

The dependence of body weight in copepodite stages of *Pseudocalanus* spp. on variations of ambient temperature and food concentration

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Abstract

Quantitative expressions are presented describing the effects of temperature and food concentration on the mean body weight of copepodite stages of *Pseudocalanus* spp. The calculations were made on the basis of experimental data from the literature for three geographically separate populations of *Pseudocalanus* from Puget Sound (Washington, USA), from the southern North Sea and the Baltic Sea. Relationships were obtained between the coefficient of daily exponential growth of body weight of *Pseudocalanus* sp. from Puget Sound and temperature in the 8–15.5°C range and food concentrations from 10 mgC m⁻³ to excess, as well as for *Pseudocalanus elongatus* from the southern North Sea at high food concentrations and in the 4–15°C temperature range. Also computed was the mean body weight for stages CII to CV of *P. elongatus* from the southern Baltic Sea at 5°C. The empirical models presented here can be used with good precision in mathematical models of pelagic communities. The results presented here indicate that *Pseudocalanus* sp. from Puget Sound (a species resembling *Pseudocalanus minutus*) is similar to *P. elongatus* from the southern North Sea and the English Channel with respect to growth parameters in the studied range of temperatures for excess food. *P. elongatus* collected in the Baltic Sea (Gulf of Gdańsk) differs from *P. elongatus* from the southern North Sea.

The complete text of the paper is available at <http://www.iopan.gda.pl/oceanologia/>

1. Introduction

Mathematical models of pelagic communities, particularly of the lower trophic levels represented by plankton, require detailed descriptions of the various relationships between the rates of physiological processes of the dominant species and environmental factors. In the literature there are considerable amounts of experimental data on these aspects for several species of zooplankton. This information can be used to give an idea of the functional relations which could be used to simulate the response of zooplankton to variations in their environment. The development of such theoretical descriptions is critical to the inclusion of these animals, as animals, in more general simulations of ecosystems. Planktonic copepods (*Pseudocalanus*, *Temora*, *Acartia*) are important components of the diet of a number of different species of fish in the North Sea and adjacent waters, i.e. the Baltic Sea and English Channel (Paffenhöfer & Harris 1976, Last 1978a, b, Thompson 1982, Witek 1995, Möllmann et al. 2000) as well as in Puget Sound, Nova Scotia and Canadian Arctic waters (Corkett & McLaren 1978, Vidal 1980a, b, Landry 1983, McLaren et al. 1989). The copepod *Pseudocalanus* is one of the more abundant zooplankton species in these waters.

Experiments on the growth rate of the copepodite stages of *Pseudocalanus* spp. suggest that it is directly proportional to food concentration (Paffenhöfer & Harris 1976, Corkett & McLaren 1978, Vidal 1980a, Klein Breteler et al. 1995) and is strongly influenced by food quality (Koski et al. 1998). The development of *Pseudocalanus* spp. was also found to increase with temperature (McLaren 1965, Vidal 1980a, Thompson 1982, Klein Breteler et al. 1995). However, the combined effects of food concentration and temperature as a function of these two parameters on growth rate and development time was established for *Pseudocalanus* spp. by Dzierzbicka-Głowacka (2004). Vidal (1980a) did describe such a dependence for the growth rate of *Calanus pacificus*, his data were insufficient to do likewise for *Pseudocalanus*. This is a key statement, being the motivation and justification for the present study, which is a continuation of Dzierzbicka-Głowacka (2004). The present work advances the idea of establishing the combined effect of temperature and food concentration on the body weight of *Pseudocalanus* spp. Its main object is to derive quantitative expressions for describing the coefficient of daily exponential growth of body weight as a function of food concentration and temperature for copepodite stages of *Pseudocalanus* spp.

2. Material and methods

The present analysis is based on the calculations made in Dzierzbicka-Głowacka (2004), which were based on literature data. The data discussed in the present paper were obtained on the basis of materials collected in Puget Sound, Washington, USA (Vidal 1980a, b) and from the southern North Sea (Thompson 1982) and Baltic Sea (Ciszewski & Witek 1977). *Pseudocalanus* sp. from Puget Sound (a species resembling *Pseudocalanus minutus*; suggestion by B. W. Frost – see Vidal (1980a) and Dzierzbicka-Głowacka (2004)) was collected with a plankton net (215 μm mesh size) hauled through the upper 30 m. Copepodite stages were cultured at 15.5, 12 and 8°C, the cultures being started with Stages CI or CII. All experiments were done with single-cell, pillbox-shaped diatoms *Thalassiosira eccentrica* isolated from the main basin of Puget Sound. *T. eccentrica* (ϕ – 20 μm ; 100%, 15.5 and 8°C; 50%, 12°C) and *T. eccentrica* (ϕ – 34 μm , 50%, 12°C) were used as food sources. The cell sizes, carbon contents, and concentrations of diatoms used in the experiments are shown in Table 1 in Vidal (1980a), where 1 ppm (food concentration) = 92 mgC m⁻³ for *T. eccentrica* of diameter 20 μm and 1 ppm = 72 mgC m⁻³ for *T. eccentrica* of diameter 34 μm . Vidal (1980a) published the values of the growth rate parameters (maximum growth rate g_{max} and slope of the growth curve σ) of *Pseudocalanus* sp. for development stages CII to CV cultured at 3 temperatures: 8, 12 and 15.5°C. *Pseudocalanus elongatus* from the North Sea (Thompson 1982) was collected with supplies of live plankton using a standard 61 μm mesh Fine International Net. The temperature of the cultures was kept at 4–15°C. All stages were fed with *Isochrysis galbana* at a concentration of 300 000 cells ml⁻¹. The development rates obtained in the experiments described in Thompson (1982) were probably not limited by food availability, and it can be assumed that they are near to the maximum rates which could occur under experimental conditions.

P. elongatus the from the Baltic Sea was collected in the Gulf of Gdańsk (Ciszewski & Witek 1977). The station was located in the center of the Gdańsk Deep, and the water temperatures in the layers where *P. elongatus* occurred, ranged from 3 to 10.5°C. Growth rate tests with *P. elongatus* were done at 5°C. The phytoplankton concentration in the sea, depending on the season in which the experiment took place, varied from 100 000 cells l⁻¹ in February to 5 000 000 cells l⁻¹ in April and decreased to 250 000 cells l⁻¹ in October. *Kirchneviella obesa*, *Microcystis aemginosa*, *Euglena* sp., *Navicula* sp., and *Gymnodinium* sp. were dominant.

A detailed description of the culture techniques used for *Pseudocalanus* sp. from Puget Sound can be found in Vidal (1980a); similarly,

those used for *P. elongatus* from the North Sea can be found in Thompson (1982) and from the southern Baltic Sea in Ciszewski & Witek (1977).

In the present work, the relationships between the stage duration calculated by Dzierzbicka-Głowacka (2004) and temperature and food concentration were found by performing linear regression following appropriate transformation of these data.

The stage duration, D , of *Pseudocalanus* sp. for stages CII–CV was used to express numerically the coefficient of daily exponential growth. D was found to be very sensitive to changes in temperature and food concentration (see the subsection ‘Stage duration’ in Dzierzbicka-Głowacka (2004)). Transformation of these data for D to natural logarithms gave a linear relationship between time and food concentration. This was described by the equation:

$$\ln(D - D_{\min}) = a + b \text{ Phyt.} \quad (1)$$

The values of a , b , and r , the correlation coefficient (in the range 0.790–0.989) for each developmental stage CII–CV and for the total period of growth from CII to CV at temperatures ranging from 8 to 15°C are given in Table IV in Dzierzbicka-Głowacka (2004). The coefficients a and b of the equations describing D as a function of food concentration were obtained as a function of temperature by means of a linear-log and an exp-linear regression on the data for coefficients a and b , respectively ($a = a_1 + b_1 \log T$; $e^b = a_2 + b_2 T$). The regression equations for each stage with the correlation coefficients (in the range 0.730–0.965) are given in Table V in Dzierzbicka-Głowacka (2004).

D_{\min} is the minimum value for which the development rates were not limited by food availability. The common logarithm of D_{\min} for *Pseudocalanus* sp. as well as *P. elongatus* from the southern North Sea was related linearly to the common logarithm of temperature:

$$\log D_{\min} = a + b \log T. \quad (2)$$

The values of a , b , and r , the correlation coefficient (in the range 0.957–0.996 for *Pseudocalanus* sp., 0.902–0.992 for *P. elongatus*) for stages CII–CV are given in Table III in Dzierzbicka-Głowacka (2004). By substituting a , b and D_{\min} in eq. (1) for the equations in Table V and III in Dzierzbicka-Głowacka (2004), D for stages CII to CV of *Pseudocalanus* sp. becomes a function of both food concentration and temperature in the 8–15.5°C range (see Dzierzbicka-Głowacka 2004):

$$\begin{aligned} \text{for CII } D &= 36.98 \times 10^{-0.988 \log T} + \\ &+ e^{-1.29+3.07 \log T+\ln(0.958+0.001124 T) Phyt}, \end{aligned} \quad (3)$$

$$\begin{aligned} \text{for CIII } D &= 29.92 \times 10^{-0.911 \log T} + \\ &+ e^{-1.63+3.30 \log T+\ln(0.954+0.001483 T) Phyt}, \end{aligned} \quad (4)$$

$$\begin{aligned} \text{for CIV } D &= 27.73 \times 10^{-0.987 \log T} + \\ &+ e^{-1.19+2.87 \log T+\ln(0.954+0.001319 T) Phyt}, \end{aligned} \quad (5)$$

$$\begin{aligned} \text{for CV } D &= 11.56 \times 10^{-0.559 \log T} + \\ &+ e^{-2.02+3.98 \log T+\ln(0.941+0.002832 T) Phyt}, \end{aligned} \quad (6)$$

$$\begin{aligned} \text{for Total CII - CV } TD &= 99.50 \times 10^{-0.860 \log T} + \\ &+ e^{0.58+2.53 \log T+\ln(0.934+0.003362 T) Phyt}. \end{aligned} \quad (7)$$

The values calculated with eqs. (3)–(7) for stage duration of *Pseudocalanus* sp. were used to obtain the mean value of α for the period CII–CV. α was calculated from the expression $W_t = W_0 e^{\alpha t}$ and is thus constant for all development stages (e.g. Paffenhöfer & Harris 1976, Huntley & Lopez 1992), where W is the mean body weight for copepodite stages CII to CIV and t is the time interval in days ($t = D$). The sets of stage duration curves computed with eqs. (3)–(7) of *Pseudocalanus* sp. for developmental stages CII–CV are shown in Fig. 4 in Dzierzbicka-Głowacka (2004).

3. Results

This subsection describes the coefficient of daily exponential growth of body weight, α , of *Pseudocalanus* sp. and *P. elongatus* from the southern North Sea and the Baltic Sea. The coefficient of daily exponential growth of body weight α of *Pseudocalanus* from Puget Sound for copepodite stages CII to CV was determined at different food concentrations and temperatures in the 8–15.5°C range and is given in Table 1. The food concentration and temperature exerted a significant influence on the coefficient of daily exponential growth. This effect was similar to that in the case of the stage duration. α increased with rising food concentration. Transformation of these data with Table 1 to exponents gave a linear relationship between the

common logarithm of food concentration and coefficient of daily exponential growth. This relationship was described by the equation:

$$e^\alpha = a + b \log Phyt. \quad (8)$$

Table 1. Coefficient of daily exponential growth α for developmental stages CII–CV of *Pseudocalanus* sp. from Puget Sound at different temperatures and food concentrations; for *Pseudocalanus elongatus* from the North Sea at 12.5°C for two periods of life: from CI to CIII/IV (*A*) and from CIII/IV to 50% adult (*B*) after Paffenhöfer & Harris (1976), and α_{\max} for *P. elongatus* obtained here according to Thompson’s (1982) data (*Th*) (last column)

Temperature [°C]	Phytoplankton concentration [mgC m ⁻³]						
	10	25	50	100	200	max	max Th
4.9							0.08799
8.6	0.06898	0.09826	0.12939	0.14908	0.15137	0.15137	0.14341
9.7	0.04705	0.09290	0.13249	0.15661	0.15270	0.16222	0.14666
10.8	0.04007	0.08661	0.12994	0.17322	0.17206	0.17694	0.16596
12.6	0.03613	0.07734	0.12201	0.16596	0.18707	0.19285	0.19375
14.5	0.03093	0.06820	0.11317	0.16398	0.19938	0.22211	0.19412
12.5 ^A		0.11	0.26-0.38	0.20-0.32	0.17		
12.5 ^B		0.10	0.07	0.19	0.16		

The values of a , b , and r , the correlation coefficient, together with the regression equations are given in Table 2. The coefficients a and b of the

Table 2. Equations describing the relationship between the coefficient of daily exponential growth α and food concentration $Phyt$ [mgC m⁻³] for developmental stages CII–CV of *Pseudocalanus* sp. from Puget Sound at 5 temperatures

Temperature [°C]	a	b	r	Equation
8.6	1.00003	0.07583	0.9742	$=\ln(1.00003 + 0.07583 \log Phyt)$
9.7	0.96226	0.09650	0.9549	$=\ln(0.96226 + 0.09650 \log Phyt)$
10.8	0.92277	0.12296	0.9746	$=\ln(0.92277 + 0.12296 \log Phyt)$
12.6	0.89755	0.13640	0.9947	$=\ln(0.89755 + 0.13640 \log Phyt)$
14.5	0.87096	0.15073	0.9934	$=\ln(0.87096 + 0.15073 \log Phyt)$

equations describing α as a function of food concentration (Table 2) were related linearly to the common logarithm of temperature in the 8–15.5°C range:

$$a = 1.512 - 0.5581 \log T, r = -0.986, \quad (9)$$

$$b = -0.2248 + 0.3274 \log T, r = -0.981. \quad (10)$$

By substituting a and b in eq. (8) for eqs. (9) and (10), the coefficient of daily exponential growth becomes a function of both food concentration and temperature (Fig. 1):

$$\alpha = \ln \{1.5124 - 0.5581 \log T + (-0.2248 + 0.3274 \log T) \log Phyt\}. \quad (11)$$

This equation is true for $10 < Phyt < Phyt_{\max} = -345.06 + 506.27 \log T$, $r = 0.992$.

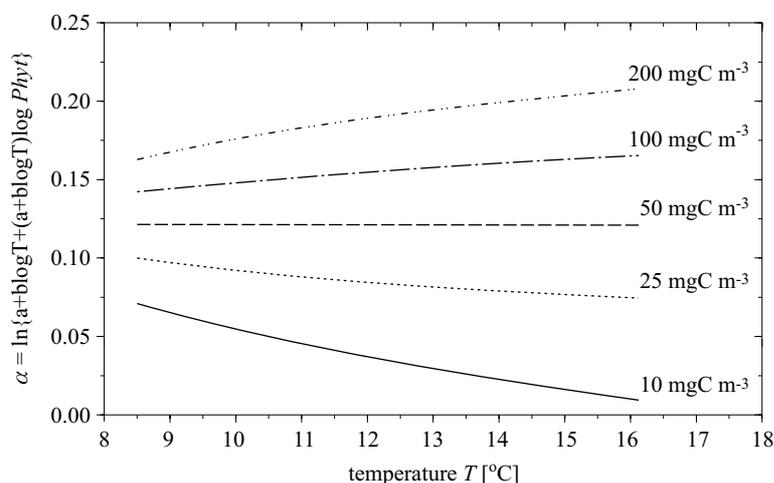


Fig. 1. Relationship between the coefficient of daily exponential growth α and temperature T [°C] for developmental stages CII–CV of *Pseudocalanus* sp. from Puget Sound for different food concentrations $Phyt$ [mgC m^{-3}]

The sets of α curves computed with eq. (11) for the copepodite stages of *Pseudocalanus* sp. cultured at different food concentrations and temperatures are shown in Fig. 2. α increased with rising temperatures and food concentrations for $Phyt > 50 \text{ mgC m}^{-3}$; but at low food concentrations ($10 < Phyt < 50 \text{ mgC m}^{-3}$) α was inversely related to temperature.

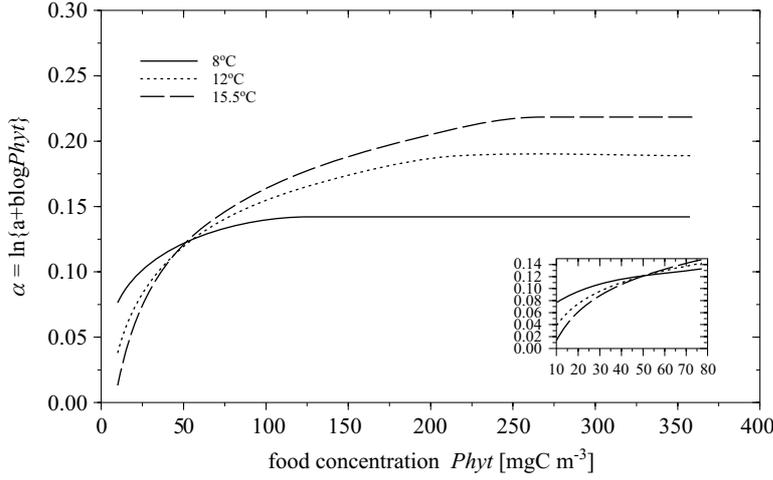


Fig. 2. Relationship between the coefficient of daily exponential growth α and food concentration $Phyt$ [mgC m^{-3}] for developmental stages CII–CV of *Pseudocalanus* sp. from Puget Sound at 3 temperatures: 15.5, 12 and 8°C

The body weight of an animal does not increase when the population starves (if $Phyt \rightarrow 0$, then $\alpha \rightarrow -\infty$, which then causes $W_t = W_0 e^{\alpha t} \rightarrow 0$). However, as food concentrations rise to high values, α tends towards a constant value ($\alpha = \alpha_{\max}$ for $Phyt \rightarrow Phyt_{\max}$ – excess food). The phytoplankton concentration at which the daily coefficient growth assumed the maximum value increased with the logarithmic increase in temperature. In this case, the coefficient α for *Pseudocalanus* from Puget Sound was determined by the equation:

$$\alpha = \begin{cases} \sim 0 & \text{for } Phyt \rightarrow 0 \\ \text{eq. (11)} & \text{for } 10 < Phyt \leq Phyt_{\max} = -345.06 + 506.27 \log T \\ \alpha_{\max} & \text{for } Phyt > Phyt_{\max} = -345.06 + 506.27 \log T. \end{cases} \quad (12)$$

The minimum stage duration D_{\min} (see equations in Table III in Dzierzbicka-Głowacka (2004)) was used to obtain the mean value of the coefficient of daily exponential maximum growth, α_{\max} , for stages CII to CV of *Pseudocalanus* sp. and *P. elongatus*, for which the development rates were not limited by food availability. α_{\max} was expressed as a function of temperature for: *Pseudocalanus* sp. from Puget Sound

$$\alpha_{\max} = -0.09851 + 0.26632 \log T, \quad r = 0.998, \quad (13)$$

P. elongatus from the southern North Sea

$$\alpha_{\max} = -0.08166 + 0.24062 \log T, \quad r = 0.987. \quad (14)$$

According to the calculations, α_{\max} for the two species increased with increasing temperature; but for *Pseudocalanus* sp. α_{\max} attained higher values than for *P. elongatus* from the North Sea with increasing temperature. Slight differences in α_{\max} were found between the two species, but they disappeared with decreasing temperature. For example, α_{\max} for *Pseudocalanus* sp. was 0.219 at 15.5°C and 0.142 at 8°C, however for *P. elongatus* from the North Sea was 0.205 at 15.5°C and 0.136 at 8°C.

On the basis of materials collected in the Gulf of Gdańsk (Baltic Sea), Ciszewski & Witek (Ciszewski & Witek 1977, Witek 1995) calculated the maximum growth rate, g_{\max} , of the copepods of *P. elongatus*. g_{\max} for developmental stages of *P. elongatus* obtained by Ciszewski & Witek (1977) is given in Table 3. Knowing the values of the maximum growth rate g_{\max} and mean body weight W_i for successive copepodite stages, we can obtain the minimum stage duration D_{\min} for each stage from CII to CV. Assuming that the mean body weight for copepodite stages of *P. elongatus* from the Gulf of Gdańsk is equal to 0.66 for CII, 0.94 for CIII, 1.69 for CIV, 2.96 for CV and 4 μgC for adults (Witek 1995, for $\text{gC}/\text{g}_{\text{w.w.}} = 0.064$), the minimum stage duration D_{\min} for stages CII to CV at 5°C was computed by the numerical solution of polynomials of unknown degrees D_{\min} . The polynomials for each successive stage from CII to CV at the given temperature were described by

$$(W_i + W_i g_{\max})(1 + g_{\max} + g_{\max}^2 + \dots + g_{\max}^{n-1} + g_{\max}^d) = W_{i+1},$$

where W_i [μgC] is the known mean body weight for successive copepodite stages, g_{\max} [% day^{-1}] is the known maximum growth rate for successive copepodite stages, and $D_{\min} = n + d$ [day] is the stage duration (e.g. when

Table 3. Parameters g_{\max} (given by Ciszewski & Witek 1977), D_{\min} and α_{\max} (obtained here) of growth for developmental stages CII–CV of *Pseudocalanus elongatus* from the Baltic Sea (Gulf of Gdańsk)

Stage	g_{\max} [% day^{-1}]	D_{\min} [day]	α_{\max}
CII	5.8	6.25	0.057
CIII	4.1	14.57	0.041
CIV	3.4	16.73	0.034
CV	2.6	11.71	0.026

$D = 5.36$ days, $n = 5$ and $d = 0.36$) and is an unknown quantity. The values of D_{\min} were used to obtain the coefficient of daily exponential maximum growth of body weight for stages CII to CV and are given in Table 3. The mean value of α_{\max} for copepodite stages of *P. elongatus* from the Gulf of Gdańsk is equal to 0.039. For example, α_{\max} for *P. elongatus* from the southern North Sea was 0.081 at 5°C; hence, it is about twice as high as in Baltic Sea waters. This situation is caused by low salinity in the Baltic Sea. Faunal and floral biodiversity in the Baltic Sea is controlled by salinity (Vuorinen et al. 1998). Similarly, the rate of physiological processes of organisms in this sea is also controlled mainly by salinity. However, salinity is controlled by river run-off (Launiainen & Vihma 1990) and Atlantic water pulses (Matthäus & Schinke 1994), both of which are ultimately regulated by meteorological factors.

The mean body weight of copepodite stages of *Pseudocalanus* sp. at time t as a function of both food concentration and temperature was described by the equation (Fig. 3):

$$W_t = \begin{cases} \rightarrow 0 & \text{for } Phyt \rightarrow 0 \\ e^{\alpha t} & \text{for } 10 < Phyt \leq Phyt_{\max} = -345.06 + 506.27 \log T \\ e^{\alpha_{\max} t} & \text{for } Phyt > Phyt_{\max} = -345.06 + 506.27 \log T. \end{cases} \quad (15)$$

Fig. 3 illustrates the growth of *Pseudocalanus* sp. obtained with eq. (15) at the six food concentrations and at three temperatures. The effect of food concentration on the mean weight of the copepodite stages of *Pseudocalanus* sp. was more pronounced in later developmental stages than in early copepodites. The growth of early copepodites was only slightly retarded at suboptimal food conditions, but that of older stages was strongly suppressed. The effect of temperature was most evident at the highest and lowest food levels. Low temperatures retarded the growth of early copepodites. This is seen by comparing the initial slopes of the curves of weight in Fig. 3. However, temperature had a moderate effect on copepods of intermediate and large body weights. The growth of small copepods was probably controlled by temperature rather than food concentration, but that of the larger ones was more sensitive to changes in food concentration.

However, the mean body weight for stages CII to CV of *P. elongatus* from the North Sea as a function of temperature and from the Baltic Sea at 5°C can be also described by the equation

$$W_t = W_0 e^{\alpha_{\max} t} \quad \text{for excess food,} \quad (16)$$

where α_{\max} for *P. elongatus* from the North Sea is defined by eq. (14)

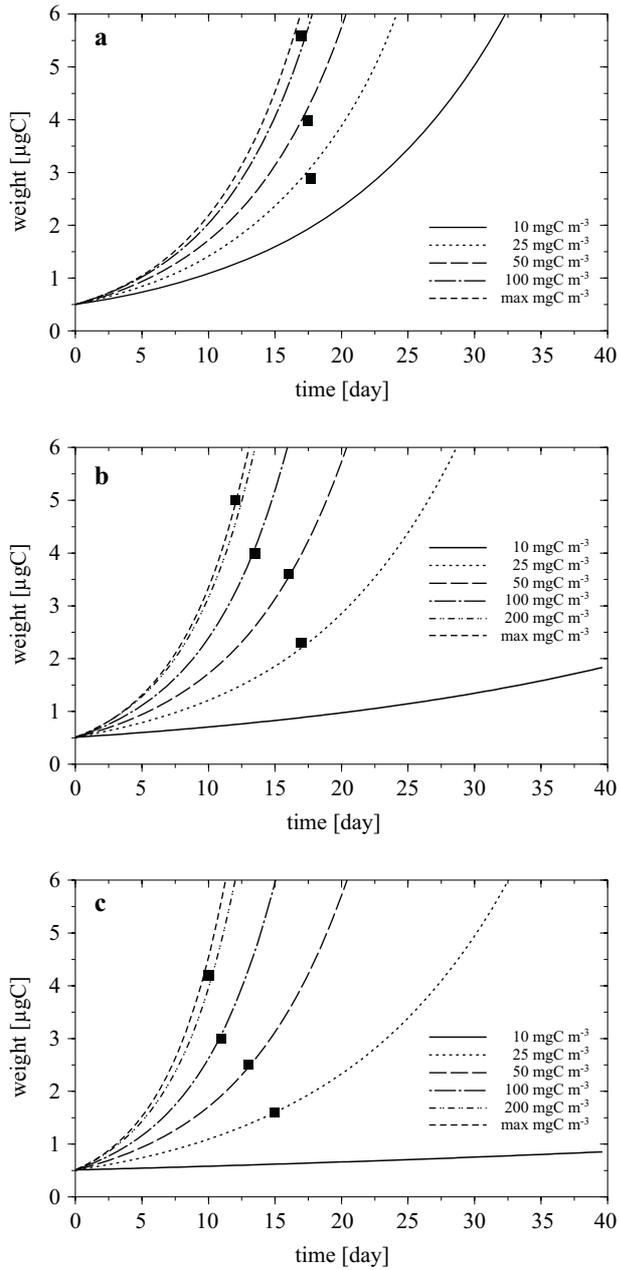


Fig. 3. Growth of *Pseudocalanus* sp. from Puget Sound. Weight W [μgC] as a function of time t [day] at different food concentrations $Phyt$ [mgC m^{-3}] at 3 temperatures: 8°C (a), 12°C (b) and 15.5°C (c). Mean body weight of *Pseudocalanus* sp. from Puget Sound for CVI after Vidal (1980a) (squares)

and for *P. elongatus* from the Baltic Sea by the values given in Table 3. Fig. 4 illustrates the growth at high food levels (for which the development rate was not limited by food availability) for copepodite stages of *P. elongatus* from the North Sea computed with eq. (16) at four temperatures (5, 8, 12 and 15°C) and from the Baltic Sea at 5°C as well as the experimental data given by Ciszewski & Witek (1977) for body wet weight of older stages of copepodite *P. elongatus* at 5°C. This figure shows that mean body weight was very sensitive to changes in temperature and rose with decreasing temperature but increasing body size was more pronounced at high than at low temperatures. The present results indicate that growth of stages CII to CV of *P. elongatus* from the North Sea and of *Pseudocalanus* sp. was similar over the studied range of temperatures for excess food. However, the growth of *P. elongatus* from the Baltic Sea at 5°C is similar to the literature data and is about half that of *P. elongatus* from the southern North Sea.

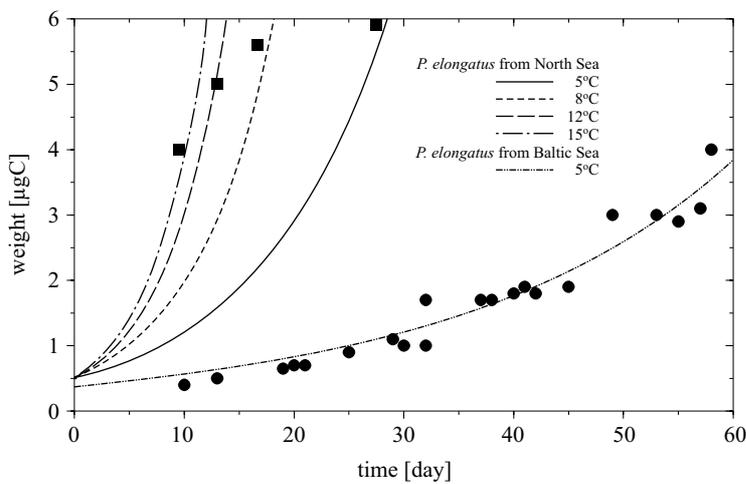


Fig. 4. Weight W [μgC] as a function of time t [day] at excess food *Phyt* [mgC m^{-3}] for developmental stages CII–CVI of *Pseudocalanus elongatus* from the North Sea at 4 temperatures (5, 8, 12 and 15.5°C) and *P. elongatus* from the Baltic Sea (Gulf of Gdańsk) at 5°C. Experimental data of body weight for copepodite stages of *P. elongatus* from the Baltic Sea (circles) and for adults of *P. elongatus* from the North Sea (squares)

4. Discussion

Copepods of the genus *Pseudocalanus* often dominate the zooplankton in the temperate-boreal neritic seas of the Northern Hemisphere (Corbett & McLaren 1978). Despite the apparent ecological significance of

Pseudocalanus species and the substantial interest in their physiology, behavior, genetics, and population biology, the genus is so poorly defined taxonomically that there is no operational means of identifying species (Frost 1989). Indeed, in most recent reports, species have been referred to as *Pseudocalanus* (e.g. Vidal 1980a, b, Klein Breteler & Gonzalez 1982, Ohman et al. 1983, Davis 1984, Frost 1985) and such caution is justified, for there are indications that two or more species of *Pseudocalanus* co-occur in some areas (Corkett & McLaren 1978). Furthermore, studies of unnamed *Pseudocalanus* in Nova Scotian waters have suggested that they do not form a panmictic population based on genetic variability in demographically important traits (Corkett & McLaren 1978), size-assortative mating (Hart & McLaren 1978), and differences in the DNA contents of adult somatic nuclei (Robins & McLaren 1982). Frost (1989) concluded on the basis of morphological criteria other than size that there are seven species within the genus *Pseudocalanus*: *Pseudocalanus minutus*, *Pseudocalanus elongatus*, *Pseudocalanus acuspes*, *Pseudocalanus major*, *Pseudocalanus moultoni*, *Pseudocalanus newmani* and *Pseudocalanus mimus*. There are only minute differences between some of these species, particularly *P. acuspes*, *P. moultoni* and *P. elongatus*. For instance, no absolute morphological criterion has been found to distinguish adult females of *P. acuspes* and *P. moultoni*. The validity of these two species was inferred from trends in several morphological characters (Frost 1989). However, Sévigny et al. (1989) studied allozyme variation at the glucose phosphate isomerase locus (GPI) to determine whether the morphological species defined by Frost (1989) represent groups that are also genetically distinct. On the basis of the GPI locus, Sévigny et al. (1989) were unable to detect any temporal variations in *P. newmani*, *P. acuspes* and *P. minutus*. The populations of *P. newmani* and *P. moultoni* from the Atlantic and Pacific coasts of North America have apparently diverged. No such divergence was detected among samples of *P. acuspes* from Nova Scotia, the Canadian Arctic and the Baltic Sea (Kiel Bay), and of *P. minutus* from Nova Scotia and Hudson Bay. *P. elongatus* collected in the English Channel differed from *P. acuspes* from the Baltic Sea (Kiel Bay). However, the results in Dzierzbicka-Głowacka (2004) and those presented here indicate that *Pseudocalanus* sp. from Puget Sound (a species resembling *P. minutus*) is similar to *P. elongatus* from the southern North Sea and English Channel with respect to growth parameters in the studied range of temperatures for excess food. *Pseudocalanus* collected in the Baltic Sea (Gulf of Gdańsk) identified as *P. elongatus* differs from *P. elongatus* from the southern

North Sea and the English Channel. On the basis of results given by Sévigny et al. (1989) and Frost (1989) as well as in this paper, one can not assume that *P. acuspes* from Kiel Bay is similar to *P. elongatus* from the Gulf of Gdańsk, because, as shown here, *P. elongatus* from the Gulf of Gdańsk differs from *Pseudocalanus* sp. (*P. minutus*) from Puget Sound.

One important interaction of broad biological and ecological significance was obtained in the present study. The body weight (the coefficient of daily exponential growth of body weight) of *Pseudocalanus* spp. for developmental stages CII to CV as a function of food concentration and temperature was expressed on the basis of results given in Dzierzbicka-Głowacka (2004). This author attempted to draw general inferences about the growth process (growth rate, development time) in *Pseudocalanus* sp. from Puget Sound (a species resembling *P. minutus* – suggestion given by B.W. Frost (see Vidal 1980a) and Dzierzbicka-Głowacka (2004)) by integrating the experimental data in Vidal (1980a,b) with those in other papers (Paffenhöfer & Harris 1976, Thompson 1982, Klein Breteler et al. 1995, Koski et al. 1998). The growth rates of *Pseudocalanus* sp. for stages CII–CV computed as a function of food concentration and temperature were similar to the experimental data given by Vidal (1980a) at all temperatures. For the smallest-sized *Pseudocalanus* sp. and *P. elongatus* from the southern North Sea, the maximum growth rate, g_{\max} , increased rapidly with rising temperature, but with advancing stage of development the effect of temperature decreased, and the larger copepods attained similar g_{\max} values regardless of temperature. The slight differences in g_{\max} between *Pseudocalanus* sp. and *P. elongatus* suggest that the total duration of stages CII–CV is similar in these two species over the studied range of temperatures, as Dzierzbicka-Głowacka (2004) has shown. The results in Dzierzbicka-Głowacka (2004) indicate that the average time to reach a given stage becomes shorter as the ambient temperature increases with food concentrations higher than $Phyt_c$ (critical food concentration) for each stage, but at lower phytoplankton concentrations, temperature clearly has no effect on D . Values of D computed in Dzierzbicka-Głowacka (2004) for *Pseudocalanus* sp. are similar to the original results given by Vidal (1980a) at much the same range of temperature and food concentration, except for $Phyt < 50 \text{ mgC m}^{-3}$, where the D values for the particular stages were a little higher at all temperatures. Dzierzbicka-Głowacka (2004) also showed that the total duration of stages CII–CV of *Pseudocalanus* sp. was 9.7 days and for *P. elongatus* was 9.6 days after Thompson (1982) and 6.7 days after Klein Breteler et al. (1995) at 15°C and excess food, which are generally

comparable to the literature values (Vidal 1980a, b, Thompson 1982, Landry 1983, McLaren et al. 1989, Klein Breteler et al. 1995). The difference in TD is caused mainly by the fact that the food source in these cases was different. The results of the study presented in Dzierzbicka-Głowacka (2004) also demonstrate that TD of *Pseudocalanus* sp. rose with decreasing temperature in the studied range of food concentration, except that at food concentrations in the range $50 < Phyt < 100 \text{ mgC m}^{-3}$, temperature clearly had no effect on TD for *Pseudocalanus* sp.

The present work advances the idea of establishing the combined effect of temperature and food concentration on the body weight of the copepodite stages of *Pseudocalanus* spp. The results in this paper demonstrate that the coefficient of daily exponential growth, α , of *Pseudocalanus* sp. for stages CII to CV increased with food concentrations rising from 50 mgC m^{-3} to excess and temperature in the $8\text{--}15.5^\circ\text{C}$ range to the maximum value α_{\max} , except at food concentrations in the range ($10 < Phyt < 50 \text{ mgC m}^{-3}$), where α was inversely related to temperature, as the present work has shown (eq. 12, Fig. 2). This suggestion is in line with the original experimental results given by Vidal (see Fig. 2 in Vidal (1980)), although he maintained that temperature and food concentration clearly had no effect on α , as in case of *Calanus pacificus*. Values of α computed here with eq. (8) are similar to those given in Vidal (1980a) with the exception of the lower food concentration ($Phyt < 50 \text{ mgC m}^{-3}$) at which α was lower. This is caused by fact that TD at $Phyt = 25 \text{ mgC m}^{-3}$ obtained in Dzierzbicka-Głowacka (2004) was higher than the value given in Vidal (1980a).

The coefficient of daily exponential maximum growth α_{\max} , which was not related to food availability, was obtained for *Pseudocalanus* sp. as well as for *P. elongatus* from the North Sea as a function of temperature. The calculations show that the maximum coefficients for these two species increased with the logarithmic increase in temperature and were similar at all temperatures.

Data on growth rates of *P. elongatus* are also given by Paffenhöfer & Harris (1976) at different food concentrations (see Table 1). At 12.5°C the daily exponential growth rate for the periods CI–CIII/CIV was $0.11\text{--}0.32$ and from CIV to adult was $0.07\text{--}0.18$. From CI to CIII/CIV the low food concentration of 27 mgC m^{-3} resulted in a reduced growth rate. The effects of food concentration become apparent during the period from CIII/CIV to 50% adult, when growth rates at food concentrations ($21\text{--}56 \text{ mgC m}^{-3}$) are markedly below the other values. However, in the present work the daily exponential growth rate obtained for the period CII to CV ranged from 0.09 to 0.2 at 12.5°C and at much the same food concentrations

as in the experiment by Paffenhöfer & Harris (1976). These differences in α mainly are caused by the fact that Paffenhöfer & Harris's (1976) experiment referred to the two periods of growth, including stage CI and 50% adult, for which the daily exponential growth rate was higher and lower, respectively.

On the basis of material collected in the Gulf of Gdańsk (Baltic Sea), Ciszewski & Witek (1977) obtained the growth rate of *P. elongatus* at 5°C. According to these findings, α_{\max} computed here is about half that of *P. elongatus* from the North Sea after Thompson's (1982) data (Fig. 4). The significant difference in α_{\max} between the two species is due to the low salinity in the Baltic Sea. *P. elongatus* is quite euryhaline or properly, marine euryhaline, 4–5 PSU appearing to be the lowest tolerable salinity (Kinne 1963).

The exponential growth α also was estimated by Koski et al. (1998) from the observed mean dry weight at 15°C. With few exceptions, the specific growth rate shows the effect of food species similar to that shown by development time; a good coefficient of exponential growth of 0.13 to 0.18 was obtained with *Rhodomonas* sp., *N*-limited *Rhodomonas* sp. and *Gymnodinium simplex*; however, the exponential growth with *Thalassiosira weissflogii* was significantly lower (0.12). Slow or negligible growth (0.10) was found with *Dunaliella* sp. and *Amphidinium* sp. The exponential growth rate with the remaining species was variable (*Chrysochromalina polylepis*) or unreliable (*N*-limited *T. weissflogii*), and generally zero, due to high mortality and, consequently, the low number of observations (Koski et al. 1998). However, in the present work, the α values were 0.20 and 0.21 at 15°C for *Pseudocalanus* from Puget Sound and the southern North Sea, respectively.

The mean body weight for copepodite stages of *Pseudocalanus* sp. in time as a function of both food concentration and temperature was obtained with the exponential equation (eq. 15). The early phase of copepodite growth, as indicated by the initial slope of the growth curves (Fig. 3), was strongly influenced by temperature but remained relatively unaffected by food concentration. However, the growth of intermediate and late copepodites was strongly influenced by food concentration but only slightly affected by temperature. These changes were gradual, the influence of temperature decreasing as that of food concentration became more pronounced (Fig. 3). On the basis of the findings in this study and of the analyses of the above relationships it is postulated that the warmer waters are characterized by the dominance of small-sized individuals *Pseudocalanus* sp.; nevertheless, large-sized ones live in colder waters, though only when food levels are comparable. For example, the mean body

weight of adult *Pseudocalanus* from Puget Sound and the North Sea at 8°C was higher than that at 15°C at the given food concentration (see Figs 3 and 4).

Pseudocalanus spp. is a cold-water genus that is most abundant in shelf waters, and, throughout much of its geographic range, is dominant during the cold season (winter and early spring) and grows from egg to adult at low temperatures (< 8°C). Since minimum ambient food concentrations in shelf regions are typically > 100 mgC m⁻³, the *Pseudocalanus* development rate, daily exponential growth, and body weight are not likely to be affected by food concentration, but are affected by temperature (Figs 2 and 3). This means that modelers can ignore the effects of food on *Pseudocalanus* at low temperatures in many shelf regions, i.e. the phytoplankton is not needed in the model under these conditions.

Quantitative expressions describing the effects of temperature and food concentration on the mean daily coefficient growth (on mean body weight) of *Pseudocalanus* spp. have been worked out. The relationship between the growth parameter of *Pseudocalanus* sp. from Puget Sound and temperature in the range 8–15.5°C and food concentration in the range from 50 mgC m⁻³ to high levels of food can be used in mathematical models of pelagic communities. However, for food concentrations below 25 mgC m⁻³ the possibilities of verification by experimental data are insufficient. The relationship for *P. elongatus* from the southern North Sea, obtained from data in Thompson (1982), at high food concentration and at temperatures ranging from 4° to 15°C can also be used. In the present work the mean body weight for copepodite stages of *P. elongatus* at 5°C was obtained, and can be used with a good precision in mathematical models.

The results of this study are dependent on the experimental results of the cited papers. Errors or bias in those experiments, if they exist, will affect the equations derived in this paper. At present the development and application of ecosystem models and of IBMs on larval fish feeding (eg. GLOBEC-projects) are on the increase. Both could definitely benefit from a study like this.

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