Downing (1984) and modified by Polishchuk (1990). This method assumes the weight specific growth rate to be constant within a stage, i.e. :

$$g_i = \frac{1}{W_i} \frac{dW}{dt} = dLn(W_i)\, dt$$

approximated by :

$$g_i = \frac{Ln(W_i(t_2)) - Ln(Wi(t_1))}{(t_2 - t_1)}$$

When (t_2-t_1) equals the duration of stage i, the stage and weight specific instantaneous growth rate g_i can be calculated using for $W_i(t_1)$, the weight when entering stage i (W_i) and for W_i (t_2), the weight when leaving stage i (W_{i+1}). The stage duration being expressed in days, g_i is then a daily rate instead of a real instantaneous rate.

Adults reproductive effort

When reaching adulthood copepods almost stop to grow, most of their metabolism is then involved in the reproductive effort, this output as to be known for an estimate of the whole population production. At 8, 14, 17 and 20 °C, twenty couples have been followed from maturation to death and their reproductive products (eggs for the females, spermatophores for the males) have been counted and weighed.

Assuming these growth and fecundity rates representative for the field conditions (cultures supplied with naturally occurring particules) one can combine it to the biomasses measured in the field to give an estimate of the *in situ* secondary production integrated over the sampling time interval following the formula given by Polishchuk (1990) :

$$IP = \sum_i gi \frac{B_i(t_2) - B_i(t_1)}{Ln[B_i(t_2) / B_i(t_1)]} (t_2 - t_1)$$

RESULTS

Culture medium characteristics

Salinity in the culture medium was maintained between 10 and 13 ‰ corresponding to the range observed in the sampling area. The particulate spectrum measured every two days

showed no particular trend during the one week storage (Fig. 1). This rather constancy points out the efficiency of the continuous pumping in maintaining particles in suspension without affecting their size spectrum. Some microscopical examinations done on this water (C. Bakker & M. Vinck, pers. comm.) revealed a predominance of plant detritus and small phytoplanktonic cells (<10 µm ; mainly microflagellates). Throughout all this experiment, the same kind of spectrum has been observed. Moreover, the total particulate and pigment contents did not change significantly (particles : $t = 2.911$, $p<0.005$; pigments : $t = 1.204$, $p<0.25$) during and among the culture experiments (Fig. 2).

Eggs Incubation time

The eggs incubation time showed a pronounced inverse relationship with temperature with mean values of 10.3 days at 2 °C, 6.5 days at 5 °C, 4.3 days at 8 °C and 2.4 days at 14 °C. These values showed a good agreement with the formula of Corkett & Mc Laren (1970) ($D = 1640 (T + 10.4)^{-2.05}$) defined for the same species (from Halifax waters, N.S). This formula was used in what follows to calculate the egg incubation times.

Development rate

At the lower temperatures, 2 and 5 °C, the copepods did not achieved a complete development. At 2 °C, it was impossible to obtain a transition to the copepodite stage, even for

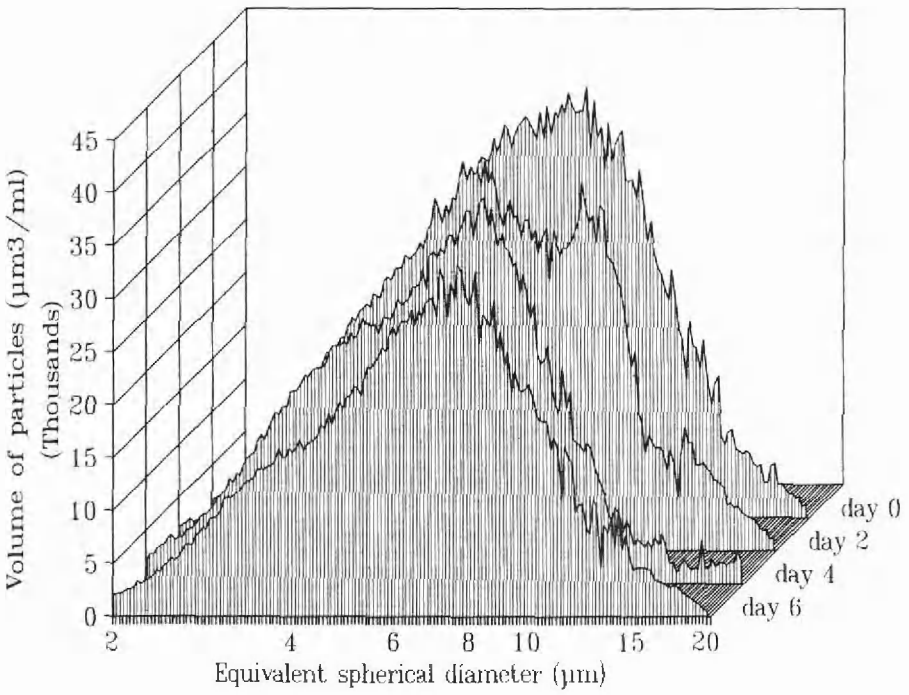

Fig. 1 : particulate spectra (Equivalent spherical diameter) of the culture medium measured during a one week storage (Coulter-Counter particles counter fitted with a 100 µm orifice tube).

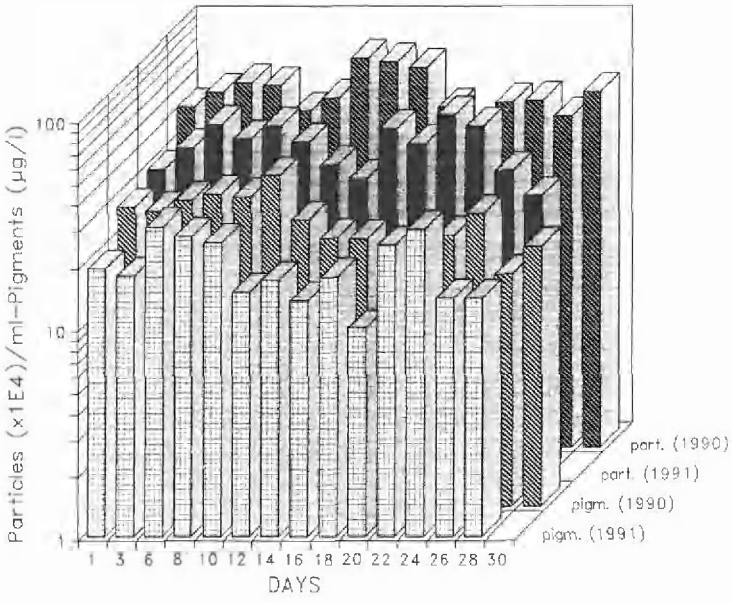

Fig. 2 : Total particulate content (2 to 60 µm E.S.D.) and pigments content in the culture medium in June 1990 and March 1991.

nauplii older than 5 weeks. Whereas at 5 °C no copepod succeeded to molt to the fifth copepodite stage even after 60 days counted from hatching. This mechanism has been inspected for nauplii by transferring a group of 36 days old nauplii raised at 2 °C in a waterbath set to 5 °C. After two days at 5 °C some of them began to molt and this molting process went on during 20 days when the last nauplii did finally molt. In a second group of nauplii kept at 2 °C and used as control, no molting was recorded. Moreover, almost 30 % of these nauplii were dead after 80 days at 2 °C. These copepods perhaps reached a physiological limit beyond which it is no more possible to survive as nauplii.

A complete developement was obtained for the temperatures over 5 °C (Tabl. II). The development rate increased with temperature from 8 to 17 °C whereas this trend was far less pronunced between 17 and 20 °C. Heip (1974) suggested the use of the following equation : $D = a \times T^b$ (D : development time, T : temperature, a and b : parameters) to modelize such temperature dependent development rate for many copepods species. The calculation of a and b resumes to a regression analysis performed after a Log-Log transformation ($Log(D) = Log(a) + bLog(T)$). The temperature dependent development functions provided mean residence times (D_i) in each development stages (i) within a continuous thermic range. A better adjustment of the a and b values has been obtained by a calibration procedure run with the Seneca modelling package (Scholten *et al.*, 1990) as described in Escaravage (submitted) (a and b calibrated values are given in Tabl. III).

TABLE II

Development stages mean durations (n : number of cultured copepods, d : mean stage duration, C.I. : *confidence interval at 95 %)*

	Temperature (°C)	n	$\bar{d}$ (days)	C.I. (95 %)
naupliar stages	8	75	15.4	0.50
	10	97	7.9	0.14
	14	81	6.0	0.31
	17	95	4.9	0.14
	20	96	4.0	0.26
Copepodite I	8	37	3.5	0.50
	10	53	3.0	0.23
	14	34	2.6	0.21
	17	32	1.8	0.18
	20	32	1.9	0.11
Copepodite II	8	37	3.9	0.50
	10	53	2.2	0.25
	14	34	1.8	0.06
	17	32	1.6	0.10
	20	32	1.6	0.19
Copepodite III	8	37	5.2	0.70
	10	53	3.0	1.01
	14	34	1.7	0.08
	17	32	1.5	0.11
	20	32	1.8	0.20
Copepodite IV	8	37	11.3	1.70
	10	53	5.1	1.51
	14	34	1.9	0.12
	17	32	1.5	0.09
	20	32	1.9	0.22
Copepodite V	8	37	14.1	1.30
	10	53	5.8	1.60
	14	34	3.5	1.19
	17	32	2.3	0.42
	20	32	2.6	0.46
egg laying to adult	8	37	57.6	5.25
	10	53	26.8	3.50
	14	34	17.4	1.94
	17	32	14.2	0.94
	20	32	13.5	1.90

Stage specific growth rates estimate

A Log/Log weight length regression was calculated from individuals sacrificed in the course of the culture experiments. No significative difference was found among the cultures (different temperatures) or between the cultures and the field. Following, all these data were pooled to establish a common weight length regression for the field and the culture

TABLE III

a and b parameters charachterizing the stage specific temperature dependent development rate (Development time = $a_i \times T^{bi}$).

Development stages i	b_i	a_i
Nauplii	- 1.60	448.781
Copepodite I	- 1.30	62.429
Copepodite II	- 1.30	64.832
Copepodite III	- 1.30	74.992
Copepodite IV	- 1.96	530.682
Copepodite V	- 1.96	791.096

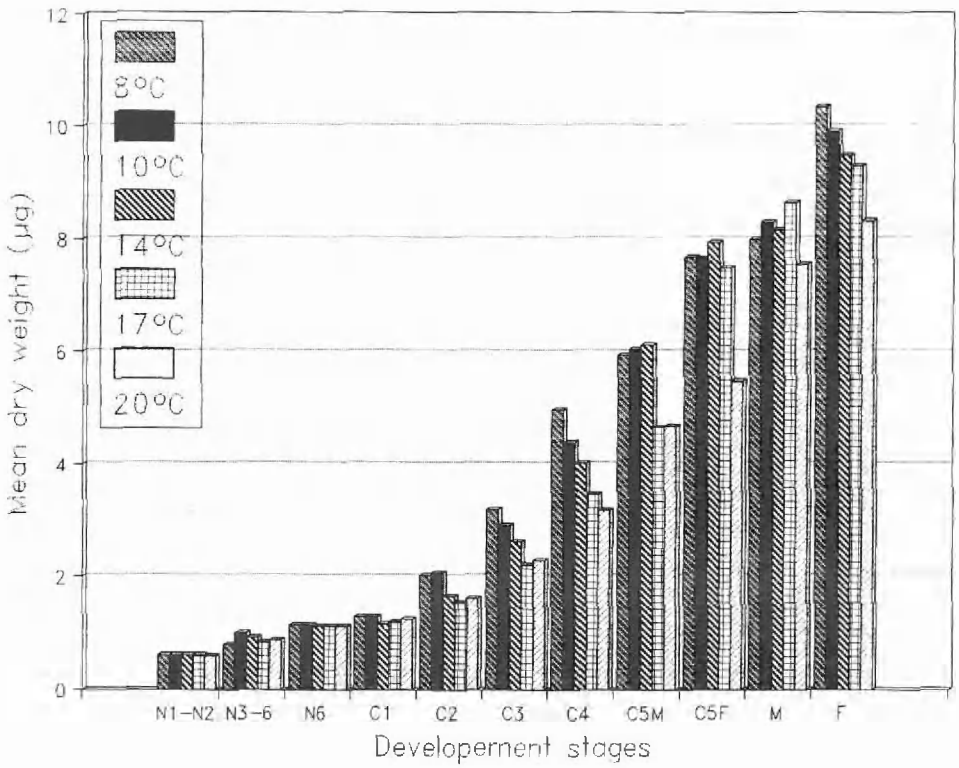

Fig. 3 : Stage specific dry weight obtained for different culture temperatures.

(Log(W) = 2.441 x Log(L) - 6.095, $r^2 = 0.97$, $p<0.05$). This relation was used to convert the molt lengths into the corresponding individual body dry weights from which were calculated the mean stage specific individual dry weights (Fig. 3).

From the mean stage development times (Tabl. II) and the mean stage individual weights were calculated weight specific instantaneous growth rates (see Methods for formulae).

The whole adult production was obtained by summing the reproductive production with the slight weight increase measured between the maturation and the death. These results were expressed in µg D.W./mg D.W./day and compared with the mean daily somatic production measured from N2 to C5 (Fig. 4). The ratio between the reproductive and the somatic productions was not constant, it varied from 50 to 150 % for the females but only from 40 to 60 % for the males. The male production reached 40 to 90 % of the female production.

Estimate of the in situ production

The *in situ* biomass evolution (Fig. 5) is characteristic for this species and can be divided in three phases : Winter emergence, Spring peak, Summer disappearance. Such pattern is supposed originated from a composiffon of internal dynamics (temperature controlled) and external control (predation, competition) (Bradley, 1975).

Combining this data set with the culture results (temperature controlled stage specific growth rates) one is able to estimate the production realized by the natural production (for-

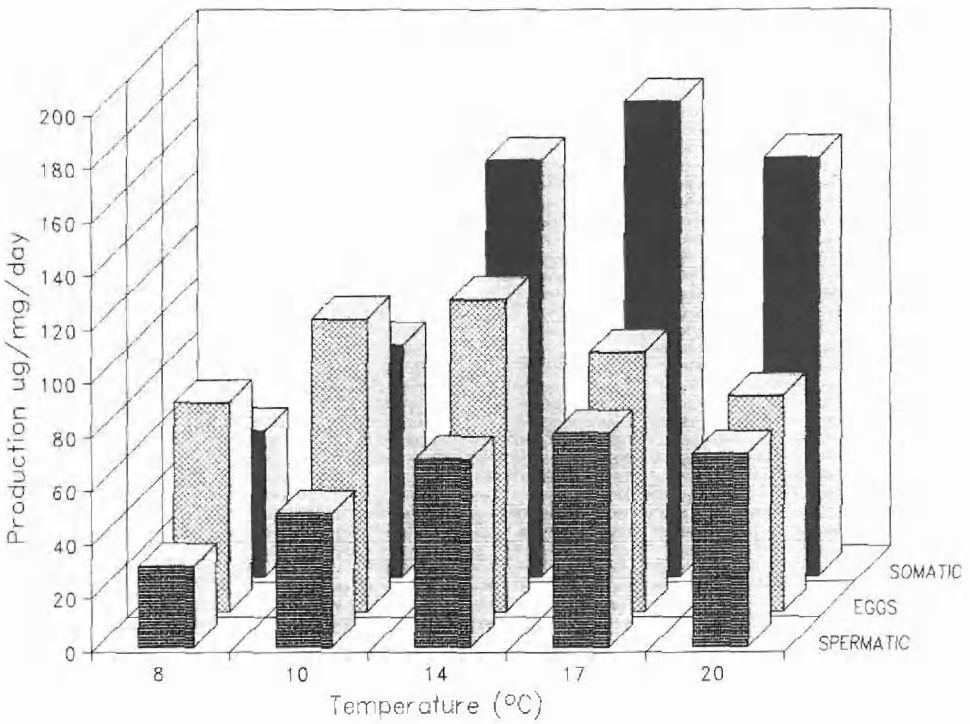

Fig. 4 : Eggs, spermatophores and somatic production expressed as weight specific daily productions.

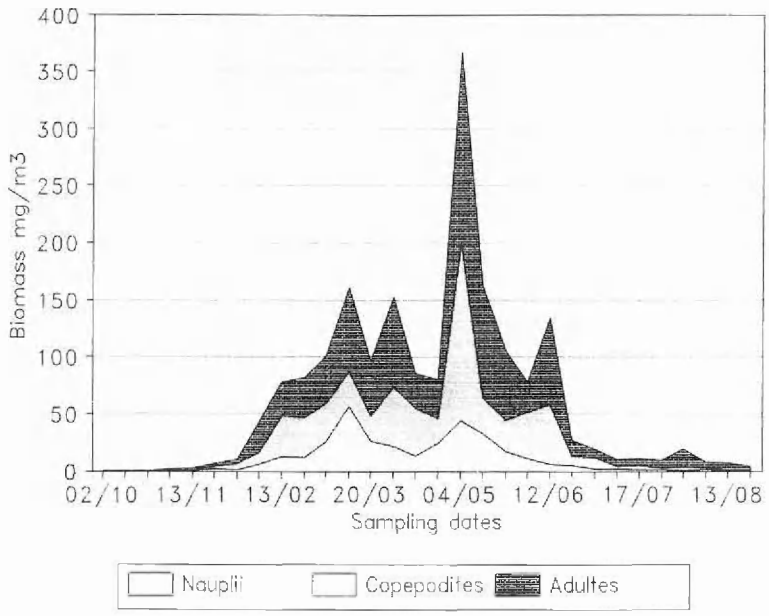

Fig. 5 : Biomass of *E. affinis* measured in the Western Schelde from October 1989 to October 1990.

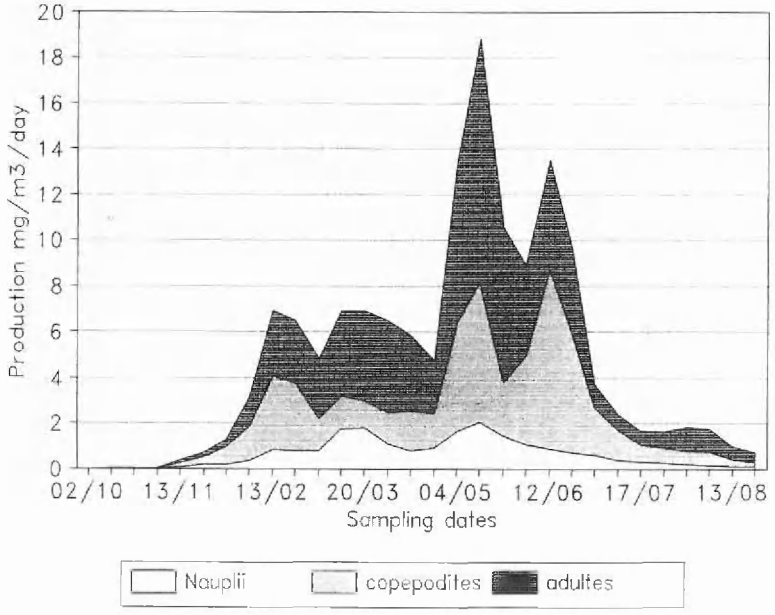

Fig. 6 : Production estimates obtained using the biomass showed in Figure 5 and the Polishchuk (1990) formula.

mulae in Methods) (Fig. 6). The production realized by the adults (including the reproductive effort) represented 50 % of the total production. The daily production was estimated by 5 mg/m^3/day and the annual integrated production by 1.6 g/m^3. A global P/B of 33 year $^{-1}$ was found for the whole population.

DISCUSSION

Culture conditions

One of the main problem arising in the course of these culture experiments was the quality of the culture medium in term of food availability. As soon as the medium was introduced in the beakers, particles began to settle, leading to an impoverishment of the water column. However observations made on *E. affinis* feeding behavior suggested this copepod able to overcome this impoverishment of the water column by switching from a typical pelagic grazing to a more benthic like foraging activity. Thus it was very common after the two days of incubation in the culture medium to see copepods, apparently in search of food, foraging among the settled particles whereas the water column was almost clear of any suspension. The following comparisons made with copepods cultures in optimal food conditions argue in favor of the efficiency of this feeding behavior plasticity.

Comparisons with other culture conditions

In previous studies *E. affinis* was cultured in an excess of algal food (Heinle & Flemer, 1975 ; Vuorinen, 1982), or as in our case with natural food directly collected in the field (Poli & Castel, 1983) (Tabl. IV, Fig. 7). The models corresponding to cultures supplied with algal food are quite similar which can lead both experiments reproduced true standardized

TABLE IV

Development times obtained for *E. affinis* in laboratory cultures.
Dn : Naupliar development (hatch to CI), Dc : Copepodite development (CI to CV),
Dt : total development = Dn + Dc (* : model adjusted on data provided by the authors).

Authorities	Locality	T°C	S ‰	*Fitted Model*
Heinle-Flemer 1975 (*)	Patuxent River	5.5-25	0-13.6	$Dt = 557.25 \times T^{-1.272}$
Vuorinen 1982	Archipelago Sea	7-20	5.5±0.1	$Dn = 278 \times T^{-1.289}$ $Dc = 272 \times T^{-1.249}$
Poli-Castel 1983	Gironde Estuary	10-25	0.5-5	$Dn\ 590 \times T^{-1.57}$ $Dc = 41 \times T^{-0.43}$
Present study	Western Scheldt	8-20	10-13	$Dt = 1146 \times T^{-1.542}$

optimal food conditions. The present experiment diverge from the food standardized cultures by the longer development times observed for lower temperatures whereas for Poli & Castel (1983) the main divergence relies on an longer development time for higher temperatures. Burkill & Kendall (1982) comparing their natural food supplied cultures of *E. affinis* with the algal supplied cultures of Heinle & Flemer (1975) found also an increase in the development time, far more pronounced at low temperature (twice as long at 5 °C but only + 15 % at 15 °C). These differences between standardized and natural experiments and even among this last group result obviously from the various quantity and quality of food used in these experiments. However it must be noticed that the development rate can in certain concitions (e.g. low temperatures in Gironde and high temperatures in Westerschelde) be similar in food saturation and in natural food supplied cultures.

The control of copepods development rate by the food availability has also been described by Vidal (1980) who concluded that the food concentration required for maximum growth was related to the temperature.

It becomes then obvious that the food quality not only controls the body size and weight of the copepods as stated by Klein-Breteler & Gonzalez (1988) but also the development rate. For this reason, Burkill & Kendall (1982) advice against the use of food optimal cultures for field extrapolations for it yields production overestimates from 10 to 80 %.

The cultures run at the lower temperatures showed an overstress of the exponential relation between temperature and development rate ressembling a development delaying for the later naupliar (N3-6) and copepodite (C4-5) stages at 2 and 5 °C. This has also been described by Poli (1982) for *E. affinis* (Gironde estuary, France) fed with naturally occurring par-

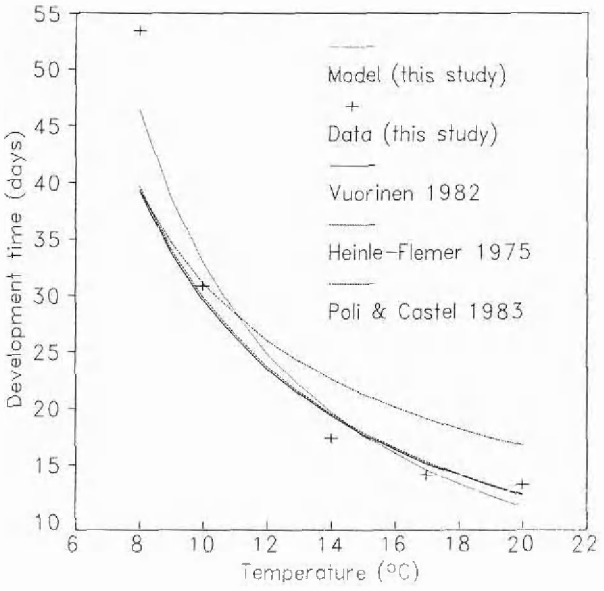

Fig. 7 : Comparison with other models found for *E. affinis* from hatching to adulthood.

ticulate matter as it was impossible to raise the copepod until adulthood at 10 °C for nauplii did not succeed to molt into first copepodite and finally died.

Production of *Eurytemora affinis*

One original result of this study is the significative production represented by the male reproductive effort, a compartment usually neglected in field production estimates. Moreover the male production seemed undergoing a similar temperature control than the juvenile growth rate (Fig. 4). Such relationship, still needing additional data to be parametrized, could be a mean to get estimate of the juvenile growth rate through short term experiments measuring the male production. Such an approach converges with the findings of Corkett & Mc Laren (1970) who established correspondances between the egg production and the juveniles growth rates for many pelagic copepods species.

Comparisons can be made between the present estimate of production and others obtained for the same species in comparable environments (Tabl. V). Whereas the biomass differed in the different areas, the P/B values showed remarkably close values. This converged with the similarities observed for the development rates obtained in cultures supplied either with natural particulate matter or with algal cultures. Both these observations underlined the ethophysiologic plasticity of the estuarine species.

TABLE V

Biomass, Production and P/B ratios measured for *Eurytemora affinis* in other estuarine locations compared with the present study.

Authorities	Locality	Biomass (mg/m^3)	Production ($mg/m^3/day$)	P/B ratio (an^{-1})
Heinle (1969)	Patuxent River	75	6.25	30.4
Allan *et al.* (1976)	Rhode River	47	3.83	29.4
Burkill & Kendall (1982)	Bristol Channel	8×10^{-3}	0.24×10^{-3}	33
Castel & Feurtet (1989)	Gironde Estuary	86	7.70	32.8
This study	Western Schelde Estuary	67.49	5	33

REFERENCES

BAKKER, C., W.J. PHAFF, M.C. EWIJK-ROSIER & N. DE PAUW, 1977. Copepod biomass in an estuarine and a stagnant brackish environment of the S.W. Netherlands. *Hydrobiologia*, 52 (1) : 3-13.

BERGMANS, M., 1981. A demographic study of the life cycle of *Tisbe furcata* (Baird, 1837) (Copepoda : Harpacticoida). *J. Mar. Biol. Ass. UK*, 61 : 691-705.

BURKILL, P.H. & T.F. KENDALL, 1982. Production of the copepod *Eurytemora affinis* in the Bristol Channel. *Mar. Ecol. Prog. Ser.*, 7 : 21-31.

BRADLEY, B.P., 1975. The anomalous influence of salinity on temperature tolerances of summer and winter populations of the copepod *Eurytemora affinis*. *Biol. Bull.* 148 (1) : 26-34.

CORKETT, C.J. & I.A. MC LAREN, 1970. Relationships between development rate of eggs and older stages of copepods. *J. Mar. Biol. Ass. UK*, 50 : 161-168.

ESCARAVAGE, V. (submitted). Analysis and modelling of the development of *Eurytemora affinis* (Poppe) in experimental culture.

CASTEL, J. & A. FEURTET, 1989. Dynamics of the copepod *Eurytemora affinis* in the Gironde estuary : Origin and fate of its production. *Scient. Mar*, 53 (23) : 577-584.

FEURTET, A., 1989. Dynamique de population. Caractérisation morphologique et production secondaire d'*Eurytemora affinis* (Copépode Calanoide) dans l'estuaire de la Gironde. Thèse de l'Université de Bordeaux I. 169 pp.

HEINLE, D.R., 1969. Effects of temperature on the population dynamics of estuarine copepods. *Dissertation, Univ. Maryland*, 132 pp.

HEINLE, D.R. & D.A. FLEMER, 1975. Carbon requirements of a population of the estuarine copepod *Eurytemora affinis*. *Mar. Biol.*, 31 : 235-247.

KLEIN BRETELER, W.C.M. & S.R. GONZALEZ, 1988. Influence of temperature and food concentration on body size, weight and lipid content of two calanoid copepod species. *Hydrobiologia*, 167/168, 201-210.

NAVARRONE, A., 1970. Influence of food organisms on the development and culture of pelagic copepods. *Helgol. Meeresunters.*, 20 : 333-345.

POLI, J.M., 1982. Contribution à l'étude de la dynamique et de l'adaptation physiologique du copepode estuarien *Eurytemora hirundoides* (Nordquist,1888). (Estuaire de la Gironde). Thèse de 3e cycle, Université de Bordeaux I, 118 pp.

POLI, J.M. & J. CASTEL, 1983. Cycle biologique en laboratoire d'un copépode planctonique de l'estuaire de la Gironde : *Eurytemora hirundoides* (Nordquist, 1888). *Vie Milieu*, 33 (2) : 79-86.

POLISHCHUK, L.V., 1990. A comment on the "theory of secondary production calculations for continuously reproducing populations" (Kimmerer). *Limnol. Oceanogr.* 32 (6) : 1645-1651.

RIGLER, H. & J.A. DOWNING, 1984. The calculation of secondary productivity. In : Downing J.A. & F.H. Rigler (eds). *A manual on methods for the assessment of secondary productivity in fresh waters* : 19-58.

SCHOLTEN, H. DE HOOP, B.J. & P.M.J. HERMAN, 1990. SENECA 1.2. A simulation environment for ecological application. *ECOMOLD REPORT EM-4*, 150 pp.

SOETAERT, K. & P. van RUSWIJK, (submitted). Spatial and temporal patterns in Westerschelde zooplankton.

VIDAL, J., 1980. Physioecology of zooplankton. I.- Effects of phytoplankton concentration, temperature and body size on the growth rate of *Calanus pacificus* and *Pseudocalanus sp.*. *Mar. Biol.*, 56 : 111-134.

VUORINEN, I., 1982. The effect of temperature on the rate of development of *Eurytemora hirundoides* (Nordquist) in laboratory culture. *Ann. Zool. Fenn.*, 19 : 129-134.