Potential rate of reproduction for some geographically separate populations of *Pseudocalanus* spp.

OCEANOLOGIA, 46 (1), 2004.
pp. 65–83.

KEYWORDS
Pseudocalanus spp.
Egg production
Temperature
Body size

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Manuscript received 18 November 2003, reviewed 5 January 2004, accepted 19 January 2004.

Abstract

Quantitative expressions are presented describing the potential reproductive rate per individual female of *Pseudocalanus* spp. in several different waters (not reduced by food limitation) as a function of both temperature and cephalothorax length of females (one equation for each studied region). The calculations were made for some geographically separate populations of *Pseudocalanus* spp. from southwest Baffin Island, Nova Scotia, Long Island Sound, Scotland, as well as the southern North Sea and its adjacent waters (e.g. the English Channel). On the basis of the findings presented in this work and from other studies, the reproductive rate was computed as the mean number of eggs per sac divided by 1.25 times the embryonic duration at the given temperature. Also computed was the amount of egg matter produced per day as a percentage of body carbon (and dry weight) of female weight for all localities. The relationships for females from the southern North Sea were obtained for 'viable eggs', but they should be treated with reserve. A more suitable expression describing egg production in the southern North Sea is the equation for females from the English Channel obtained here. Our assumptions and approximations appear to predict quite well the temperature-length of female dependent daily rates of egg production of well-fed females of *Pseudocalanus* spp. for the above waters, and we suggest that they can be used to test the hypothesis more thoroughly.

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

1. Introduction

Planktonic copepods are the major food source for fish larvae in the period of development following the utilisation of the larval yolk sac. They also form part of the basic diet of many adult pelagic fish. Feeding studies of fish larvae by Załachowski et al. (1975) and Last (1978a, b, 1980) have shown that *Pseudocalanus, Temora, Acartia* nauplius and copepodid stages are important components of the diet of a number of different species of fish in the North Sea and adjacent waters (i.e. the English Channel and Baltic Sea) as well as in Nova Scotian and Canadian Arctic waters (Corkett & McLaren 1978). The copepod *Pseudocalanus* is one of the more abundant zooplankton species in these waters.

Growth and development of *Pseudocalanus* spp. in different waters are determined mainly by temperature and food availability (Paffenhöfer & Harris 1976, Corkett & McLaren 1978, Vidal 1980a, b, Thompson 1982, McLaren et al. 1989, Klein Breteler et al. 1995, Witek 1995, Koski et al. 1998, Dzierzbicka-Głowacka 2004). Egg production of copepods in nature is generally assumed to be food-limited, while juvenile growth often seems to be dependent on temperature alone (McLaren et al. 1969, Paffenhöfer & Harris 1976, Thompson 1976, Corkett & McLaren 1978, Landry 1983).

The literature provides copious experimental data on egg production for different *Pseudocalanus* spp. This information can be used to obtain an idea of the functional relations between reproductive rate, body size of females and temperature, 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 *qua* animals in more general simulations of ecosystems. On the basis of the available information, this paper describes the general patterns determining egg production, i.e. the number eggs in a sac, the total number of sacs, embryonic duration, and the post-reproductive period in some geographically separate populations of *Pseudocalanus* spp. from southwest Baffin Island, Nova Scotia, Long Island Sound, western Scotland as well as the southern North Sea and its adjacent waters, e.g. the English Channel.

The present work advances the idea of establishing the combined effect of temperature and cephalothorax length of females on the reproductive rates of *Pseudocalanus* spp. The main objective of this paper is to derive some quantitative expressions to describe the average number of eggs produced per day by populations of satiated females of *Pseudocalanus* spp. in the above waters as a function of temperature and length of female (one equation for each region). This allowed us to express the quantity of egg matter produced per day as a percentage of body carbon (and dry weight) of female weight, which is determined by the given temperature for all localities.

2. Important terms regarding egg production

The terminology given by Corkett & McLaren (1978) is used in this work. An *egg sac* is a group of eggs clearly surrounded by an outer membrane and attached to a female. The *potential* reproductive rate is the average number of eggs produced per day by one female not reduced by food limitation.

The reproductive rate per female can be analysed in terms of five variables: (i) the number of eggs in the sacs, (ii) the rate of sac production, (iii) the total number of sacs produced during the reproductive period, (iv) the length of the post-reproductive period, and (v) the proportion of eggs in the sacs that hatch as nauplii (Corkett & McLaren 1978).

2.1. Number of eggs in a sac – E_s

Corkett & McLaren (1978) showed that the size of individual sacs may vary quite a lot during the full reproductive period of females. They suggested that exceptionally small sacs are often followed by exceptionally large females, and vice versa. Perhaps this involves withholding eggs between oogenetic cycles. The importance of female size was first explicitly recognised by Marshall (1949).

The number of eggs in a sac E_s as a function of cephalothorax length L [mm] was described by McLaren (1963) with Marshall's data from Loch Striven (Scotland) (see Table 1) (Corkett & McLaren 1978). In this paper the mean egg number in a sac for females from Nova Scotia, Long Island Sound and the Canadian Arctic was calculated on the basis of data from McLaren (1965) and Corkett & McLaren (1969, 1978). Transformation of these data to logarithms gives a linear relationship between female cephalothorax length and E_s: $\log E_s = a + b \log L$ (or $E_s = a\,L^b$). The parameters a, b and r, the correlation coefficient, are given in Table 1; the regression equations and experimental data are shown in Fig. 1.

Corkett & Zillioux (1975) found that temperatures had no effect on the sac size of females captured off Plymouth (the English Channel), and the mean number eggs per sac at all temperatures was about $E_s = 12.23$. Paffenhöfer & Harris (1976) measured the reproductive performance of a number of *Pseudocalanus* females from the North Sea reared at 12.5°C. The average number eggs in a sac was $E_s = 16.24$ for females of lengths between 1 and 1.2 mm, but there was variation within and between experiments (11.68–20.80). Thompson (1976) found that females from the southern

Table 1. Parameters a, b, and r describing the number of eggs per sac ($E_s = aL^b$) of *Pseudocalanus* spp.

Locality	Parameters			References
	a	b	r	
Scotland	19.35	3.94	0.997	McLaren (1963)
Nova Scotia	21.045	3.52	0.998	author
southwest Baffin Island	25.176	3.45	0.957	author
Long Island Sound	21.9145	3.72	0.974	author
southern North Sea	10.805	2.74	0.908	author

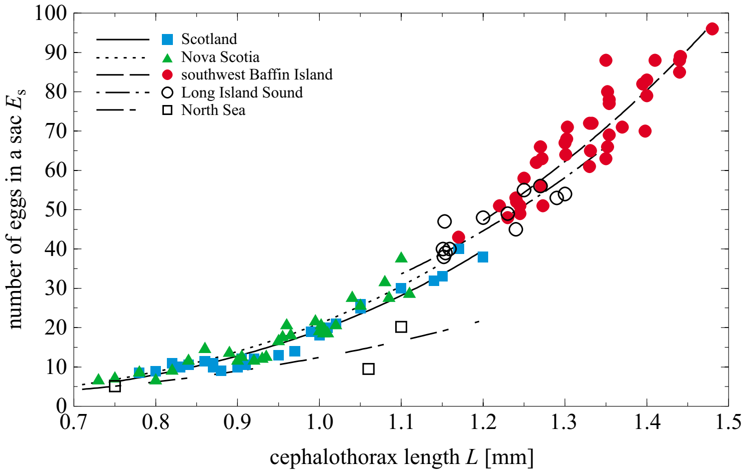

Fig. 1. Average number of eggs in a sac as a function of cephalothorax length. Lines were fitted to data using the equations in Table 1

North Sea stock produced on average about half as many 'viable eggs' per sac as might be expected from the relationship indicated by Corkett & McLaren (1969) for females from Nova Scotia or Scotland. The females of known cephalothorax lengths between 0.72 and 0.78 mm produced 5.1 eggs on average and those between 1.00 and 1.12 mm an average of 9.3 eggs. Thompson counted their eggs after hatching as nauplii, and predation by females was probably responsible for the low values (and high variance). In the present work the average number of 'viable eggs' per sac for females from the North Sea according to data given by Corkett & McLaren (1969) and Thompson (1976) as well as data after Paffenhöfer & Harris (1976) for high food levels ($Phyt = 200$ mgC m^{-3}, at which the rates of the physiological processes of egg production, growth and development were probably not limited by food availability (Paffenhöfer & Harris 1976, Dzierzbicka-Głowacka 2004)) are described by $\log E_s = a + b \log L$ (or $E_s = a\,L^b$ – see Table 1 and Fig. 1) as a result of the relevant transformation of these data. The southern North Sea results should be treated with reserve.

2.2. Total number of sacs – No_s

In the laboratory females produce a number of normal or complete egg sacs, after which they may produce smaller or infertile ones during an essentially post-reproductive period, i.e. the time between the appearance of the last sac and the female's death (after Corkett & McLaren 1978). Among females captured in nature, some will already have expended part of their reproductive potential. Those females producing maximal numbers of egg sacs are more revealing of reproductive potential.

Corkett & McLaren (1969) found that 8 of 33 females produced between 8 and 11 full-sized sacs and between 0 and 3 small, late ones. This suggests that the normal reproductive potential for females off Nova Scotia is about 10 successive sacs. However, the largest number of sacs produced by an individual captured off Plymouth (English Channel) was 9, all of which hatched successfully (Corkett & Zillioux 1975). Paffenhöfer & Harris (1976) showed that in one experiment using *Peridinium trochoideum* as food, 15 females produced an average of only 2.27 egg sacs. In another experiment 3 females produced only one, two, and two sacs respectively. This indicates that *P. trochoideum* is an unsuitable food. In another experiment using *Thalassiosira rotula* as food, 6 females produced an average of five sacs, which is lower than might be expected from the maximal performances of wild-caught females. Thompson (1976) found that seven females fertilised in the laboratory produced an average of 8.9 egg sacs, close to the potential indicated for wild females.

2.3. Embryonic duration – D_E

Bělehrádek's temperature function ($D_E = a(T + \alpha)^b$) has been extensively used to describe the embryonic duration of *Pseudocalanus* species (e.g. McLaren et al. 1969, 1989, Corkett & McLaren 1978) for appropriate food. D_E is the embryonic duration, α is related to the normal temperature regime for the species, and a is a population-specific constant. The slope of the line is described by b, which is set at -2.05 for copepod species. With this parameter constant, measurements of embryonic duration must be made at a minimum of 2 temperatures if they are to fit the function

(Corkett & McLaren 1978). The embryonic durations D_E with $b = -2.05$ for all localities are given in Table 2 (Corkett & McLaren 1969, 1978, McLaren et al. 1969, 1989, Thompson 1976).

Table 2. Parameters a, α describing the embryonic duration ($D_E = a(T + \alpha)^{-2.05}$) of *Pseudocalanus* spp.

Locality	Parameters		References
	a	α	
southwest Baffin Island	2280	13.84	[1]Corkett & McLaren (1978)
Nova Scotia[1]	2144	13.40	[2]McLaren et al. (1969)
Nova Scotia[2]	1949	12.59	McLaren et al. (1989)
Long Island Sound	2312	13.87	Corkett & McLaren (1978)
Scotland	2290	13.63	Corkett & McLaren (1978)
southern North SeaTh	1845	11.45	ThThompson (1976)
southern North Sea^{K-B}	1259	7.44	$^{K-B}$author after the data by Klein Breteler et al. (1995)

Thompson (1982) obtained the time taken in days from the production of the egg sac by the females to the hatching of nauplii for *Pseudocalanus elongatus* from the southern North Sea recorded at each temperature and described by $D_E = 9.628\, e^{-0.099\, T}$, where the correlation coefficient $r = 0.967$.

Paffenhöfer & Harris (1976) tabulate the means in four experiments to find the number of sacs produced by females, numbers of eggs per sac, and periods of nauplii production in days. In one experiment with *T. rotula* as food, four sacs (five minus one) were produced in 14.33 days, and the embryonic duration was about 2.8 days at 12.5°C. In three other experiments using *P. trochoideum*, the mean delays between the hatching of one sac and the appearance of the next were 3.3, 4.7 and 6.0 days.

Development times of seven species of planktonic marine copepods, including *Pseudocalanus* (female cephalothorax length = 1.0 mm) from Puget Sound (Washington), were determined at 15°C by Landry (1983). Eggs, nauplii and copepodids for *Pseudocalanus* make up 5.7, 43.5, and 50.8% of the generation time (=21.1 days). Hence, the embryonic duration amounted to 1.2 days and was similar to that in *Acartia tonsa*, where the time was measured relative to the midpoint between the beginning and end of egg production.

Embryonic duration was also calculated as the time for 50% of eggs to hatch for *Pseudocalanus* from northern Norway, and found to be 6.17 days at

3.3°C and 5.06 days at 4.5°C (Norrbin 1996). The parameters determined by McLaren et al. (1989) for development to first reproduction (D_{gen}) in this species at Halifax (Nova Scotia) was used, where $D_{gen} = 22591(T + 12.59)^{-2.05}$ or $11.59\,D_E$.

The duration of life stages under different conditions of temperature and food was calculated by Klein Breteler et al. (1995) for *Pseudocalanus* from the North Sea. The generation time D_{gen}, i.e. the time from laying to the time when 50% of the population had reached maturity, was obtained as a function of temperature at different food concentrations. In the present work the egg production time for the above species according to data given by Klein Breteler et al. (1995) was obtained using Bělehrádek's function $D_E = 1259(T + 7.44)^{-2.05}$, where the correlation coefficient $r = 0.999$.

2.4. The post-reproductive period – PTD and longevity – $TD + PTD$

Evidently, females can live for some time after reproduction has essentially ceased. Corkett & McLaren (1978) have suggested that the mean reproductive span of eight out of 33 wild-caught females (which carried 8–11 successive complete sacs) was 51 days, and their average life time between the appearance of the last sac and death was 41 days, i.e. the average longevity of these eight females was 92 days.

Thompson (1982) found that the seven females from North Sea reared in the laboratory had mean reproductive periods of 39 days and post-reproductive periods of 40 days, i.e. these females lived for an average of 79 days after mating, which occurred soon after maturity. However, for females producing a full complement of about 10 sacs at a maximal temperature-dependent rate, Thompson (1982) suggests that the essentially post-reproductive period can occupy the entire second half of adult life.

The period of egg production was also determined by Paffenhöfer & Harris (1976) for females feeding on either *P. trochoideum* or *T. rotula.* The mean reproductive period was 14.33 days with *T. rotula* as food and 8.4, 7.8 and 6 days with *P. trochideum* as food. Hence, female longevity may be about 29 days in the first case and about 17, 15 and 12 days in the second case in accordance with Thompson's (1976) suggestion that the post-reproductive period PTD may last as long as the reproductive period TD, i.e. $PTD = TD$.

3. Potential rate of reproduction

Corkett & McLaren (1969) concluded that embryonic durations can be estimated accurately, and that the time between successive sacs (or hatchings) might be about 25% longer than those durations when the food supply is adequate. Thus, estimating the potential rates of reproduction per individual female (not reduced by food limitation) might seem straightforward: simply divide the observed or calculated mean number of eggs in sacs by 1.25 times the embryonic duration at the given temperature, i.e.

$$\begin{aligned}
&\{\mathit{Reproduction}\} = \{\mathit{no.\ of\ eggs\ in\ sac}\}/1.25\,\{\mathit{embryonic\ duration}\}\\
&Egg = E_s/1.25\,D_E \quad \text{or}\\
&\{\mathit{Reproduction}\} = \{\mathit{no.\ of\ eggs\ in\ sac}\}\{\mathit{no.\ of\ sacs}\}/\{\mathit{reproductive\ period}\}\\
&Egg = E_s\,No_s/TD.
\end{aligned} \tag{1}$$

In this paper, the potential reproductive rate per individual female of *Pseudocalanus* (i.e. reproductive rate = no. eggs female^{-1} day^{-1}) was obtained on the basis of relationships between the number of eggs per sac and length of females as well as between embryonic duration and temperature. The calculations were made for some geographically separate populations of *Pseudocalanus*, i.e. from southwest Baffin Island, Nova Scotia, Long Island Sound, Scotland, and the southern North Sea.

Applying eq. (1), quantitative expressions ($Egg = a\,L^{\beta}(T+\alpha)^{2.05}$) describing the effects of temperature and female length on the potential rate of reproduction were obtained. The parameters a, β and α are given in Table 3 for all localities. It should be borne in mind that *Egg* in the North Sea was calculated for 'viable eggs'.

Table 3. Parameters a, β and α describing the daily number of eggs produced per *Pseudocalanus* spp. female ($Egg = aL^{\beta}(T+\alpha)^{2.05}$)

Locality	Parameters		
	a	β	α
southwest Baffin Island	0.0088	3.45	13.84
Nova Scotia^1	0.00785	3.52	13.40
Nova Scotia^2	0.00864	3.52	12.59
Long Island Sound	0.0076	3.72	13.87
Scotland	0.00676	3.94	13.63
southern North SeaTh	0.003644	1.737	11.45
southern North Sea^{K-B}	0.00534	1.737	7.44

$^{1,\,2,\,Th,\,K-B}$ – see Table 2.

Corkett & Zillioux (1975) found that the females captured off Plymouth (English Channel) at higher temperatures tended to release more of their eggs prior to hatching times. Here, the mean number of eggs produced per female from the English Channel per day was described after data given by Corkett & Zillioux (1975) (see Fig. 2d) as a function of temperature by

$$Egg_{ECh} = 0.712\, e^{0.1047\, T} \text{ with the correlation coefficient } r = 0.957.$$

The results of the present work indicate that the potential rate of reproduction for females of various lengths from Nova Scotia computed using D_E given by McLaren et al. (1969, 1989) was similar at all temperatures. The calculations also show that *Egg* values for females from Long Island Sound and Nova Scotia are similar at all temperatures. However, egg production for females from western Scotland is slightly lower than that from Nova Scotia. For example, females from Nova Scotia of lengths between 0.8 and 1.1 mm produce about 0.2–0.3 eggs female^{-1} day^{-1} more than those from Scotland at 5°C and about 0.8–1.2 eggs female^{-1} day^{-1} more at 14°C (see Figs 2b and 2c).

The studies presented here demonstrate that the reproductive rates for females of various lengths from the North Sea which were obtained using D_E given by Thompson (1976, 1982) and after the data by Klein Breteler et al. (1995) are comparable at all temperatures. It also turns out that the mean number of 'viable eggs' in the southern North Sea (*Egg*) for small females is slightly lower than in western Scotland at all temperatures, and for large ones is equal to about two thirds of this value. For example, females from the southern North Sea between 0.8 and 1.1 mm in length produce about 0.2–1.7 eggs female^{-1} day^{-1} fewer than those from Scotland at 5°C, and about 0.4–2.9 eggs female^{-1} day^{-1} fewer at 14°C (see Figs 2c and 2d).

The theoretical rate of reproduction for females from southwest Baffin Island and Nova Scotia obtained in this work as a function of temperature and female length and the data given by Corkett & McLaren (1978) (see Fig. 21 in Corkett & McLaren (1978) and Fig. 2 in this paper) differ slightly at all temperatures and various lengths. The reproductive rate for females from Baffin Island computed here (Fig. 2a) is about 0.8 eggs day^{-1} higher (for the largest females) than the figure given by Corkett & McLaren (1978). However, the calculated egg production for females from Nova Scotia (Fig. 2b) is slightly higher than that given by Corkett & McLaren (1978) at temperatures higher than 8°C. This difference for large females is about 0.7 eggs day^{-1}, but for smaller ones is about 0.3 eggs day^{-1}. These slight differences in *Egg* between the values calculated here and those in Corkett & McLaren (1978) are probably caused by the fact that the latter authors

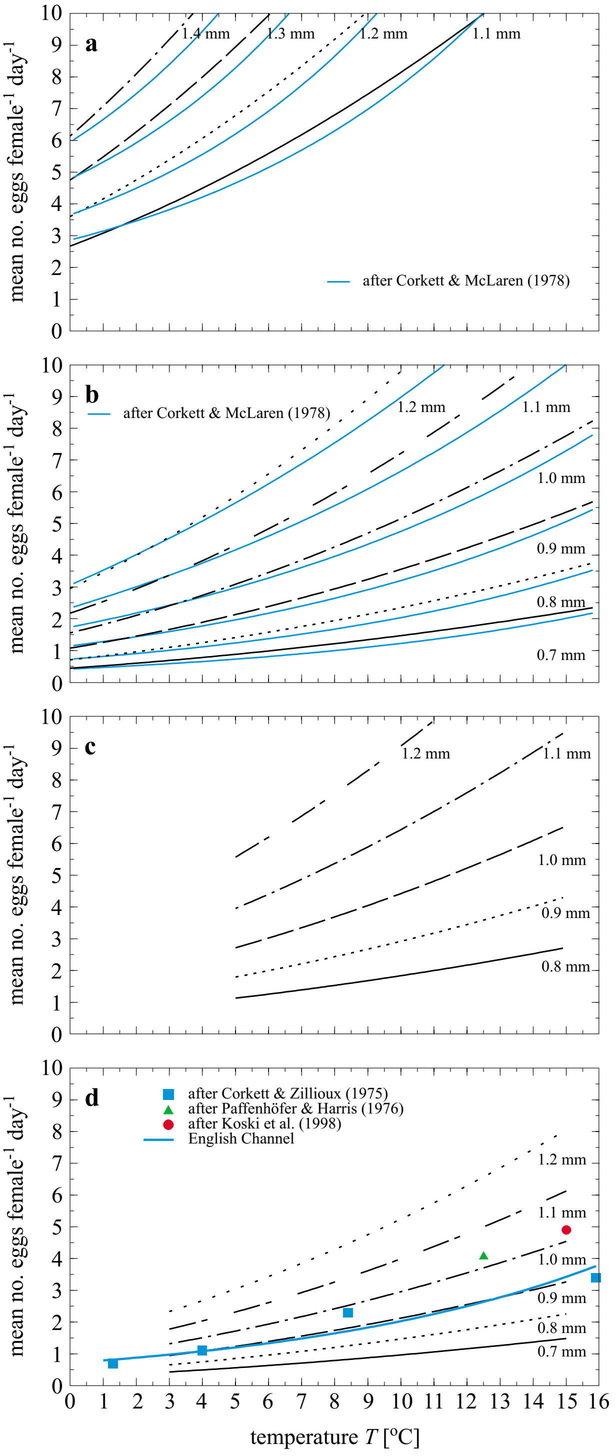

Fig. 2. Average number of eggs produced per day by one female of various lengths as a function of temperature for satiated populations. Curves are for females from southwest Baffin Island (a), Nova Scotia (b), Scotland (c) and the southern North Sea and the English Channel (d). The black lines were fitted to the equations in Table 3; the blue lines were fitted to the data given by Corkett & McLaren (1978) – see Fig. 21 in their paper. Experimental data after Corkett & Zillioux (1975), Paffenhöfer & Harris (1976) and Koski et al. (1998) are shown for high food levels

based the reproductive rate on the number of eggs per sac for females from Loch Striven (Scotland). Therefore, the value of *Egg* in western Scotland obtained here was similar to that obtained by Corkett & McLaren (1978) in Nova Scotia.

For example, the values of *Egg* computed with the above equations (see Table 3) for *Pseudocalanus* spp. of various female length at different temperatures from southwest Baffin Island Sound, Nova Scotia, Scotland, the southern North Sea and English Channel are shown in Fig. 2. The slope of the lines steepened significantly with increasing female length. These figures show the effects of interactions between temperature and female length on the average number of eggs produced per female of this species. Naturally, a large animal that produces many more eggs per day than a small one at a given temperature will produce a larger increment of eggs per day with a given rise in temperature.

4. Rate of production of egg matter

The potential rate of reproduction obtained in the above section can be converted to the equivalent amount of egg matter produced per day as a percentage of female weight for all localities (see McLaren & Leonard 1995):

$$Prod\ Egg = (W_{egg}/W_{female})\, Egg. \qquad (2)$$

In this study the weight of an egg W_{egg} is taken to be that from southwest Baffin Island, i.e. 0.30–0.31 μg dry weight per egg (McLaren et al. 1969). The dry weight (d.w.) of adult females W_{female} is calculated from the weight-length relationship of *Pseudocalanus* (for CIII, CIV, CV and adult) from the Canadian Arctic:

$$W_{female} = 11.9\, L^{3.64}, \qquad (3)$$

where W_{female} is in μg dry weight and L is the cephalothorax length in mm. Corkett & McLaren (1978) suggest that the above formula is much the most reliable available. Thus the rate of production of egg matter [μg μg^{-1} female^{-1} day^{-1}] can be expressed as a function of temperature T [°C] and cephalothorax length L [mm]:

$$Prod\ Egg_{\mathrm{d.w.}} = a\, L^{\beta}(T+\alpha)^{2.05}. \qquad (4)$$

The calculations were made for some geographically separate populations of *Pseudocalanus*, i.e. from southwest Baffin Island, off Halifax, Nova

Table 4. Parameters a, b, β and α describing the rate of egg matter production in *Pseudocalanus* spp. obtained in this paper ($Prod\ Egg_{\mathrm{d.w.}} = a\,L^{\beta}(T+\alpha)^{2.05}$; $Prod\ Egg_C = b\,L^{\beta}(T+\alpha)^{2.05}$)

Locality	Parameters			
	$a \times 10^{-4}$	$b \times 10^{-4}$	β	α
southwest Baffin Island	2.292	2.525	−0.19	13.84
Nova Scotia	2.178	2.479	−0.12	12.59
Long Island Sound	1.915	2.18	0.08	13.87
Scotland	1.704	1.939	0.3	13.63
southern North Sea	1.389	1.581	−0.51	11.45

Scotia, Long Island Sound, Scotland and the southern North Sea. The parameters a, β and α of eq. (4) are given in Table 4.

In this paper, the amount of egg matter produced per day as the percentage of body carbon of female weight for all localities was determined from

$$Prod\ Egg_C = b\,L^{\beta}(T+\alpha)^{2.05}, \tag{5}$$

where parameters b, β, and α are given in Table 4. The carbon content of the copepods was assumed to be 41% of the dry weight (Williams & Robins 1982) and that of the eggs 0.14 μgC egg^{-1} (Frost 1989). However, it should be remembered that *Prod Egg* for females from the southern North Sea (see Table 4) was obtained for 'viable eggs' (see section 2.1).

Relationships between female size and environmental temperatures in various localities were obtained on the basis of data from McLaren et al. (1969) and Corkett & McLaren (1978):

$$\text{– Canadian Arctic :}\quad L = 1.0592\,e^{-0.05\,T},\quad r = -0.985; \tag{6}$$

$$\text{– Long Island Sound :}\quad L = 1.2672\,e^{-0.033\,T},\quad r = -0.998; \tag{7}$$

$$\text{– Scotland :}\quad L = 1.8305\,e^{-0.066\,T},\quad r = -0.999. \tag{8}$$

However, using Thompson's (1976) data, Corkett & McLaren (1978) gave the cephalothorax length of an adult female from the southern North Sea as a function of temperature when greater than 8°C as

$$L = 0.939 - 0.0322(T - 11.57). \tag{9}$$

By substituting L in eq. (5) for eq. (6), (7), (8) and (9) for females from Baffin Island, Long Island Sound, Scotland and the southern North Sea respectively, we obtain the amount of egg matter produced per day as a percentage of female weight, which is determined by the given temperature in the range 8–15.5°C; this is depicted in Fig. 3. The values of $Prod\ Egg_C$ as % body carbon of female weight per day at 8, 10, 12.5, 15°C for females from Long Island Sound, Scotland and the North Sea are given in Table 5.

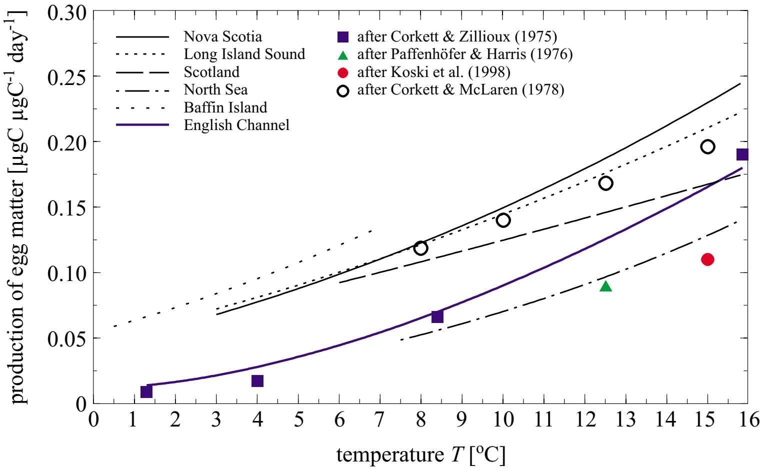

Fig. 3. The average daily production of egg matter per female as a function of temperature for satiated populations. Curves are for females from Baffin Island, Nova Scotia, Long Island Sound, Scotland, the English Channel and the southern North Sea with eq. (5). Lines were fitted to the equations in Table 5 for $Prod\ Egg_C$. Experimental data after Corkett & Zillioux (1975), Paffenhöfer & Harris (1976), Corkett & McLaren (1978) and Koski et al. (1998) are shown for high food levels

Table 5. The amount of egg matter produced per day as % body carbon of female weight from Long Island Sound, Scotland and the southern North Sea

	Production rate of egg matter [% body carbon female^{-1} day^{-1}]		
T [°C]	Long Island Sound	Scotland	southern North Sea
8	12.14	10.82	6.75
10	14.45	12.73	8.53
12.5	17.61	14.59	10.16
15	21.05	16.75	13.34

Let us look at the problem from another point of view. Corkett & McLaren (1978) gave a general relationship for the dry weight of eggs in a sac W_{sac} [μg d.w.]:

$$W_{sac} = 6.35L^{4.19}, \tag{10}$$

where L is the cephalothorax length in mm. The time between sacs is assumed to be 1.25 multiplied by the duration of sacs (Corkett & McLaren 1978). Thus, the production rate of egg matter $Prod\ Egg$ and rate of reproduction Egg by one female can be described by

$$Prod\ Egg_{\text{d.w.}} = W_{sac}/(1.25\, D_E\, W_{female}) = 0.4269\, L^{0.55}/D_E \tag{11}$$

and

$$Egg = W_{sac}/(1.25\, D_E\, W_{egg}) = 16.93\, L^{4.19}/D_E. \tag{12}$$

The results obtained with relationships (11) and (12) are in good agreement with the values calculated with equations in Table 3 and 4 for all localities except the southern North Sea. This situation results from the fact that (i) equations (11) and (12) were expressed using eq. (10), which describes the dry weight of eggs per sac for females from Baffin Island, Nova Scotia, Long Island Sound and Scotland, and (ii) the equations given in Table 3 and 4 for females from the North Sea are for 'viable eggs'

Substituting eq. (12) in eq. (2), the amount of egg matter produced per day as % body carbon of female weight from the southern North Sea can be obtained from

$$\begin{aligned} Prod\ Egg_C = 0.26329 \times 10^{-3}\ \times \\ \times\ (0.939 - 0.0322(T - 11.57))^{0.55}(T + 11.45)^{2.05}. \end{aligned} \tag{13}$$

These values are 11.89, 14.04, 16.79, 19.56% body carbon per day at 8, 10, 12.5 and 15°C respectively and are similar to the mean values of $Prod\ Egg_C$ in Long Island Sound and Scotland (see Table 5 and Fig. 3). However, these values are higher than the ones given in Table 5 for 'viable eggs' in the North Sea. In our opinion, the eqs. (11), (12) and (13) for the North Sea do not quite represent reality (these values are higher than the literature data – see Fig. 3 and section 5).

5. Discussion

On the basis of analyses of relationships between the number of eggs in a sac and length of females, as well as embryonic duration and temperature from other studies, the *potential* rate of reproduction per individual female *Pseudocalanus* spp. (not reduced by food limitation) was calculated as the mean number of eggs per sac divided by 1.25 and multiplied by the embryonic duration at the given temperature.

Quantitative expressions describing the effects of temperature and cephalothorax length on the potential rates of reproduction *Egg* of *Pseudocalanus* spp. presented in this work for some geographically separate populations of *Pseudocalanus* spp. are indispensable to the formulation of mathematical models of pelagic communities.

The calculations made here show that the mean daily number of eggs produced per female from Canadian Arctic waters of lengths between 1.1 and 1.4 mm ranged from 4 to 10 at 5°C. However, for females from waters off Nova Scotia of short lengths between 0.7 and 0.8 mm, the egg production was about 1 egg female^{-1} day^{-1} at 5°C and about 2.5 eggs female^{-1} day^{-1} at 12.5°C; but for longer females between 1.1 and 1.2 mm in length it was about 5 eggs female^{-1} day^{-1} at 5°C and about 10 eggs female^{-1} day^{-1} at 12.5°C. Values of *Egg* computed here for *Pseudocalanus* from southwest Baffin Island and Nova Scotia are similar to the results given by Corkett & McLaren (1978) (see Figs 2a and 2b).

The studies described in the paper demonstrate that the rate of reproduction for females from Long Island Sound and Nova Scotia were similar for various female lengths and temperatures. However, the potential production of 'viable eggs' in the southern North Sea is about 30% lower than the mean number of eggs for large females from Scottish waters; but, for small ones these values are similar. On the basis of the findings in this study, this potential rate of reproduction for females of *Pseudocalanus* from the southern North Sea of lengths between 0.7 and 1.2 mm ranged from 0.6 to 3 eggs female^{-1} day^{-1} at 5°C and from 1.3 to 6.7 eggs female^{-1} day^{-1} at 12.5°C, which is generally comparable to the literature data for high food levels (Corkett & Zillioux 1975, Paffenhöfer & Harris 1976, Koski et al. 1998) (see Fig. 2d).

Corkett & Zillioux (1975) examined the effects of temperature on egg production by *Pseudocalanus* from off Plymouth. The mean numbers of eggs produced per female per day was 0.7, 1.1, 2.3 and 3.4 eggs female^{-1} day^{-1} at 1.3, 4, 8.4 and 16°C respectively. These values lie within the range of *Egg* for 'viable eggs' for females from the southern North Sea as presented here.

Paffenhöfer & Harris (1976) found that the total number of 'viable eggs' produced by a *Pseudocalanus* female from the North Sea ranged from 2 to 136. The period of egg production varied from 3 to 29 days, and the rate of production during this period for females of lengths between 1 and 1.2 mm ranged from 3.1 to 4.1 nauplii female^{-1} day^{-1} at 12.5°C and for food concentrations ranged from 25 to 200 mgC m^{-3}. It shows that the egg production is not significantly dependent on food concentration and is lower (by about 0.8 eggs female^{-1} day^{-1} at high food level) than computed here at 12.5°C for $L = 1.1$ mm.

Egg production in *P. elongatus* was also measured in the laboratory by Koski et al. (1998) in relation to the taxonomy and physiology of algal food at 15°C. The reproductive rate was highest with *Rhodomonas* sp. and *Thalassiosira weissflogii* used as food sources (at high food levels), 5 eggs female^{-1} day^{-1} for females of lengths between 0.9 and 1.1 mm. A somewhat lower egg production (2.4 eggs female^{-1} day^{-1}) was observed with *Tetraselmis suecica* and *Gymnodinium simplex*. Egg production was lower still (<1 egg female^{-1} day^{-1}) with *Dunaliella* sp. and *Amphidinium* sp. No eggs were produced in any of the *Chrysochromulina polylepis* experiments or in experiments with filtered sea water with or without lipid supplement (Koski et al. 1998).

The reproductive rate in the North Sea for females of lengths between 0.89 and 1.1 mm obtained in this work ranges from 3.4 to 6.1 eggs female^{-1} day^{-1} at 15°C and is comparable to the data given by Koski et al. (1998) (with *Th. weissflogii* and *Rhodomonas* sp. as food sources). The egg production given by Koski et al. (1998) is about 1.6 eggs female^{-1} day^{-1} (with *Th. weissflogii*) higher and 1.1 egg female^{-1} day^{-1} lower (with *Rhodomonas* sp.) than computed here.

In the present work, the rate of production of egg matter as a function of both temperature and cephalothorax length was obtained for all localities. The amount of egg matter ($Prod\ Egg_C$) produced per day was also expressed as % body carbon of female weight, which is determined by the given temperature for females from Baffin Island, Long Island Sound, Nova Scotia, Scotland, and the North Sea. One should remember that Egg and $Prod\ Egg$ in the southern North Sea were calculated for 'viable eggs'. The results indicate that the daily production rate of egg matter for females from Nova Scotia, Long Island Sound and Scotland except the North Sea are similar to the data given by Corkett & McLaren (1978) in the studied range of temperature (see Fig. 3 and Table 5). 'Viable egg' production in the southern North Sea at 8°C is about 4% body carbon female^{-1} day^{-1} lower than the mean egg production in Scotland and at 15°C is about 2.5% body carbon female^{-1} day^{-1}. The values of $Prod\ Egg_C$ in the southern North Sea given in Table 5 are comparable to the literature data (see Corkett & Zillioux 1975, Paffenhöffer & Harris 1976, Koski et al. 1998). In this paper the carbon content of eggs and females used in the calculations is the same as in Koski et al. (1998). After Koski et al. (1998), $Prod\ Egg_C$ at 15°C was high with *Rhodomonas* sp. and *T. weissflogii* (c. 11% body carbon day^{-1} for $W_{females} = 18$ and 8.0 $\mu g_{\text{d.w.}}$ corresponding to $L = 1.12$ and

0.89 mm respectively), but only intermediate (5% body carbon day^{-1}) with the other good-food species, *Gymnodinium simplex* and *T. suecica.* With the poor-food species, egg production was always low. On the basis of data given by Paffenhöffer & Harris (1976), $Prod\ Egg_C$ ranged from 6% to 9% body carbon of female weight at 12.5°C; however, after Corkett & Zillioux's data (1975), $Prod\ Egg_C$ is about 6.6% at 8.4°C and 19.2% body carbon of female weight at 16°C assuming the carbon content of the eggs and females to be as in this paper.

The quantitative expressions presented in this work describing the effects of temperature and cephalothorax length on the potential rate of reproduction of an individual female and the rate of production of egg matter can be used with good precision in mathematical models. It should be borne in mind that relationships for females from the North Sea were obtained for 'viable eggs' and these results should be treated with reserve (see section 2.1). In our opinion, on the basis of literature data, the real values of Egg and $Prod\ Egg$ for females from the southern North Sea are higher than the ones obtained here for 'viable eggs' and lower than those from Scotland. A more appropriate expression describing the effect of temperature on egg production for females from the southern North Sea is the equation Egg_{ECh} for females from the English Channel computed in this paper (see section 3).

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