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Development of *Pseudocalanus elongatus* (Copepoda, Calanoida) cultured at different temperature and food conditions

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ABSTRACT: The pelagic copepod *Pseudocalanus elongatus* Boeck was bred 3 times from nauplius stages I and II to maturity at 5, 10, 15 and 20°C and at 4 different rations of autotrophic and heterotrophic food. The rate of development of the copepods increased with increasing temperature and food supply. The shortest generation times (from egg to adult) were 59 d at 5°C and 19 d at 15°C. The generation time nearly doubled when food concentration was very low. At 20°C mortality rates were high and development did not proceed faster than at 15°C. At all food levels the stage duration was generally constant (nearly isochronal), but the last 1 or 2 developmental stages took longer. The relationship between development time and temperature is described by Bělehrádek's functions at different food levels. This relationship predicts a generation time of approximately 45 d during spring bloom conditions in the North Sea and about 30 d during summer due to food limitation. Field estimates from the literature are too scarce to evaluate the presumption of food limitation during summer conditions. Some evidence of a low critical food level was found compared to other North Sea copepod species. Together with a fast development rate at low temperatures, this may explain the numerical dominance of *P. elongatus* in the North Sea and the northeast Atlantic Ocean.

KEY WORDS: *Pseudocalanus* · Copepods · Cultivation · Development · Temperature · Food

INTRODUCTION

Growth and productivity of copepods in temperate seas are mainly governed by temperature and food availability. McLaren (1978) discussed the possibility that development rates of copepods in nature are not influenced by variations in food level and that they are predictable from temperature alone. From published data at a wide range of temperatures, Huntley & Lopez (1992) calculated that temperature alone explained more than 90% of the variance in growth rate for 33 species of copepods. Although they admitted that the food factor may have been masked by selective predation on slower growing individuals, they proposed that, throughout the ocean, copepods are always able to find sufficient food to grow at maximal rates. This was based on the assumption that micro patches of food in the sea enable zooplankton to graze efficiently, even at low mean food concentrations that are suboptimal only in the laboratory. However, a body of evidence from *in situ* observations on development, length, weight, condition factor and egg production rates of *Acartia* spp., *Temora longicornis*, *Oithona similis* and *Calanus chilensis* shows that in temperate seas food can be limiting during a significant part of the season (cf. review by Klein Breteler & Schogt 1994).

Food limitation may not occur to the same extent in all species of copepods. In particular, different species of the genus *Pseudocalanus* seem to have a low susceptibility to food limitation, which may account for their high abundance in many seas around the world. Compared to the large *Calanus* spp., grazing rate and egg production in adult *Pseudocalanus* spp. was satiated at lower food concentrations (Frost 1985). The same was found for development rate at naupliar stages (Green et al. 1991) and for growth rate at copepodite stages (Vidal 1980a). Comparing similar sized species, egg production in *P. minutus* appeared to be less sensitive to discontinuous food availability than in *Centropages typicus* and *Acartia tonsa* (Dagg 1977).

Body length in *P. elongatus* is another indicator of food limitation (Klein Breteler & Gonzalez 1982, 1988). In the North Sea there was no effect of food concentration on body length of *P. elongatus*, in contrast to *Temora longicornis* (Evans 1981). Also in Dabob Bay (Washington, USA) food did not seem to influence body size, growth, development and reproduction of *Pseudocalanus* sp. (Ohman 1985). However, in Greenland fjords, in the absence of significant seasonal temperature changes, seasonal variations of body size of *P. minutus* were observed that could only be ascribed to differences in the availability of food (Ussing 1938). Obviously, a low sensitivity to food limitation does not mean that *Pseudocalanus* spp. is food satiated in every area and season. This makes *P. elongatus* a particularly interesting species in which to study the development rate through all stages at controlled conditions of temperature and food concentration. The results can be compared with similar estimates on the small copepods *T. longicornis* (Klein Breteler & Gonzalez 1986) and *Acartia clausi* (Klein Breteler & Schogt 1994).

Until now, no systematic laboratory analyses on the influence of temperature and food on the rate of development of *Pseudocalanus elongatus* have been made. The generation time of different species of *Pseudocalanus* was estimated in the laboratory at a constant temperature and excessive food (Crawshay 1915, Katona & Moody 1969, Corkett 1970, Sazhina in Corkett & McLaren 1978, Landry 1983). To establish a new method for estimating median development time, Klein Breteler et al. (1994) added another set of data at a constant temperature and excess food. Different concentrations of food at a constant temperature were used by Paffenhöfer & Harris (1976), Klein Breteler et al. (1982) and Davis (1983) and different temperatures at excess food by Thompson (1982). The only record on development of *Pseudocalanus* spp. in relation to both temperature and food concentration is by Vidal (1980b), but that study was restricted to the last 3 copepodite stages. The present study attempts to determine the generation time of *P. elongatus* from the rate of development measured in the laboratory at different conditions of both temperature and food. A temperature range of 5 to 20°C was chosen, which covers the habitat of *P. elongatus* throughout the year in its geographic area of distribution (Colebrook 1982, Frost 1989, Fransz et al. 1991). The relationship can be used to interpret field data on the development, with respect to the trophic state, of *P. elongatus* in the sea.

MATERIAL AND METHODS

The calanoid copepod *Pseudocalanus elongatus* was continuously cultured in the laboratory under conditions of 15°C and optimal food (>300 µg C l^{-1}) consisting of the autotrophic algae *Rhodomonas* sp. and *Isochrysis galbana* and the heterotrophic dinoflagellate *Oxyrrhis marina* (Klein Breteler 1980, Klein Breteler et al. 1982, Klein Breteler & Gonzalez 1986, 1988). Two chemostat cultures of *Rhodomonas* sp. (mean Equivalent Spherical Diameter, ESD, 6.7 µm, mean concentration 1.5×10^6 cells ml^{-1}, 33.1 pg C $cell^{-1}$) and one of *I. galbana* (4.9 µm, 4.2×10^6 cells ml^{-1}, 11.7 pg C $cell^{-1}$) were kept at 15°C on f/2 medium (Guillard 1975) at a dilution rate of 0.17 d^{-1}. *O. marina* lived together with the copepods in the cultures and developed there depending on the supply of autotrophic food and on grazing by the copepods. This organism was also cultured in a 2 l continuous culture (14.0 µm, 1×10^5 cells ml^{-1}, 215.8 pg C $cell^{-1}$) that was kept in the dark and fed from a *Rhodomonas* sp. culture at a dilution rate of 0.23 d^{-1}.

A brood from the parental copepod stock was raised to maturity in 3 independent experiments, each at 4 different temperatures and 4 food supplies of the same food mixture as in the stock culture. The cohorts raised represented the 12th, 20th, and 23th generations bred from February to December 1986.

At the beginning of each experiment, larvae were separated from the parental culture by sieving part of the water through a nylon screen with a mesh of 112 µm, allowing NI and II with a few eggs to pass. A more synchronised cohort, starting with eggs of known age, was not practical due to the large scale of the experiment. The larvae were concentrated in 3.5 l of the old culture water, mixed well and equally divided into sixteen 25 l Fiberglas containers. Sea water of about 30‰ was added up to 22 l through a Whatman Gamma 12 tube filter (pore size <2 µm) to a final concentration of 30 to 60 larvae l^{-1}. The temperature was maintained at 5, 10, 15 and 20°C (±0.2°C), respectively, by keeping the copepod containers in racks immersed in temperature controlled water basins.

Twice daily time-regulated peristaltic pumps fed 0, 2, 6 and 30 ml of the mixture of algae to the copepod cultures, representing the Food Supplies 0, 1/16, 1/4 and 1, respectively. Food Supply 0 merely means that no autotrophic algae were supplied, but it still allowed some copepod growth due to the presence of detritus and small heterotrophic flagellates. These flagellates and the heterotrophic dinoflagellate *Oxyrrhis marina* occurred in all copepod cultures, since they were introduced with the larvae at the start of the experiments. The trophic state of the cultures depends upon the speed of the food pump and is characterised by a rapidly changing dominance from the small autotrophic flagellates to the larger heterotrophic one. This shift in food species is adequate to meet the changing food size spectrum (Gruzov 1985) of the developing

larvae (Klein Breteler et al. 1990). After reaching its level, depending on the supply of auto-trophic food, the concentration of *O. marina* remains more or less constant (Fig. 4 in Klein Breteler & Laan 1993). During this time *O. marina* constituted the dominant food source (45 to 90% of the total food biomass) and was probably the main food during the later part of the copepod's development (Klein Breteler et al. 1990). When *O. marina* was dominant, its grazing kept the concentration of *Rhodomonas* sp. below 10% of the total food biomass. The remaining particles consisted of *Isochrysis galbana* and similar sized or smaller colourless flagellates and detritus.

Concentrations of algae and *Oxyrrhis marina* were measured weekly using an Elzone particle counter (Particle Data Inc.). In addition, the concentration of *O. marina* was regularly checked by microscopy by roughly counting the number of living cells present in each sample collected for copepod counting. When the concentration had obviously fallen below the normal level, *O. marina* was added from the continuous culture described above. This manual addition of *O. marina* was sometimes necessary at the end of the experiments, when copepod survival had been high and the grazing capacity of the abundant, almost full-grown survivors exceeded the growth rate of the heterotrophic flagellate.

There was a clear relation between the microscopic and the electronic counts. However, when no cells were visible the particle counter still recorded some 100 particles ml^{-1} (~22 µg C l^{-1}) within the size range of *Oxyrrhis marina*. Also, from the particle distribution, it was clear that particles other than the 3 species used as food were present, particularly in the small size range of *Isochrysis galbana*. Probably these particles were comprised of detritus and small colourless flagellates. At Food Supply 1 these background particles obviously played no important role (<10% of total food biomass), but at the lowest 2 supplies their number may have contributed considerably. Since they also seem to have a food value for the copepods, no attempt was made to correct for their presence. It was assumed that their carbon content was similar to that of the corresponding size class of the regular food. Obviously, the food biomass estimated at lower food supplies was only a rough approximation of the true food level.

The carbon content of the autotrophs was assumed to be constant, since it was obtained from measurements in continuous cultures similar to those of the present experiments. However, *Oxyrrhis marina* mainly developed in the copepod containers under different conditions. Particle size analyses indicated up to 1.1 µm larger cell sizes (mean ESD) at lower temperatures and a high food supply and up to 1.1 µm smaller cells at high temperature and low food supply, relative to the size of *O. marina* in the continuous culture. Therefore, the carbon content of *O. marina* was corrected for the corresponding volume deviation.

The concentration and stage of development of the copepods were determined 1 to 3 times per week, depending on the culture conditions. The sampling schedule was chosen so that 9 to 10 samples were taken at regular time intervals during completion of a generation. After stirring, samples were taken with a PVC tube (diameter 4 cm) reaching almost to the bottom of the tank. A stopper with a hole on the top and a removable sieve (50 µm) on the bottom of the tube allowed easy sampling and collection of the animals in a small petri dish. As a rule 4 samples of 0.25 l were taken, but additional samples were taken if fewer than 15 individuals were caught.

Median development time of copepod life stages was determined as the time when 50% of the population reached a particular stage (Landry 1975, 1983). Until recently, no satisfactory, objective method was available to estimate the median development time. For this reason publication of the present data was suspended until an improved method had been established (Klein Breteler et al. 1994), while data on body size, weight and lipid content of the same experiments were already presented by Klein Breteler & Gonzalez (1988). According to the new method, Gamma distribution functions were used to fit the cumulative stage frequency data against time. From these functions the median development time of the stages was calculated for each individual culture. Stage duration was calculated as the difference of the median development time of 2 successive stages.

Sexes were discerned, but not treated separately in the calculations. Previous (unpubl.) observations did not indicate any relation between sex ratio and the present culture conditions. Moreover, in contrast to Landry (1983), accurate observations did not reveal a difference in development time between the sexes in 3 species of copepods, including *Pseudocalanus elongatus* (Klein Breteler et al. 1994).

The number of estimates of stage duration was generally 3 (1 per experiment) for each stage at each culture condition. However, at the youngest naupliar stages, due to their relatively fast development, our sampling frequency appeared to be too low to estimate the median development time. At older stages there were also data gaps when cultures died prematurely. At the most severe condition of 20°C and Food Supply 0, the duration of most stages could not be estimated. The durations of the youngest and some missing older stages were derived from the data on the remaining stages. To achieve this, accurate data collected at 15°C and excess food (Klein Breteler et al. 1994) were used, assuming equiproportional development (Corkett 1984). Similarly,

incomplete records from the literature were extrapolated to full generation time using the present results at Food Supply 1 at 5, 10 and 15°C. Temperature corrections were made using the Bělehrádek function calculated at Food Supply 1. The duration of eggs and of the pre-feeding first and second naupliar stage was assumed to be optimal and, at the temperature concerned, not influenced by the food regime.

The generation time (D, d) was calculated as the sum of the duration of all stages, i.e. the time from egg laying to the time when 50% of the population had reached maturity. The relation with temperature (T, °C) was estimated at different food supplies using Bělehrádek's function:

$$D = a(T - \alpha)^b$$

according to McLaren (1963, 1965), who showed that a good fit could be obtained at a common value of parameter b. However, when trying this we often did not obtain standard errors of the parameters, due to highly correlated parameters. Guerrero et al. (1994) suggested using a model with only 2 parameters to avoid over-fitting. However, both the Arrhenius and the Tauti models they suggested gave bad fits of our data points. Therefore, we simplified Bělehrádek's function to a linear model by adopting a fixed value of parameter α. Although this had very little influence on the curves fitted, it enabled confidence intervals (of the regression line) and prediction intervals (of the data) to be calculated. When estimating the 3 parameters iteratively at a common α, the best estimate of α was found to be –8.0°C. Therefore, we fixed α at a value of –8°C. The parameters of this Bělehrádek's function were estimated by a single linear regression analysis of the form:

$$y_{ij} = a'_i + b_i(x_{ij} - \bar{x}_{ij}) + \varepsilon_{ij}$$

in which $y = \ln D$, $x = \ln(T + 8)$, $a'_i = \ln a - b\bar{x}$, ε_{ij} is the error which is normally distributed with mean zero and variance σ^2, and i and j are the food supplies and temperatures used, respectively.

In this model $(T + 8)$ was corrected for its mean value, to avoid intercepts and slopes that were correlated. Since a single regression analysis was performed for the total data set of all food levels together, the same number of degrees of freedom and the same number of residual mean squares pertain to all food supplies. Hence, the confidence or prediction intervals will be equal, although they will differ proportionally after back transformation.

RESULTS

The total food biomass increased at higher levels of the supply of autotrophic food (Table 1). The low amount at Food Supply 0 represents a basic concentration of detritus and heterotrophic flagellates, including *Oxyrrhis marina*. At lower temperatures the total food concentration tended to increase, probably as a result of reduced grazing by the copepods. During the experiments there was no obvious systematic trend, since overall changes of the food concentration were on average close to zero.

The stage duration of *Pseudocalanus elongatus* in the different experiments is shown in Table 2. The development proceeded at different rates, depending on temperature and on food supply (Fig. 1). At Food Supply 1 the rate was generally at maximum, but the difference with Food Supply 1/4 was small. At 20°C the development was slightly faster at Food Supply 1/4 than at Food Supply 1. However, the low number of observations at Food Supply 1/4 makes this difference doubtful. From NIV to CIV development was almost isochronal, as is shown from the almost linear progress of development over time, irrespective of the food conditions. However, at 10°C this nearly isochronal development was less clear at the higher 3 food supplies. The duration of the first feeding stage NIII was often longer than the other stages (Table 2). At most conditions also the duration of CV was longer than at younger stages.

The generation time (D, d) is plotted against temperature (T, °C) at different food supplies (Fig. 2). The data at 20°C were problematic, because at the lowest food supply the duration of only a few stages was

Table 1 Mean total biomass (µg C l^{-1}) of food at different temperatures and food supplies in cultures of *Pseudocalanus elongatus*. SD: standard deviation; n: number of observations. Food supply is the rate of supplying autotrophic algae; at Supply 0 some food in the form of detritus and heterotrophic flagellates is present

Food supply	5°C			10°C			15°C			20°C		
	Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD	n
0	64	25	20	54	32	19	60	26	13	54	23	5
1/16	77	22	24	59	14	16	59	13	12	67	18	7
1/4	196	77	22	91	32	11	106	26	9	106	27	7
1	655	195	21	363	133	11	310	80	8	221	54	8

Table 2. *Pseudocalanus elongatus*. Duration (d) of life stages at different conditions of temperature and food. Data estimated from median stage development time observed in 3 separate experiments. Mean values indicated, or, when no data were available, derived [in brackets] from the duration of the other stages at the same condition and from separate experiments at 15°C (cf. 'Material and Methods'). Generation time calculated as the sum of the stage duration of all stages; missing values taken from the column 'Mean' •Missing estimate of development time of individual stages; hence mean stage duration given of the combined stages. Food supply is the relative pump speed feeding autotrophic algae; at Supply 0 some food in the form of detritus and heterotrophic flagellates is present

Temp. (°C)	Stage	Food supply: 0				1/16				1/4				1			
		Expt 1	Expt 2	Expt 3	Mean	Expt 1	Expt 2	Expt 3	Mean	Expt 1	Expt 2	Expt 3	Mean	Expt 1	Expt 2	Expt 3	Mean
5	Egg				[7.1]				[7.2]				[7.2]				[7.1]
	1				[1.8]				[1.8]				[1.8]				[1.8]
	2				[2.7]				[2.7]				[2.7]				[2.7]
	3	17.9	24.8	16.3	19.6	9.4	13.2	10.7	11.1	6.8•	6.6	6.5	6.6	8.4	6.4	6.8	7.2
	4	9.7	8.5	14.2	10.8	6.4	4.3	5.2	5.3	6.8•	5.4	5.0	5.8	4.4	6.7	4.2	5.1
	5	9.8		17.7	13.7	7.5	5.8	2.7	5.3	5.7	5.7	3.9	5.1	3.2•	3.4	6.1	4.2
	6	6.2		14.2	10.2	3.1	3.0	4.2	3.4	1.8	1.8	2.9	2.2	3.2•	2.9	1.3	2.5
	7			−0.5	−0.5	6.2	7.1	6.8	6.7	7.8	6.0	5.4	6.4	5.3	5.7	6.6	5.9
	8				[10.5]	3.9	4.7	4.5	4.4	3.9	4.9	7.6	5.5	6.3	4.1	4.4	5.0
	9				[10.3]	5.2	5.7	5.1	5.3	4.6	4.2	5.8	4.9	5.0	4.0•	3.9	4.3
	10				[10.5]	13.1	6.3	4.2	7.8	7.8	8.1	3.4	6.4	4.7	4.0•	4.0	4.2
	11				[14.6]	11.1	8.4	10.5	10.0	5.3	7.2	5.5	6.0	6.7	12.9	8.3	9.3
Generation		100.5	114.1	119.3	111.3	77.4	70.0	65.4	71.0	61.9	61.6	57.5	60.4	58.9	61.7	57.2	59.3
10	Egg				[3.7]				[3.7]				[3.7]				[3.7]
	1				[1.0]				[1.0]				[1.0]				[1.0]
	2				[1.4]				[1.4]				[1.4]				[1.4]
	3				[7.6]	4.8		5.4	5.1	4.7	4.5	4.0	4.4	3.8	4.1	3.6	3.8
	4		6.4	7.5	6.9	4.3	3.8	3.7	3.9	2.0	2.1	1.9	2.0	2.7	1.6	2.2•	2.2
	5	12.1	14.2•	13.0	13.1	2.8	2.8	1.4	2.3	2.5	1.6	2.1	2.1	2.4	2.0	2.2•	2.2
	6	4.4	14.2•	1.8	6.81	1.3	1.6	1.1	1.3	2.3	1.9	1.2	1.8	2.8	2.6	0.9	2.1
	7	2.0	0.8	4.2	2.3	1.8•	4.0	5.4	3.7	1.8	3.6	3.4	2.9	1.5	2.2	3.5	2.4
	8	6.2•	3.5	3.7	4.4	1.8•	3.4•	2.4	2.5	4.5	2.4	2.6	3.2	1.6	2.0	2.5	2.0
	9	6.2•	0.8	8.0	5.0	4.1	3.4•	2.3	3.3	3.2	2.5	2.7	2.8	3.2	2.6	2.1	2.6
	10		0.3	6.1	3.2	7.5	3.4•	2.7	5.1	4.2	2.9	2.6	3.2	3.1	2.9		3.0
	11				[8.4]	10.3	7.5	4.9	7.6	4.0	6.1	4.7	4.9	4.8	4.3		4.5
Generation		63.0	62.2	66.4	63.8	44.6	41.1	35.3	40.3	35.0	33.7	31.2	33.3	31.8	30.2	30.4	30.8
15	Egg				[2.1]				[2.1]				[2.1]				[2.1]
	1				[0.5]				[0.5]				[0.5]				[0.5]
	2				[0.8]				[0.8]				[0.8]				[0.8]
	3				[4.7]				[4.0]		1.9		1.9		1.6	1.9•	1.7
	4	6.4		4.2	5.3		2.3•		2.3	2.1	2.3		2.2		1.9	1.9•	1.9
	5		10.2		10.2		2.3•		2.3	1.7	1.7	2.2	1.9	1.4•	1.2	1.3	1.3
	6		1.5		1.5	1.6	1.6		1.6	1.2	1.4	1.5•	1.3	1.4•	1.7	1.1	1.4
	7		3.1		3.1	3.9	3.4		3.7	2.7	1.8	1.5•	2.0	1.4•	1.9	2.0	1.8
	8		2.9		2.9	3.2	1.4		2.3	2.2	1.7	2.1	2.0	1.4•	1.3	1.5	1.4
	9		3.6		3.6	3.5	4.5		4.0	1.3	1.3	1.6	1.4	2.4	1.5	1.4	1.8
	10		1.8		1.8	1.9	6.6		4.2	3.5	2.4	1.6	2.5	2.2	1.5	1.8	1.8
	11		2.4		2.4	6.5	2.4		4.4	2.1	2.6	5.1	3.3	2.7	2.6	3.0	2.7
Generation					38.8	32.6	31.6		32.1	22.0	20.5	22.9	21.8	20.0	18.5	19.1	19.2
20	Egg				[2.9]				[2.9]				[2.9]				[2.9]
	1				[0.7]				[0.7]				[0.7]				[0.7]
	2				[1.1]				[1.1]				[1.1]				[1.1]
	3								[3.4]				[2.2]	2.6	2.4		2.5
	4		3.5	4.0	3.8	3.8	2.9	2.2	2.9	1.8	1.5		1.7	2.5	1.9		2.2
	5							3.3	3.3	1.1	2.3		1.7	1.4	2.2	1.2•	1.6
	6							1.7	1.7	1.6	0.4		1.0	1.1	1.4	1.2•	1.2
	7							2.5	2.5	3.1	2.9•		3.0	2.7	2.3	1.7	2.2
	8								[2.7]	1.0•	2.9•		2.0	1.6	1.3	2.4	1.8
	9								[2.7]	1.0•	0.7		0.8	1.6	2.0	2.5	2.0
	10								[2.7]	1.5			1.5	2.9	2.8	2.1	2.6
	11								[3.8]	3.4			3.4	2.4	2.6	3.9	3.0
Generation									30.4	21.3	22.2		21.8	23.4	23.6	24.3	23.7

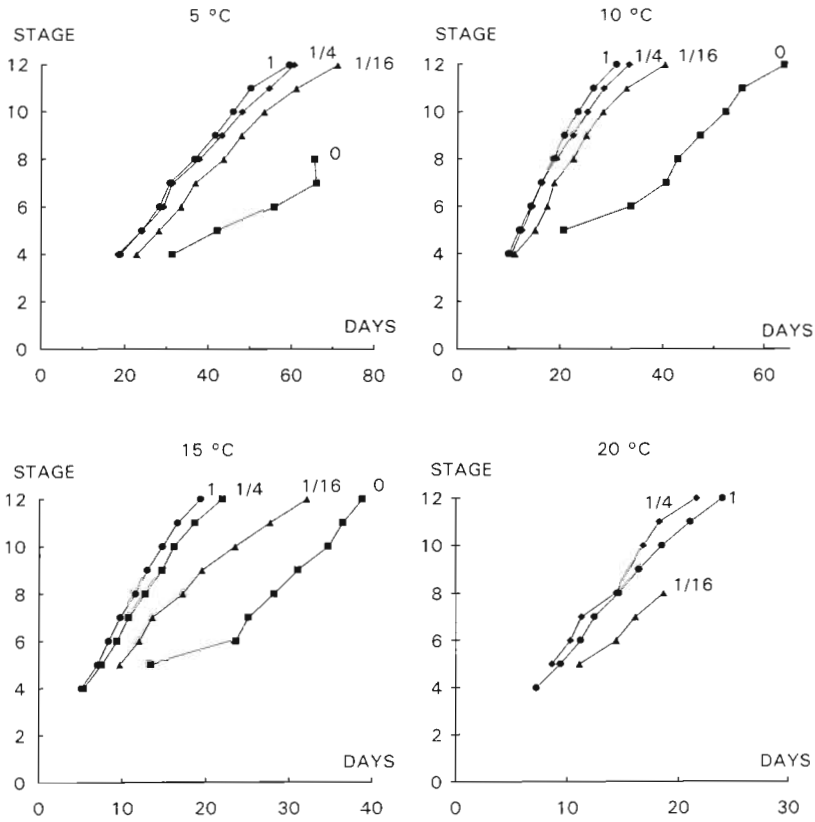

Fig. 1. *Pseudocalanus elongatus*. Development at 5, 10, 15 and 20°C and relative food supplies 0, 1/16, 1/4 and 1. Note that at Food Supply 0 some edible particles are present. Mean age (d) of stages calculated from independently estimated stage duration in each of 3 or fewer experiments of similar conditions. Age at first stage shown estimated from older stages and from separate experiments (cf. 'Material and Methods')

determined (Table 2), and at the higher 2 food supplies the generation time was longer than at 15°C. Together with the high mortality observed at this temperature (see Table 4), this points to high physiological stress in *Pseudocalanus elongatus* at the edge of its natural thermal range. Therefore, the data at 20°C have not been used in subsequent calculations.

The relationship between generation time and temperature was estimated using Bělehrádek's function, which was transformed to a linear model using a fixed value of $\alpha = -8$°C (cf. 'Material and methods'). The parameters a, a' and b are given in Table 3. After back-transformation of the linear model, the curves describe the data points between 5 and 15°C very well (Fig. 2). Since the data at 20°C were not used, the curves should not be extrapolated beyond 18°C.

The effect of the different food supplies was well established (Fig. 2). Above 6°C the 95% confidence interval of the curve of Food Supply 1/16 does not overlap with that of excess food. There was only a small (nonsignificant) difference between the curves at Food Supplies 1/4 and 1, indicating that Food Supply 1 was excessive. This was similar in experiments with *Temora longicornis* (Klein Breteler & Gonzalez 1986) and *Acartia clausi* (Klein Breteler & Schogt 1994). At the higher 3 food levels the curves run almost parallel. They maintain a gentle slope at lower temperatures,

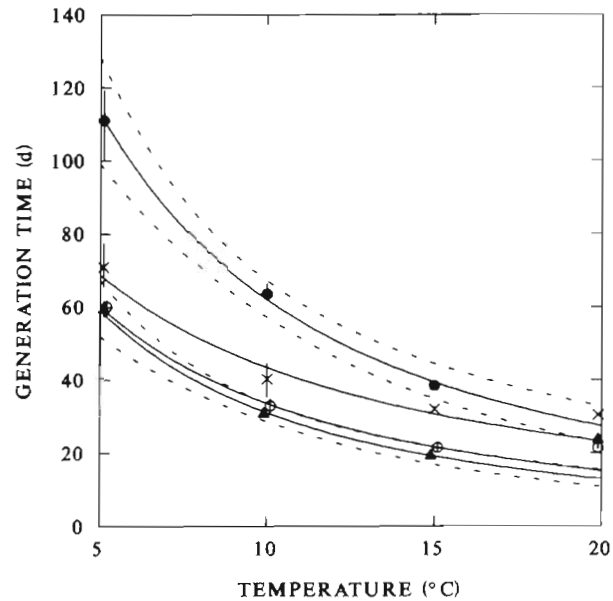

Fig. 2. *Pseudocalanus elongatus*. Generation time from egg to adult plotted against temperature at Food Supplies 0 (●), 1/16 (×), 1/4 (○) and 1 (▲). Mean values and range (bars), when available, in different experiments (cf. Table 2). Bělehrádek's functions (excluding data at 20°C) fitted. 95% confidence intervals at Food Supplies 0 and 1 given. Intervals at other food supplies not shown since they differ only proportionally

Table 3. Parameters of Bělehrádek's function $D = a\,(T - \alpha)^b$ of generation time (D, d) and temperature (T, °C) at different food concentrations and $\alpha = -8$°C. a' is the intercept of the linear function. SE: standard error; L: lower limit; H: higher limit

Food supply	a'	SE(a')	a	L(a)	H(a)	b	SE(b)
0	4.18	0.029	12684	9567	16730	−1.84	0.123
1/16	3.81	0.029	2566	1935	3385	−1.41	0.123
1/4	3.56	0.029	5873	4475	7824	−1.79	0.123
1	3.49	0.029	9398	7158	12518	−1.98	0.123

which points to the ability of *Pseudocalanus elongatus* to develop relatively quickly at a low temperature.

Mortality was generally constant during the culture period. The rate of mortality (Z) was calculated during the complete culture period in each culture according to $N_t = N_0\,e^{-Zt}$, in which N_0 and N_t are the concentration of ind. l^{-1} at time 0 and t, after correction for mortality due to the sampling, and t is the time of cultivation in d (Table 4). At higher food supplies between 5 and 15°C mortality was generally low and, with 1 exception, varied between 0.034 and 0.016 d^{-1}. However, at the lowest food supplies rather high mortalities occurred. At 20°C mortality was high at all food supplies, particularly at the lowest supply, which led to extinction of some cultures.

DISCUSSION

Laboratory estimates

In the laboratory generation time of *Pseudocalanus elongatus* has been estimated by different workers at temperatures between 5 and 15°C (Fig. 3). When comparing these with the present results, it should be remembered that our prediction intervals are not very sensitive due to the low number of data points on which they are based. Therefore, non-significant differences should be considered with caution. Our previous experiments at 15°C (Klein Breteler et al. 1982), after using the present calculation techniques to estimate median development times, show more or less similar generation times at the same food conditions. At excessive food the generation time was 3 d longer than in the present experiment. However, recent experiments at similar conditions (Klein Breteler et al. 1994) showed that at 15°C the minimum generation time can be 2 d shorter than in the present experiments. Although these data points are within the 95% prediction interval (Fig. 3), it is felt that small differences in the culture conditions occurred, possibly connected with the quality of the autotrophic or heterotrophic food. Probably, the shortest generation times represent the optimum conditions.

Obviously, the results by other workers at excessive food conditions give longer generation times than the present results (Fig. 3). Most of the observations are above or just at the edge of the higher 95% prediction limit of excessive food. The observations by Thompson (1982) between 5 and 15°C on *Pseudocalanus elongatus* clearly support the present relationship between generation time and temperature. However, the 4 to 13 d higher level suggests that the single food species *Isochrysis galbana* she used, was not really optimal. Using *I. galbana* as the excessive but sole food source, we also observed (unpubl. obs.) a (significant) delay of the generation time of *P. elongatus* by about 6 d compared to the present food mixture at 15°C . Green et al. (1991) raised *P. elongatus* from NI to CI. At the 4 highest food levels of *I. galbana* and after extrapolation to full generation time (cf. 'Material and methods'), their data also point to a slightly suboptimal generation time (difference almost significant, $p = 0.05$). Paffenhöfer & Harris (1976), using *Thalassiosira rotula* as a single food source, reported a generation time of *P. elongatus* that is 5 d longer ($p = 0.05$) than in our present results at excessive food. Gruzov (1985) explained that the retention efficiencies of different sizes of food is not the same for all life stages. Clearly, the different stages do not have the same qualitative demand of food (Klein Breteler et al. 1990, Peterson et al. 1991). Hence, a narrow size range of a single food species seems to hamper the growth of copepods during particular stages of development. Nevertheless, Katona & Moody (1969), using a

Table 4. *Pseudocalanus elongatus*. Average mortality rate d^{-1} at different temperatures and food concentrations. Standard errors in parentheses; n = 3

Food supply	5°C	10°C	15°C	20°C
0	0.089 (0.003)	0.095 (0.008)	0.189 (0.030)	0.555 (0.036)
1/16	0.030 (0.007)	0.034 (0.012)	0.092 (0.058)	0.336 (0.027)
1/4	0.023 (0.002)	0.031 (0.003)	0.049 (0.017)	0.308 (0.024)
1	0.016 (0.005)	0.026 (0.007)	0.030 (0.010)	0.187 (0.008)

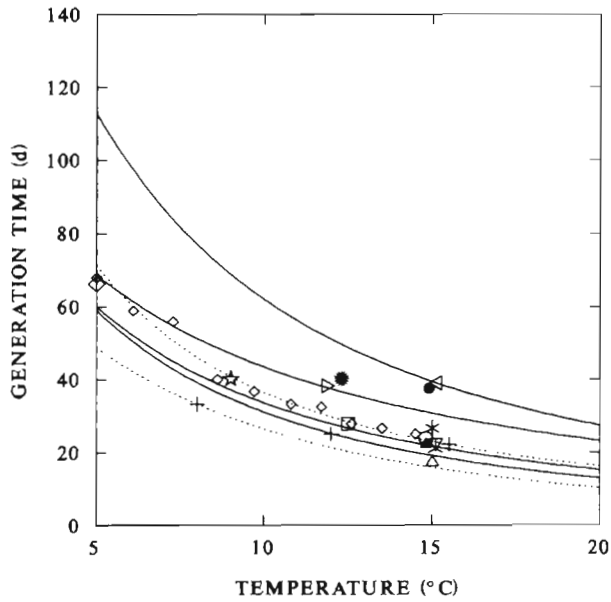

Fig. 3. *Pseudocalanus* spp. Laboratory estimates of generation time plotted against temperature. Observations by Klein Breteler et al. (1982) at Food Supplies 0 (●), 1/16 (∗), 1/4 (○) and 1 (▲) and at excess food by Crawshay (1915) (•), Katona & Moody (1969) (◁), Corkett (1970) (▷), Paffenhöfer & Harris (1976) (□), Sazhina in Corkett & McLaren (1978) (☆), Vidal (1980) (+), Thompson (1982) (◇), Davis (1983) (◇), Landry (1983) (⅄), Green et al. (1991) (▽), and Klein Breteler et al. (1994) (△). Most data slightly corrected for missing embryonic development time; those of Green et al. and of Vidal extrapolated for missing development time of all naupliar and copepodite stages, respectively (cf. 'Material and Methods'). Bělehrádek's functions of Fig. 2 at different food supplies (——) and 95% prediction interval at Supply 1 (·····) for comparison

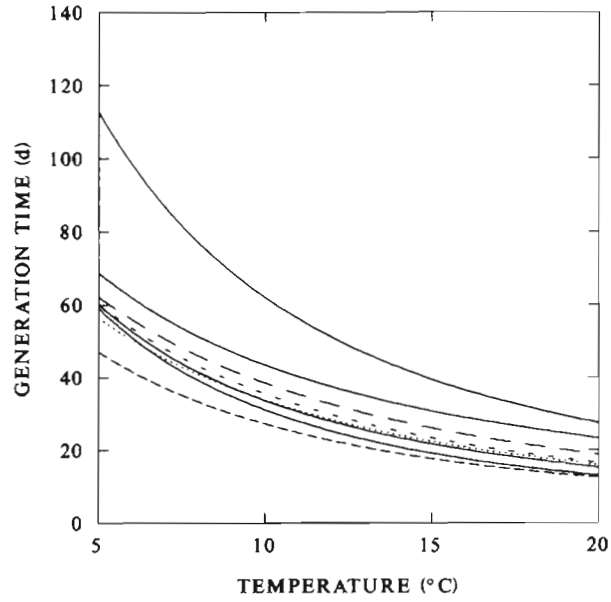

Fig. 4. *Pseudocalanus* spp. Laboratory estimates of the relation between generation time and temperature by McLaren et al. (1989): *P. minutus* (— —), *P. moultoni* (- - -), *P. acuspes* (·····) and *P. newmani* (– –). Bělehrádek's functions of Fig. 2 at different food supplies (——) for comparison

mixture of food organisms including ciliate protozoans, observed an extremely long generation time (Fig. 3), which may be explained by the biochemical composition of the food.

Data of unknown or different species of *Pseudocalanus* (Corkett 1970, Sazhina in Corkett & McLaren 1978, Davis 1983, Landry 1983) generally indicate a similar generation time as observed by the other workers for *P. elongatus* (Fig. 3). The latter 2 observations are within the 95% prediction interval of excessive food. The data from Vidal (1980b) were derived by extrapolation of his observations from 100% CII to 50% CVI. At 8 and 15.5°C his extrapolated data are just at the lower and higher limit of the prediction interval of excessive food, respectively. Also Vidal recognised that the generation time at 8°C was suspiciously short and he mentioned the low number of observations as a possible explanation. However, Vidal raised his larvae to CII at a temperature of 12 or 15.5°C and at excess food prior to the measurements at older stages. Hence, particularly at 8°C, adaptation to the new temperature and food conditions may have biased his results, which may also explain the equally rapid development he noticed at this temperature at low food levels (not shown here).

After the taxonomic status of the genus *Pseudocalanus* had been clarified, McLaren et al. (1989) studied the development time of the 4 eastern Canadian species separately at temperatures between 0 and 12°C at an excess of food supply consisting of a mixture of algae. The Bělehrádek curves he calculated for *P. minutus*, *P. moultoni* and *P. acuspes* run parallel to our curves at Food Supplies 1 and 1/4 at temperatures beyond 8°C up to 20°C (Fig. 4). Above 7, 8 and 10°C, respectively, the curves of these species predict generation times that are significantly longer ($p < 0.05$) than we observed at Food Supply 1. Below these temperatures the curves increase less steeply, resulting in a generation time of around 60 d at 5°C, just as we observed in *P. elongatus*. This is remarkable, since *P. minutus* and *P. acuspes* are species that are considered to be well adapted to the Arctic environment (McLaren et al. 1989). The fourth species *P. newmani*, however, developed faster at low temperatures. At 15°C its generation time was between the present estimate and the one by Klein Breteler et al. (1994) (Fig. 3), but below 13°C the curves predict a development time of *P. newmani* that is significantly faster ($p < 0.05$). It is not known what part of the difference among these closely related species must be attributed to the exper-

imental technique, which can be considerable (Fig. 3). However, observations of embryonic duration (McLaren et al. 1989) support the idea that at least part of the differences may be explained by a different adaptation to the temperature.

Field estimates

Our experimental observations on the generation time of *Pseudocalanus elongatus* cover most of the natural range of temperatures and quantity of food. Hence, the Bělehrádek functions calculated permit the interpretation of field estimates of development time with regard to food availability at the prevailing temperature conditions. Unfortunately, only few field estimates of development time of *Pseudocalanus* spp. are available. Under semi-natural conditions in 4 large enclosures, Hay et al. (1988) estimated the development time from NI to CVI at a temperature increasing from 7.5 to 11°C. Their estimates, increased by 3.6 d for embryonic development, lead to generation times that are clearly longer than our estimate at excess food (Fig. 5). Of the 4 differences, 3 are significant ($p < 0.05$). In 2 of the enclosures food must have been severely limiting.

In the southern North Sea, Daro et al. (1982) estimated the generation time at temperatures increasing from 7°C in April to 16°C in June. Interpolating these temperatures and after correction for egg development as above, their data show optimal or slightly suboptimal development from May to July, but in April/May the development was 8 d faster than has ever been shown in the laboratory (Fig. 5). In April/May and July the differences with the curve at excess food were significant ($p < 0.05$). This suggests that food was limiting in July, but the unrealistically rapid development rate in April/May points to methodological errors. Although these authors did not specify the temperature accurately, uncertainties of the temperature are not so great since this area of the North Sea is well mixed. However, sampling occurred at one station in an area with considerable vertical advection, so bias due to sampling in water with different phases of development of the copepods is a realistic possibility.

McLaren (1978) used the data of Marshall (1949) to estimate the generation time of *Pseudocalanus minutus* in Loch Striven during spring and summer. Note that this species probably is *P. elongatus* (Frost 1985, 1989). McLaren explained that his estimate contained uncertainties about the depth distribution of the copepods and about the ambient temperature that was 2.5 to 6°C different between 0 and 30 m depth. Since Marshall's data pertain to only 1 vertical haul per occasion at 2 depth strata, nothing is known of the

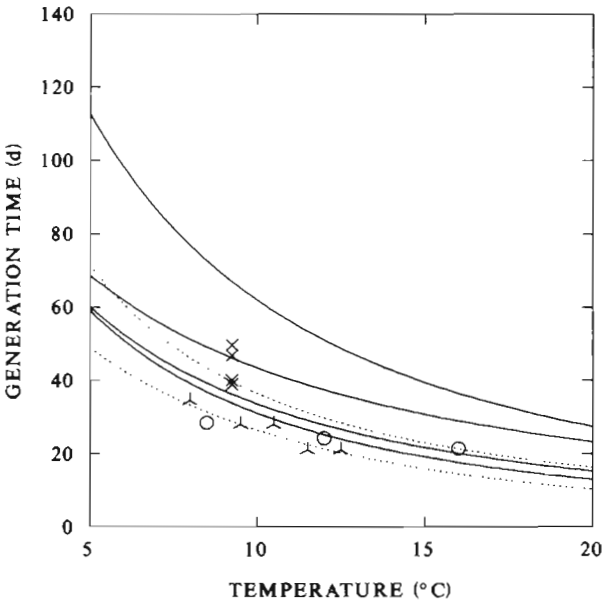

Fig. 5. *Pseudocalanus elongatus*. Field estimates of generation time observed at different temperatures (°C). Data in Loch Striven from Marshall (1949) by McLaren (1978) (⅄), in the southern North Sea (Daro et al. 1982) (O) and in large enclosures in a Scottish sea loch (Hay et al. 1988) (×). In the latter 2 corrections were applied for missing egg development time. Bělehrádek's functions of Fig. 2 at different food supplies (——) and 95% prediction interval at Supply 1 (·····) for comparison

copepod's main residence during the day. If the temperature assumed by McLaren is correct, development in Loch Striven proceeded up to 6 d faster (2 out of 5 cases significant, $p \leq 0.05$) than was possible in the laboratory (Fig. 5). However, if the copepods responded to the surface temperature, development in Loch Striven would still have been 2 and 3 days faster in spring, but 1, 6 and 2 d slower from June to August, respectively, than at excessive food in the laboratory. Most of these differences must be considered as small relative to the accuracy that may be expected in field estimates. Therefore, assuming that the laboratory estimates at excessive food represent the maximal development rate and that the field values were estimated correctly, this would imply that the temperature response of the copepods was not in accordance with the assumed depth distribution, and that food was generally not limiting for development of *P. elongatus* during spring and summer in Loch Striven. The latter conclusion was also drawn by Frost (1985) on the basis of apparently food satiated egg production of this species in the data of Marshall (1949) during spring and summer in Loch Striven. Similar considerations for other species in the same data, however, lead to the conclusion that food was limiting in *Calanus finmarchicus* (Frost 1985) and possibly also in *Acartia*

clausi (Klein Breteler & Schogt 1994). This supports the idea that *P. elongatus* has a low sensitivity to food limitation (cf. 'Introduction').

The above comparisons between laboratory and field data make it apparent that for a proper interpretation of field data, precise knowledge is required on the distribution and the temperature history of the copepod population. Well-mixed areas with small temporal and spatial temperature gradients include the risk of sampling in different populations. In stratified areas, even when the daily migratory behaviour is known, it will be difficult to estimate an 'average' temperature to which the copepods will physiologically respond during their development. With regard to *Pseudocalanus* spp. too few field data were available to conclude whether or not food limitation is a general phenomenon in the sea. In a comparable study on *Acartia clausi* (Klein Breteler & Schogt 1994) sufficient data were available to conclude that food is generally in short supply during summer.

The present references of unrealistically rapid development may also point to methodological problems in properly estimating the development of copepods in the field. Errors may arise during summer and autumn due to the difficulty to distinguish the successive cohorts when reproduction is continuous (e.g. Krause & Trahms 1983). This may bias available field estimates towards data that are collected in spring, when the first generation is still clearly discernible. Such over-representation of data in spring, at a surplus of food, might obscure the influence of the food factor during the rest of the season. Moreover, since food concentration and temperature tend to be inversely related during the season, it is difficult to discern the true causal relationship with either temperature or food. For these reasons doubt may arise about the conclusion drawn from literature data that generation time and, derived from this, the growth rate of copepods is determined by temperature alone (Huntley & Lopez 1992). Too much evidence from field observations, as reviewed by Klein Breteler & Schogt (1994), is available to generalise and reject food concentration as a limiting factor.

Comparison with other North Sea species

Temperature had a major influence on development of *Pseudocalanus elongatus*. At a low temperature of 5°C the generation time was about 59 d when food was abundant. This is comparable to the results obtained with *Temora longicornis* in similar experiments (Klein Breteler & Gonzalez 1986). However, *Acartia clausi* developed some 20 d slower at this low temperature (Klein Breteler & Schogt 1994). At a high temperature of 20°C, differences in development rate were obscured by high mortalities in *P. elongatus* and *T. longicornis*, but not in *A. clausi*. These differences in development rate at low temperatures and in mortality rate at high temperatures are indicative of a species specific physiological adaptation to the temperature. A low tolerance of high temperatures in *P. elongatus* may have contributed to its high mortality observed in the Westerschelde estuary (Soetaert & Herman 1994) and explain its low abundance during summer in coastal waters (Eriksson 1973, Fransz & Van Arkel 1983).

Limiting levels of food concentration were clearly found in the present experiments with *Pseudocalanus elongatus*. Our Food Supply 1/4 only slightly (10 and 15°C, about 100 µg C l^{-1}) or hardly (5°C, 192 µg C l^{-1}) reduced the rate of development, but at Food Supply 1/16 (about 70 µg C l^{-1}) and lower, development was significantly depressed. In former experiments an optimal development at Food Supply 1/4 was also observed at 15°C (Klein Breteler et al. 1982). Therefore, between 100 and 200 µg C l^{-1} seems to be a critical food level for development in our experiments with *P. elongatus*. In 3 other species of copepods the rate of development seemed to be more clearly depressed at this food level (Klein Breteler et al. 1982, Klein Breteler & Gonzalez 1986), although the difference was not very large, particularly with *Acartia clausi* (Klein Breteler & Schogt 1994). Therefore, the present results give some support to the low critical food value observed for development and growth in *Pseudocalanus* spp. compared to *Calanus* spp (cf. 'Introduction'). However, growth measurements include the change of weight, which, just as body length and lipid content, was generally significantly reduced by food at Food Supply 1/4 in the present experiments (Klein Breteler & Gonzalez 1988). Hence, with regard to growth the critical food level will be approximately 200 µg C l^{-1}, which corresponds well with the observations by Vidal (1980a) at the last copepodite stage, but it is clearly higher than found for egg production in *Pseudocalanus* sp. by Frost (1985).

The critical food level also seems to depend on the quality of the food. Using the chain-forming diatom *Thalassiosira rotula* as food, Paffenhöfer & Harris (1976) observed a lower development rate of *Pseudocalanus elongatus* only at 25 µg C l^{-1}, whereas data of Green et al. (1991), using the small flagellate *Isochrysis galbana*, provide evidence of reduced naupliar development time at 176 µg C l^{-1}. In another undefined species of *Pseudocalanus* fed with single cells of *T eccentrica*, Vidal (1980b, his Fig. 3) showed a reduced development rate of copepodite stages at 140 µg C l^{-1}, whereas Davis (1983) reported this at concentrations below 100 µg C l^{-1} of a mixture of food algae.

During summer, phytoplankton concentrations of 30 and 70 µg C l^{-1} are typical in the North Sea offshore and along the coast, respectively (Baars & Fransz 1984, W. Gieskes & G. Kraay pers. comm.). At the comparable Food Supplies 0 and 1/16 and a summer temperature of about 18°C the present data predict a generation time of *Pseudocalanus elongatus* of 31 and 26 d, respectively. This is 5 to 9 d faster than observed in *Temora longicornis* and 7 to 19 d faster than in *Acartia clausi* at similarly low food conditions. At spring conditions of about 7°C and ad libitum food a generation time of 45 d would be expected, which is only 4 d slower than *T. longicornis*, but 17 d faster than *A. clausi* (Klein Breteler & Gonzalez 1986, Klein Breteler & Schogt 1994). These characteristics of a rapid development during spring and summer conditions may explain the numerical dominance of *P. elongatus* in the stratified part of the North Sea and the northeastern Atlantic (Colebrook 1982). First, a possibly low critical food level may help to maintain a larger population during periods of food shortage in autumn and winter and, perhaps, also in summer. Since *P. elongatus* is able to store energy in the form of lipid droplets, the energy reserves collected during winter may contribute to a quick reproductive response at the onset of the spring phytoplankton bloom. Combined with rapid development at low temperatures, an early development of the population may be expected, which is in agreement with the short lag-time after the phytoplankton bloom development compared to *A. clausi* (Colebrook 1982).

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