Factors controlling the temporal dynamics of egg production in the copepod *Temora longicornis*

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ABSTRACT: The factors controlling the temporal dynamics of egg production rate (EPR) in *Temora longicornis* were investigated during a 3 yr study. *T. longicornis* produced eggs all year round, with an annual maximum (EPR_{max}) between 27 and 48 eggs female^{-1} d^{-1} during spring/summer and minimum of 1.4 eggs female^{-1} d^{-1} in autumn/winter. The highest EPR values were measured when copepods were heaviest and *in situ* chlorophyll *a* (chl) increased above ~1 to 3.5 µg l^{-1}, irrespective of ambient temperature. EPR was positively related to copepod body weight (BW) and chl, whereas it was negatively related to suspended particulate matter (SPM) and temperature. Stepwise multivariate analysis showed that copepod BW, chl and SPM explained most of the variability associated with fecundity, outweighing the effect of temperature. Moreover, the lower EPR_{max} measured in spring 1996, as compared to 1997 and 1998, suggests that food nutritional quality was probably another important factor affecting copepod fecundity. Since BW was inversely related to temperature, by controlling copepod BW, temperature indirectly determined the maximum potential reproductive output of *T. longicornis*. Acting on at least *in situ* physical parameters like temperature and SPM, climate change could represent an important modulator of secondary production in this and other copepod species.

KEY WORDS: Fecundity · *Temora longicornis* · Body weight · Suspended sediment · Chlorophyll *a* · Temperature · Microplankton · Food limitation

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INTRODUCTION

Egg production rate (EPR) is one of the most studied vital rates in copepods, and yet there is still incomplete understanding about the importance of the different physiological and environmental variables controlling the reproductive output of these organisms *in situ*. Previous studies have indicated that food ration (Kiørboe & Nielsen 1994), food quality (Kleppel & Hazzard 2000, Jónasdóttir et al. 2002), cell size (Dam & Peterson 1991), temperature (White & Roman 1992) and suspended sediments (Burdloff et al. 2000) are all important variables affecting copepod fecundity.

Body weight (BW) represents an intrinsic variable known to affect the rates of physiological processes (e.g. feeding, metabolism, growth) of invertebrates

including reproduction (Schmidt-Nielsen 1991). So far, however, research has mostly focused on the effect of temperature (Hirakawa 1991, White & Roman 1992) and food quantity and quality (Jónasdóttir 1994, Kiørboe & Nielsen 1994), whereas the dependence of fecundity on copepod size has received limited attention (Kiørboe & Sabatini 1995, Hopcroft & Roff 1998, Bunker & Hirst 2004). The relationship between copepod BW and EPR has been investigated for multi-species data (Kiørboe & Sabatini 1995, Hopcroft & Roff 1998, Bunker & Hirst 2004), but investigations at the level of a single species and in relation to a range of environmental variables are lacking. Multi-species studies have reported scaling of fecundity with BW for some data sets (Bunker & Hirst 2004), but not for others (Kiørboe & Sabatini 1995). On the other hand, single-

species studies have found contrasting results for the factors affecting fecundity in general even for the same species (Halsband & Hirche 2001, Maps et al. 2005). Using multi-species or limited data sets may obscure subtle and important relationships between variables (Bunker & Hirst 2004), particularly when simple statistical analysis is employed to resolve the complexity of data characterised by high variability, like fecundity. In this respect, multivariate statistical analysis can be a very powerful tool to establish relationships between variables (Dam & Peterson 1991, Hopcroft & Roff 1998).

Using a 3 yr time series the present study investigated the factors controlling the *in situ* fecundity of *Temora longicornis*, one of the most abundant copepod species in many coastal areas of the northern hemisphere (Fransz et al. 1992, Peterson & Kimmerer 1994, Williams et al. 1994). The EPR of *T. longicornis* in the field has been studied in the past, but there is still disagreement regarding which factors control the fecundity of this species (Halsband & Hirche 2001, Maps et al. 2005). In particular, we addressed the following questions: (1) is *in situ* EPR related to copepod BW and (2) how important is BW for fecundity compared to other environmental factors like food availability, temperature and suspended sediments?

MATERIALS AND METHODS

Sampling. Plankton was collected weekly, between March 1996 and November 1998, using a 200 µm mesh WP-2 plankton net fitted with a non-filtering cod-end from the St. George Pier, Menai Strait (53° 13′ N, 4° 09′ W) in the eastern Irish Sea. The sample was immediately transferred to an opalescent, polypropylene aspirator containing 10 l of natural seawater; it was pre-screened through 250 µm to exclude predators, and copepods were sorted within 1 h of collection.

Temperature (*T*, °C) and salinity (*S*, ppt) were measured with a CTD (Braystoke, Series 600) throughout the water column during each sampling. Chlorophyll *a* (chl, µg l^{-1}) and microplankton samples were collected with a 2 l Niskin bottle from ~2 m depth. Chl concentration was determined from water samples of 100 to 750 ml, filtered onto GF/F filters, extracted in neutralised 90% acetone solution for 24 h at 4°C in the dark and measured using a Turner 10 fluorometer in accordance with the recommendations of Tett (1987). Microplankton was immediately fixed with Lugol's iodine to 2% final concentration (Kiørboe & Nielsen 1994), stored into 100 ml dark glass bottles in the dark at 4°C and analysed by the Utermöhl (1958) technique within 1 mo. Cellular dimensions of a minimum of 30 cells for each type were determined with an ocular micrometer (× 400) and used to calculate cell volume

by assigning taxa to simple geometrical shapes. Cell volumes were converted to cell carbon with the equations of Strathmann (1967) for phytoplankton, Putt & Stoecker (1989) for oligotrichous ciliates and Bartram (1980) for other heterotrophic protists. Data for total suspended particulate matter (SPM) were estimated from settled microplankton samples by looking at the percentage of the slide area covered by the detritus and assigning scores from 1 to 6, corresponding to ~0 to 50 mg l^{-1} (Buchan et al. 1967 and SPM data for 1996, from Kratzer et al. 2000).

Egg production rates. Between 25 and 30 intact active female *Temora longicornis* were randomly selected from the catch, using a large bore plastic pipette. Individuals were placed into 250 ml crystallising dishes filled with natural, 53 µm pre-screened seawater. Measurements from single females were used to estimate individual variability in EPR and the proportion of reproductively active females (RAF) in the population. The dishes were kept for 24 h in a temperature-controlled water bath at the ambient surface temperature ±0.2°C (i.e. 1 m depth), under artificial lighting, with an ambient light/dark regime. After incubation, the females were gently removed from the crystallising dishes with the pipette, the content of each dish was filtered through a 53 µm sieve, and the eggs and nauplii were retained, stained with Lugol's iodine and counted in a Bogorov tray under a dissecting microscope. Copepods found dead or moribund at the end of the incubation time were not included in the analysis. EPR was converted to carbon production rates (EPR$_c$) on the basis of monthly measurements of the diameter of 30 eggs with a high power microscope and conversion of egg volume to carbon, assuming 0.14 × 10^{-6} µg C µm^{-3} (Kiørboe et al. 1985). Egg hatching success was also measured, and results have already been reported elsewhere (Castellani & Lucas 2003). The proportion of RAF for each sampling date was calculated as the ratio between the number of females producing eggs and the total number of females incubated.

The prosome length (PL, µm) of the females incubated was sized with an eye-piece graticule under a dissecting microscope, and length was converted to dry weight (DW, µg) with the relationship ln DW = 2.75 × ln PL – 15.9 (r^2 = 0.85, p < 0.001, df = 29) (Castellani 2002). Copepod DW was then converted to carbon by assuming a weight-specific carbon content of 40% (Omori & Ikeda 1984).

Data analysis. Both simple and forward stepwise multiple regression were used to examine the relationship between the dependent variable EPR$_c$ (µg C female^{-1} d^{-1}) and the independent variables BW (µg C), chl concentration (µg l^{-1}), *T* and total SPM (ordinal scale of 1 = minimum to 6 = maximum). Chl was chosen as the only proxy for food availability, as

the measurements made on specific microplankton groups were limited.

The analysis was carried out using both individual measurements and means of EPR according to sampling date, including the zero values to compare these 2 different analytical approaches. Using individual measurements allows one to take into account more accurately the effect of body weight, particularly when its variation within a sampling event is large. However, this type of data may contain a large number of zero values (i.e. copepods which did not produce eggs) arising as a result of a methodological artefact, i.e. the females needing a longer incubation time than the standard 24 h to produce eggs. Under these circumstances the statistical analysis of individual values may overestimate the natural variability of the data and lower the slope estimated by the regression analysis between the variables. Mean estimates, on the other hand, although they may represent a more appropriate descriptor of the fecundity of the population, will artificially reduce the variability of the data and increase the explanatory power of the regression analysis. Thus, both analytical approaches were used for comparative purposes.

To examine the effect of the different variables in more detail, the data were analysed for smaller intervals of BW (µg C, >3 to ≤8; >8 to ≤12; >12 to ≤16; >16 to ≤20; >20 to 28), SPM concentrations (1 to 6) and temperature ranges (T, ≤10°C, >10°C). If an independent variable did not contribute significantly to the prediction, it was excluded, and the regression was completed using the remaining variables.

RESULTS

Hydrography and environmental conditions

The sampling station is characterised by shallow water depths mostly between 1 and 5 m (maximum 20 m), strong tidal currents and high tidal ranges (3.4 to 6.6 m), and therefore it is thoroughly mixed throughout the year. The water temperature recorded between 1996 and 1998 in the Menai Strait varied from a minimum of 2°C in winter to a maximum of 18°C in summer (Fig. 1a). The greatest inter-annual variation occurred between January and April, with the temperature in 1996 being ~3.5 and ~4.5°C lower than in 1997 and 1998, respectively. Salinity changed little, reaching maximum values of 34.1 ppt in summer and a minimum of 31.7 ppt in autumn, during the highest local annual rainfall (i.e. 110 to 126 mm mo^{-1}, Royal Meteorological Society, Weather Log 1996 to 1998).

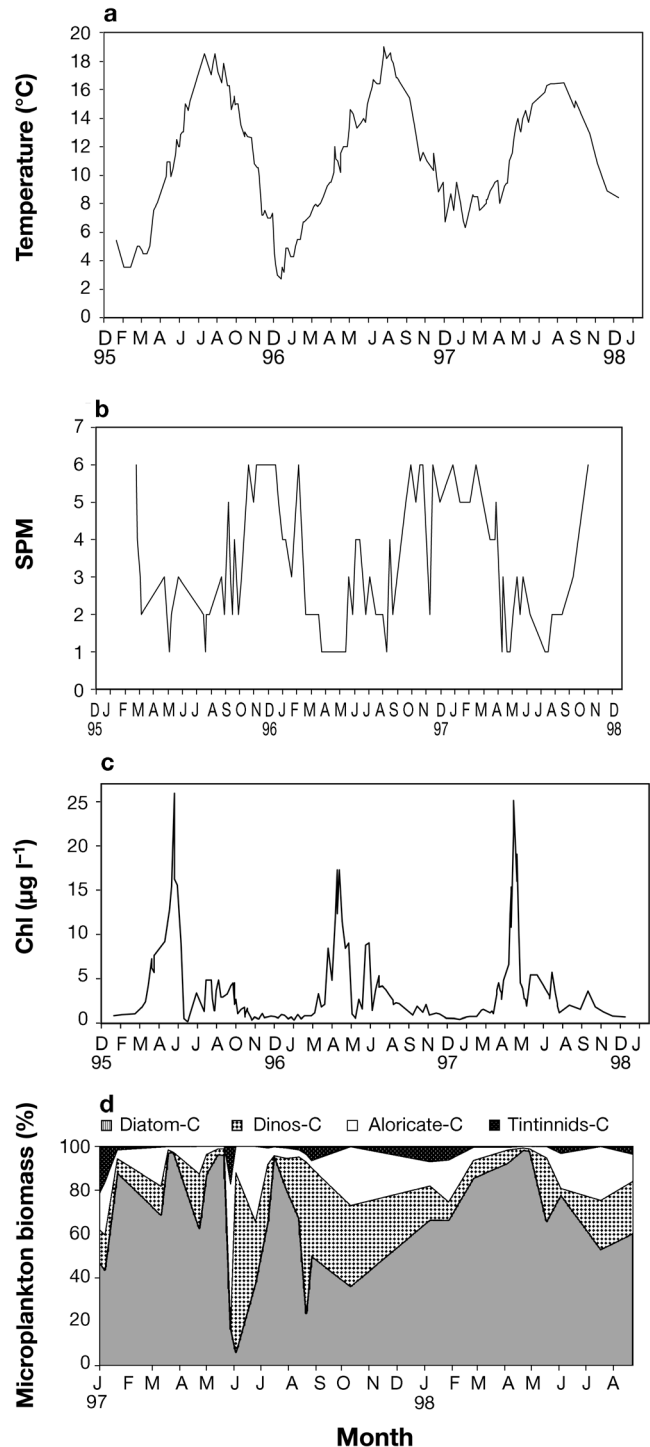SPM concentration varied with wind strength, tidal range and season, with maximum values of ~5 to 50 mg

Fig. 1. Seasonal changes in (a) temperature, (b) suspended particulate matter (SPM, ordinal scale), (c) chlorophyll *a* (chl) and (d) microplankton biomass composition in the Menai Strait

l^{-1} in autumn/winter, minima of ~0.5 to 3 mg l^{-1} in late spring/early summer and intermediate concentrations of ~3 to 5 mg l^{-1} in late summer (Fig. 1b, Kratzer et al. 2000).

Chlorophyll *a* and microplankton

The seasonal changes in the *in situ* chl concentration and the biomass composition of the main microplankton groups are shown in Fig. 1c,d. The early spring increase of chl from the low winter concentration of 0.5–0.9 to ~3–8 µg l⁻¹ was almost exclusively diatomaceous and included species like *Ditylum brightwelli*, *Skeletonema costatum*, *Chaetoceros* sp., *Asterionella* sp. and *Thalassiosira* sp.. Between April and June the microplankton community was replaced by the mixed diatom–flagellate bloom of *Phaeocystis* sp.–*Rhizosolenia delicatula*, and chl increased to ~16–26 µg l⁻¹. The spring bloom was followed by an increase in euglenoids and cryptomonas-like flagellates. A series of monospecific diatom blooms of *Leptocylindrus danicus*, *Rhizosolenia styliformis* and *Guinardia flaccida* developed in summer and autumn, with chl ranging between ~3 and 8 µg l⁻¹. Ciliate biomass, mostly belonging to the genus *Strombidium*, also peaked between spring and early summer and was correlated to chl concentration (r = 0.67, p < 0.05, df = 33). Dinoflagellates, on the other hand, peaked in the summer, after the chl maxima.

Seasonal and inter-annual variation in fecundity

Temora longicornis produced eggs all year round, with mean (±SE) EPR ranging from ~1.3 ± 0.5 eggs female⁻¹ d⁻¹ in autumn/winter to ~48 ± 7 eggs female⁻¹ d⁻¹ in spring/summer (Fig. 2). EPR also differed from year to year. In 1996 a fecundity maximum of ~23 ± 3 eggs female⁻¹ d⁻¹ occurred in June, and was approximately half of that measured in May of 1997 (44 ± 6 eggs female⁻¹ d⁻¹) and 1998 (48 ± 7 eggs female⁻¹ d⁻¹). Mean (±SE) copepod BW also varied seasonally, with the lightest (4.5 ± 0.9 µg C) copepods in summer/autumn and the heaviest (18.7 ± 2.5 µg C) in winter/spring (Fig. 2). Thus, BW was inversely correlated with *in situ* temperature (Fig. 2, Table 1). Over the year individual females produced from 0 to 116 eggs female⁻¹ d⁻¹, and the proportion of reproductively active females also varied seasonally, from up to 100% in spring/summer to just 21% in autumn/ winter (Fig. 3).

The general decrease in RAF to <50% in winter and at the end of summer indicates that, at this time, the environmental and/or the physiological conditions of the copepods were not optimal to induce maximal reproduction in the population.
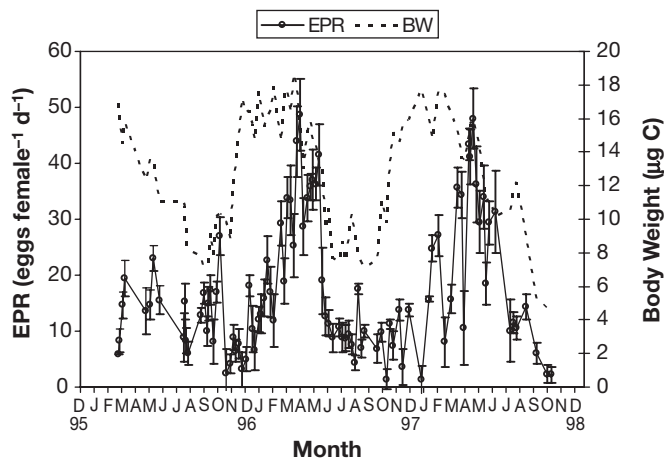

Fig. 2. *Temora longicornis.* Seasonal change in mean (±SE) egg production rate (EPR) and copepod body weight (BW)

EPR versus BW, chl, SPM and *T*

Tables 1 & 2 summarise the relationships found for fecundity versus BW, chl, SPM and *T* and BW versus *T*. The scatterplot in Fig. 4 shows that EPR increases with BW according to a linear relationship. The apparent decline in EPR for copepod body weight > 22 µg C may be an artefact due to the limited number of observations available for the largest copepods.

Fecundity also increased with chl, and both a linear and an asymptotic relationship could describe the relationship equally well. A series of Ivlev's curves was fitted to the mean EPR for different BW groups. The curves show that both maximum fecundity (EPR$_{max}$) and the concentration of chl required to reach EPR$_{max}$ increase for all the BW groups, suggesting that food availability represents a limiting factor for fecundity across the size range (Fig. 5, Table 3).

The relationship between EPR and *T* is more complex, and appears to be described by a dome shape, with EPR$_{max}$ occurring between 9 and 14°C (Fig. 6).

Table 1. *Temora longicornis*. Regression analysis of EPR$_c$ (egg production rate, µg C female⁻¹ d⁻¹) versus suspended particulate matter (SPM, ordinal scale), body weight (BW, µg C), chlorophyll *a* (chl, µg l⁻¹) and temperature (*T*, °C), and BW versus *T*. Significance level: ***1%; n: number of observations; standard error given in parentheses

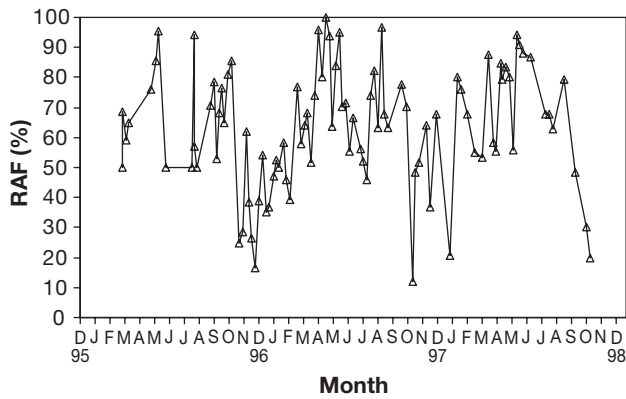| Variables	n	Intercept		Slope		r²	*F*
EPR$_c$ vs. SPM	2228	1.119***	(0.034)	−0.142***	(0.009)	9.4	230.30
EPR$_c$ vs. BW	2228	0.040	(0.046)	0.049***	(0.005)	8.3	201.72
EPR$_c$ vs. chl	2228	0.451***	(0.021)	0.057***	(0.004)	8.5	207.03
EPR$_c$ vs. *T*	2228	0.879***	(0.048)	−0.020***	(0.004)	1.1	25.37
BW vs. *T*	2228	20.2	(0.219)	0.673	(0.018)	38.7	1410.6

Fig. 3. *Temora longicornis.* Seasonal variation in the proportion of reproductively active females (RAF)

Fecundity was also inversely related to SPM over the year (Table 1) and to mean tidal range (r = −0.99, p < 0.001, df = 4, Fig. 7). This result suggests that an increase in suspended sediment may affect EPR by interfering with the feeding behaviour (i.e. food handling and/or ingestion efficiency) and/or decreasing the quality of the food ingested by the copepod.

Stepwise multiple regression

The results of the stepwise multiple regression analysis between copepod fecundity, BW, chl, T and SPM are shown in Table 4. The best fit was found for non-transformed data.

Tables 2 & 4 show that there were no significant differences between the slopes of the single and multiple regressions estimated from either means or individual measurements of fecundity. It is also noteworthy that, using individual estimates, the effect of temperature could be clearly identified, whereas this variable was not significant using the mean fecundity values (Table 4). The multiple regression analysis of individual measurements shows that fecundity was positively related to BW and chl, whereas it was negatively related to SPM concentration and T. The most important variables explaining the variability in fecundity
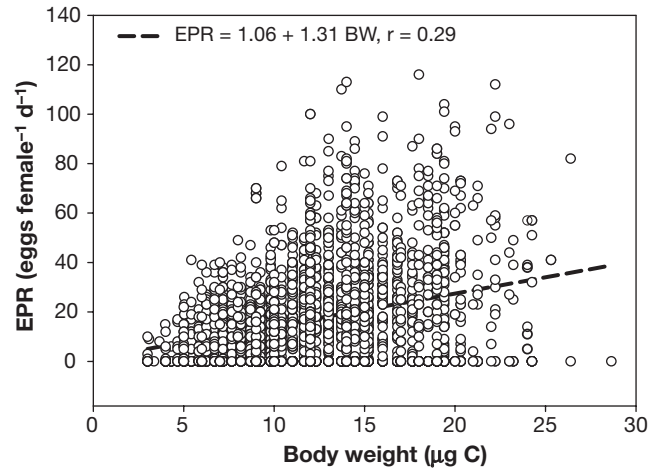

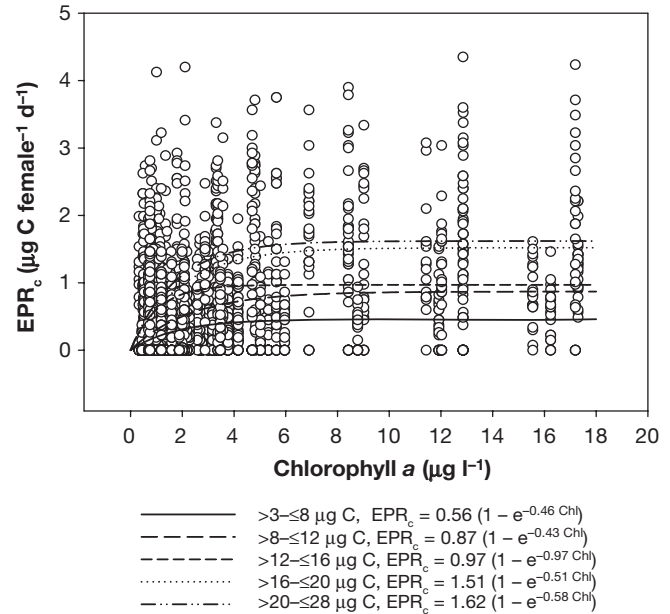Fig. 4. *Temora longicornis.* Scatterplot of egg production rate (EPR) and copepod body weight (BW)

Fig. 5. *Temora longicornis.* Scatterplot of egg production rate (EPR) expressed as carbon EPR_c versus chlorophyll *a*. Ivlev's curves, $EPR = EPR_{max} \times (1 - e^{k \times chl})$, fitted to mean EPRs for different copepod size groups (BW, μg C); k is the rate at which EPR approaches its asymptote (EPR_{max})

Table 2. *Temora longicornis.* Comparison of regression slopes for EPR (eggs female^{-1} d^{-1}) versus BW, in terms of (1) individual EPR, (2) mean EPR according to sampling date (irrespective of BW) and (3) mean EPR of different BW groups (irrespective of sampling date). Further details as in Table 1

Regression type (EPR vs. BW)	n	Intercept	Slope	r^2	Comparison of slopes	t-statistic
(1) Individual EPR values	2228	1.06 (1.22)	1.32*** (0.093)	8.3	–	–
(2) Mean EPRs (sampling date)	95	−0.37 (3.97)	1.42*** (0.31)	18.5	1–2	0.17
(3) Mean EPRs (BW group)	24	−0.71 (2.36)	1.41*** (0.15)	80.8	1–3	0.16

Table 3. *Temora longicornis.* Relationship between EPR_c (µg C female^{-1} d^{-1}) and chl (µg l^{-1}). Ivlev's curves $EPR_c = EPR_{max} \times (1 - e^{-k \times chl})$, fitted to the mean EPR for different copepod size groups (BW, µg C). Max: maximum; k: the rate at which EPR approaches its asymtote (EPR_{max}); further details as in Table 1

BW	n	k	EPR_{max}	r^2
>3 to ≤8	39	0.46 (0.331)	0.56 (0.191)	12.4
>8 to ≤12	90	0.43 (0.127)	0.86 (0.105)	10.5
>12 to ≤16	83	0.97 (0.294)	0.96 (0.975)	13.3
>16 to ≤20	55	0.51 (0.134)	1.51 (0.155)	32.9
>20 to ≤28	38	0.58 (0.212)	1.62 (0.196)	30.7

Fig. 6. *Temora longicornis.* Scatterplot of egg production rate (EPR) versus field temperature

Fig. 7. *Temora longicornis.* Mean (±SE) egg production rate (EPR) versus tidal range egg production rate (EPR), measured between November 1996 and January 1997

significant for different SPM concentrations, whereas chl and *T* have no or less consistent explanatory power. Moreover, there is a tendency for the strength of the relationship between EPR and the other variables to decrease with increasing SPM (Table 5). Similarly, the effect of SPM was consistently negative and significant across the different BW groups, whereas the relationship between fecundity, chl and *T* was not (Table 6). Considering the 2 temperature intervals above and below 10°C, the relationship between EPR, BW, chl and SPM was consistent with the results reported above, and the explanatory power of these variables appears stronger within each data subset (Table 7).

DISCUSSION

The present study has investigated the factors controlling the fecundity of *Temora longicornis* over a 3 yr survey. The data set was compiled by measuring individually the EPRs of 2228 females of body weights between 3 and 29 µg C, over a wide range of *in situ*

were SPM, BW and chl, whereas *T*, although significant, made the least contribution (Tables 1 & 3).

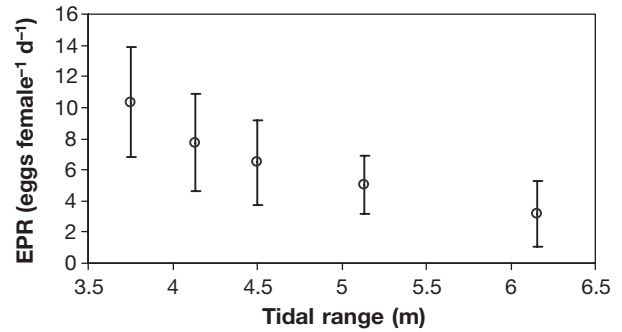The results of the multiple regressions carried out on the SPM data subsets show that BW was consistently

Table 4. *Temora longicornis.* Stepwise multiple regression analysis ($EPR_c = a + b_1$ SPM + b_2 BW + b_3 chl + b_4 *T*) between either individual EPR_c (1 to 4, in µg C female^{-1} d^{-1}) or mean EPR_c for each sampling date (5) and SPM (ordinal scale), BW (µg C), chl (µg l^{-1}) and *T* (°C). Significance levels: *10%; ***1%. Further details as in Table 1

Estimated model	n	Intercept (a)	SPM (b_1)	BW (b_2)	Chl (b_3)	*T* (b_4)	r^2	F
(1) $EPR_c = a + b_1$ SPM	2228	1.119*** (0.035)	−0.142*** (0.009)				9.4	230.30
(2) $EPR_c = a + b_1$ SPM + b_2 BW	2228	0.482*** (0.049)	−0.158*** (0.009)	0.055*** (0.003)			19.7	273.36
(3) $EPR_c = a + b_1$ SPM + b_2 BW + b_3 chl	2228	0.316*** (0.055)	−0.126*** (0.010)	0.052*** (0.003)	0.028*** (0.004)		21.3	200.6
(4) $EPR_c = a + b_1$ SPM + b_2 BW + b_3 chl + b_4 *T*	2228	0.816*** (0.125)	−0.150*** (0.011)	0.040*** (0.004)	0.027*** (0.004)	−0.023*** (0.005)	22.0	156.72
(5) EPR_c (mean) = a + b_1 SPM + b_2 BW (mean) + b_3 chl + b_4 *T*	95	0.625* (0.349)	−0.15*** (0.023)	0.046*** (0.013)	0.023*** (0.008)	−0.013 (0.0132)	61.5	35.88

Table 5. *Temora longicornis.* Stepwise multiple regression analysis (EPR$_c$ = a + b_1 BW + b_2 chl + b_3 T) between EPR$_c$ (µg C female^{-1} d^{-1}), BW (µg C), chl (µg l^{-1}) and T (°C) for different SPM concentrations (ordinal scale). Significance levels: *10%; **5%; ***1%. Further details as in Table 1

SPM	n	Intercept (a)		BW (b_1)		Chl (b_2)		T (b_3)		r^2	F
1	303	1.160**	(0.49)	0.072***	(0.02)	−0.017	(0.013)	−0.061**	(0.025)	15.9	18.84
2	633	0.739***	(0.22)	0.031***	(0.008)	0.034***	(0.006)	−0.042***	(0.01)	20.7	54.70
3	414	−0.2	(0.275)	0.068***	(0.011)	0.029***	(0.011)	0.004	(0.013)	18.2	30.43
4	276	0.383	(0.28)	0.023*	(0.013)	−0.015	(0.022)	−0.009	(0.015)	6	5.80
5	220	−0.406	(0.256)	0.054***	(0.011)	−0.014	(0.028)	0.021	(0.014)	13	10.74
6	382	0.042	(0.125)	0.018***	(0.005)	0.119**	(0.048)	−0.018**	(0.009)	5.3	7.08

Table 6. *Temora longicornis.* Stepwise multiple regression analysis (EPR$_c$ = a + b_1 SPM + b_2 chl + b_3 T) between EPR$_c$ (µg C female^{-1} d^{-1}), SPM (ordinal scale), chl (µg l^{-1}) and T (°C) for different copepod BW (µg C) ranges. Significance levels: **5%; ***1%. Further details as in Table 1

BW	n	Intercept (a)	SPM (b_1)	Chl (b_2)	T (b_3)	r^2	F
>3 to ≤8	400	−0.072 (0.24)	−0.057*** (0.016)	0.024 (0.011)	0.009** (0.011)	15.8	18.54
>8 to ≤12	714	0.153 (0.27)	−0.117*** (0.019)	0.013** (0.007)	−0.023*** (0.008)	15.2	31.84
>12 to ≤16	585	1.224** (0.47)	−0.200*** (0.023)	0.009 (0.008)	−0.024** (0.010)	17.2	30.09
>16 to ≤20	418	0.982 (0.64)	−0.172*** (0.029)	0.046*** (0.012)	−0.009 (0.017)	22	29.07
>20 to ≤28	111	1.841 (1.44)	−0.181** (0.077)	0.011 (0.027)	0.067 (0.055)	17.4	5.6

Table 7. *Temora longicornis.* Stepwise multiple regression analysis (EPR$_c$ = a + b_1 SPM + b_2 BW + b_3 chl + b_4 T) between EPR$_c$ (µg C female^{-1} d^{-1}) and SPM (ordinal scale), BW (µg C), chl (µg l^{-1}) and T (°C) for the ranges T ≤ 10°C and T > 10°C. Further details as in Table 1

T (°C)	n	Intercept (a)	SPM (b_1)	BW (b_2)	Chl (b_3)	T (b_4)	r^2	F
≤10	848	0.719*** (0.19)	−0.175*** (0.021)	0.024*** (0.008)	0.048*** (0.012)	0.037*** (0.015)	22.7	62.99
>10	1315	1.073*** (0.20)	−0.118*** (0.014)	0.047*** (0.006)	0.014*** (0.005)	−0.048*** (0.010)	25.6	112.69

variables, like chlorophyll *a* (0.3 to 17.3 µg l^{-1}), temperature (2.5 to 18.5°C) and suspended sediments (0.5 to 50 mg l^{-1}). As such, the present research is one of the most comprehensive studies ever conducted on the fecundity of this copepod species.

Our data show that *Temora longicornis* breeds continuously throughout the year, with EPRs following a seasonal pattern and magnitudes comparable to those reported for other temperate areas (Kiørboe & Nielsen 1994, Peterson & Kimmerer 1994, Peterson & Dam 1996, Halsband & Hirche 2001). The results of the stepwise multiple regression analysis, from the present study, suggest that BW, chl and SPM are key parameters controlling the EPR of *T. longicornis*, whereas the effect of *T*, although significant, is less important (Tables 1 & 3).

Effect of body weight on fecundity

Temora longicornis reproduced at a maximum rate (EPR$_{max}$) during spring when copepods where heaviest and at a minimum rate (EPR$_{min}$) in summer/autumn when copepods were lightest (Figs. 2 & 4). As a result,

fecundity was positively related to BW, which accounted for a large part of the variability explained by the multiple regression analysis (Tables 1 & 3). The positive, significant relationship found between EPR and BW, in the present study, contrasts with results from previous investigations (Halsband & Hirche 2001, Maps et al. 2005). Maps et al. (2005) argued that food availability rather than BW was the main factor regulating the fecundity of *T. longicornis* in the Gulf of St. Lawrence, while Halsband & Hirche (2001) could not find any significant correlation between EPR, PL and chl for this species in the North Sea. However, based on a significant correlation between clutch size and PL, Halsband & Hirche (2001) speculated that body size rather than food sources regulated the fecundity of *T. longicornis*.

BW has already been reported as an important determinant of egg mass for several copepod species (Runge 1985, Bunker & Hirst 2004). Nevertheless, not many investigations have explored the relationship between fecundity and body weight. In addition, the majority of the studies to date have limited their analysis to multiple rather than single species (Kiørboe &

Sabatini 1995, Hopcroft & Roff 1998, Bunker & Hirst 2004). The lack of correlation between variables reported is probably due to the fact that none of the previous studies on *Temora longicornis* has thoroughly investigated the combined effects of BW, chl and *T* at the high frequency (i.e. weekly) measurements and over the full range of variables reported by the present study. For instance, Maps et al. (2005) conducted their field study over a restricted part of the year, and, thus, the lack of relationship they reported between EPR and BW was probably due to the similarity in the size of the copepods they studied (see their Table 2). Similarly, the lack of scaling between EPR and BW reported for multiple copepod species by Kiørboe & Sabatini (1995) has been attributed to the use of a limited data set (Bunker & Hirst 2004). In addition, both Halsband & Hirche (2001) and Maps et al. (2005) used simple correlation analysis on means rather than on individual observations. By using this approach, they reduced both the sample size and the variability in their data set and, therefore, probably limited the possibility of finding a significant correlation among the variables they studied. For instance, results from the present study indicate that, although the parameters estimated using either individual or mean values are the same, temperature was significantly correlated to fecundity only when using individual values. We will return to the differences in methodological approaches used by different studies (see section 'Methodological and statistical considerations in the analysis of EPR data').

Fecundity versus temperature

The relationship between fecundity and temperature, found in the present study, was negative and weaker than that between EPR and the other variables (Tables 1 & 3). Such a relationship largely arose from the observed decrease in *Temora longicornis* EPR at field temperatures >10°C (Fig. 6, Table 7). A rise in temperature usually results in an increase in the physiological rates of poikilotherms up to an optimum beyond which conditions become sub-optimal or detrimental to life processes (Schmidt-Nielsen 1991). However, laboratory experiments have shown that, under food-saturated conditions, *T. longicornis* fecundity reaches a maximum around 18°C (Halsband-Lenk et al. 2002), i.e. greater than or equal to the maximum field temperature experienced by this species in our study area. Similarly, the low EPR measured in winter, when copepods reached their largest sizes, was probably not due to low temperature (i.e. ~3 to 8°C). Laboratory studies have indeed shown that, under food-saturated conditions, *T. longicornis* fecundity is temperature limited at 2°C (Maps et al. 2005). However, the data pre-

sented by Kiørboe & Nielsen ([1994], see their Figs. 4B & 5C) clearly show an EPR_{max} for *T. longicornis* at ~5°C during the spring phytoplankton bloom, demonstrating that, provided an adequate food source is available, this species can reproduce maximally even at such low temperatures. The minimum field temperatures encountered by *T. longicornis*, in the present study, never dropped below 5°C throughout winter, with the exception of the ~3°C measured in early January 1996 and 1997. Moreover, the high 'spring-like' temperatures of ~8.5°C we recorded in the winter of 1998 did not promote any increase in *T. longicornis* EPR until the chl concentration in the field rose >0.5 µg chl l^{-1}, suggesting that fecundity was food limited. Such a low EPR in winter might have also been exacerbated by the fact that copepods at this time of the year were heaviest and thus required more energy to meet metabolic costs (C. Castellani unpubl. data) and/or to initiate reproduction.

Other studies have reported positive scaling between the EPR of multiple species and temperature, although, consistently with our results, temperature did only have low explanatory power of copepod fecundity (Bunker & Hirst 2004). The reason for the difference and reduced effect of temperatures on EPR, across studies, is probably to be attributed in part to both the effects of BW and food limitation on fecundity. In the present study, the negative scaling between fecundity and temperature was due to the fact that at the lower temperatures copepods were larger and EPR was on average greater than at the warmer temperatures (Fig. 6). When food resources *in situ* are limiting, temperature is unlikely to accurately predict changes in copepod fecundity with BW, as any ingested/stored energy would probably be channelled towards basic metabolism rather than reproduction.

Fecundity versus chlorophyll *a*

Findings of the current study regarding *in situ* food limitation of *Temora longicornis* fecundity support what has been reported for this species by some field studies (Peterson & Bellantoni 1987, Bautista et al. 1994, Kiørboe & Nielsen 1994, Peterson & Kimmerer 1994, Maps et al. 2005), but not by others (Halsband & Hirche 2001). Although, *T. longicornis* reproduced throughout the year, EPR_{max} was only achieved at microplankton carbon values ranging from ~12 to 200 µg C l^{-1} and at chl > 1 to 3.5 µg l^{-1} (Fig. 5), a value lower but close to the value of 5 µg chl l^{-1} reported by Peterson & Bellantoni (1987) for this species in Long Island Sound. Further evidence of food limitation on fecundity, in the present study, is provided by the fact that the chl concentration at which EPR_{max} occurred

coincides with the 3.5 µg l^{-1} (for phytoplankton cells >20 µm) at which the ingestion rate of *T. longicornis* is maximum (Dam & Peterson 1991). In addition, Ivlev's relationships show a saturation of EPR with increasing chl concentration for all BW groups, indicating that food limitation was not restricted to the largest copepods, but occurred over the full BW range (Fig. 5, Table 3). In contrast, Halsband & Hirche (2001) could not find any significant relationship between EPR and chl, and concluded that the *in situ* fecundity of *T. longicornis* was not food limited. In their study, however, Halsband & Hirche ([2001], compare their Figs. 2B & 4A) recorded the highest fecundity and length of *T. longicornis* at the end of the spring phytoplankton bloom, when food sources were still sufficient (i.e. chl ~5 µg C l^{-1}) to sustain EPR$_{max}$.

The relationship between EPR and chl, found in the present study, is not as strong and consistent as that between EPR and BW (Tables 3 to 5). One reason for this is perhaps that *Temora longicornis* can reproduce and reach EPR$_{max}$ at food concentrations as low as ~0.5 µg C l^{-1} (Peterson & Bellantoni 1987, Peterson et al. 1991, Bautista et al. 1994) and ~1 µg chl l^{-1} (present study), respectively. Another possibility is that our results are based on a relationship between EPR and *in situ* rather than ingested chl and that this approach does not take into account microzooplankton as a potential food source. Being an omnivore, *T. longicornis* is able to exploit a variety of food sources, including microzooplankton, which may represent up to $\frac{1}{3}$ of the daily nitrogen requirement of this species (Peterson & Dam 1996). The largest proportion of chl during the spring phytoplankton bloom was due to *Phaeocystis* spp., a phytoplankton species, which is not usually grazed upon in large amounts by copepods (Hansen et al. 1993, Castellani et al. 2005). As ciliate biomass also peaked during the bloom, it is possible that *T. longicornis* preferentially selected microzooplankton over *Phaeocystis* spp., similar to what has been reported by Hansen et al. (1993). Thus, since *T. longicornis* may select its food according to type (O'Connors et al. 1980), size (Dam & Peterson 1991) and quality, and feed carnivorously (Hansen et al. 1993), a weaker relationship between EPR and total available chl may be expected.

During spring 1996 *Temora longicornis* EPR was consistently lower than that in 1997 to 1998 over the full range of copepod weights for comparable chl concentrations, microplankton composition and SPM loading. The observed high variability in fecundity and poor correlation between EPR and chl may also have resulted from copepods ingesting food of different qualities. The quality of food depends on the biochemical components of the diet that cannot be synthesised by the copepods, in particular long-chain fatty acids (Pond et al. 1996), amino acids (Guisande et al. 2000),

sterols (Klein Breteler et al. 1999), proteins (Kleppel & Hazzard 2000) and vitamins (Lee et al. 1999). Variations in absolute egg numbers may also be due to the different age structures in the populations, i.e. the proportion of spent females (Uye 1981). However, our data show that the percentage of RAFs found during spring was similar across years. These considerations suggest that food quality, rather than copepod size and age, may have determined the inter-annual differences in the fecundity measured.

In the present study, the weight-specific fecundity (SEPR) of *Temora longicornis* was at most 10% body carbon d^{-1} (i.e. body C d^{-1}). Thus, the daily carbon rations of this species would be at most 30% body C d^{-1}, assuming a gross growth efficiency (GGE) of ~30% (Straile 1997). Dam & Peterson (1993) constructed a carbon budget for *T. longicornis*, based on phytoplankton ingestion only, that would be consistent with this inference. However, since *T. longicornis* is an omnivore, carbon consumption is likely to be greater than the inferred ration, and the GGE is much less. Dam & Lopes (2003) have recently estimated a GGE of ~9% for *T. longicornis* fed 7 different diets, which would support this view.

Effect of SPM on EPR

Temora longicornis EPR was significantly inversely related to both SPM and tidal range (Fig. 7, Table 1). Butler (1995) has reported that all concentrations of suspended sediments significantly lowered the ability of the herbivorous freshwater copepod *Diaptomus ashlandii* to locate and ingest micro-algae. However, Gasparini & Castel (1997) have suggested that the low fecundity of *Acartia bifilosa* in the Gironde estuary may be related to poor feeding conditions associated with high suspended particulate loading. Thus, *T. longicornis* fecundity may have been reduced either directly due to suspended sediments lowering feeding efficiency or indirectly through the ingestion of food of lower nutritional quality, i.e. degraded material derived from the bottom sediments re-suspended in the water column during high tide. Nevertheless, the mechanisms through which SPM affects the EPR of *T. longicornis* are unclear at present and require further investigation.

Methodological and statistical considerations in the analysis of EPR data

Heterogeneity of results between studies might also have arisen as a consequence of using different methodological (e.g. single versus multiple animal

incubations, length of incubation) and analytical techniques (e.g. simple logarithmic transformation versus ln [$x + 1$] transformation). Several authors have already discussed the importance of standardising the methodology used to determine EPR by incubating individual females and including zero values to estimate copepod population fecundity (Runge & Roff 2000, McKinnon & Duggan 2001). Zero values can be artificially excluded from the statistical analysis by, for instance, taking into account only reproductive females and/or using simple ln transformation rather than ln ($x + 1$) (Hopcroft & Roff 1998, Bunker & Hirst 2004). Excluding zero values will both overestimate the fecundity of the population and produce an artificially higher explanatory power of the variables (as the variability of the data set will become reduced). To avoid this shortcoming, in the present study, we chose to analyse individual estimates rather than mean fecundity to fully take into account the influence of the outliers, i.e. the zero values and very high values (McKinnon & Duggan 2001). The results of our analysis show that this latter approach yielded the same regression coefficients estimated using mean values and allowed us to take into account more accurately the effect of body size and to determine more effectively the relationship between variables (Tables 1 & 3).

CONCLUSIONS

The present study has shown that body weight, food concentration and suspended particulate matter are all important variables affecting the fecundity of *Temora longicornis*. However, the relative impact of each of these factors on the total number of eggs a female copepod can produce may vary during the year. Food limitation of EPR (i.e. either low food abundance/quality or high SPM) may play a more important role during winter, when copepods are larger and require more energy to meet basic metabolic costs. On the other hand, BW may be a more important factor in setting the upper limit of reproductive output during the summer, as copepods at this time are smaller. In addition, the inverse correlation between BW and *T* suggests that temperature plays a more subtle role by indirectly determining the maximum potential reproductive output of *T. longicornis* through its control on BW. It is concluded that by regulating at least *in situ* physical parameters, such as *T* and SPM, climate change may act as an important determinant of secondary production.

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