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Journal of Experimental Marine Biology and Ecology 318 (2005) 145–162

Journal of EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY

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Effects of chlorophyll concentration and temperature variation on the reproduction and survival of *Temora longicornis* (Copepoda, Calanoida) in the Eastern English Channel

David Devreker[a], Sami Souissi[a,*], Laurent Seuront[a,b]

[a]*Ecosystem Complexity Research Group, Station Marine de Wimereux, Université des Sciences et Technologies de Lille, CNRS-UMR 8013 ELICO, 28 Avenue Foch, BP 80, F-62930 Wimereux, France*
[b]*School of Biology Sciences, Flinders University, GPO Box 2100, Adelaide 5001, South Australia*

Received 6 April 2004; received in revised form 18 June 2004; accepted 10 December 2004

Abstract

The influence of temperature and chlorophyll concentration on egg production, hatching success, female survival and body size of the copepod *Temora longicornis* was investigated in situ in the coastal waters of the Eastern English Channel. Twenty samples were collected between February and July 2003 three to four times per month. The maximum daily level of egg production of 75.5 eggs female^{-1} was observed in March, with minima of 10 eggs female^{-1} in February and July. Between February and March egg production increased with chlorophyll concentration. At the end of March a decrease in egg production corresponded to a strong increase in chlorophyll concentration that indicated a *Phaeocystis*-dominated bloom. After this period egg production closely followed the temporal variation in chlorophyll concentration with a maximum of 55.3 eggs female^{-1} in April during a second peak of chlorophyll concentration. Hatching success varied between 60% and 80% and was not influenced by chlorophyll concentration, in situ temperature or any other biological parameter considered in this study. Increases in temperature from February to July paralleled a decrease in body length and an increase in the percentage of spawning females. Mean female survival followed the variation of both temperature and chlorophyll concentration only between April and July. Temperature and chlorophyll concentration affected the reproductive parameters of *T. longicornis* differently. Female survival and body size were negatively correlated with temperature, while the highest chlorophyll concentrations were not always favourable for egg production. Therefore the quality of food should not be associated with chlorophyll quantity. Furthermore, the maximum values of egg production in this study are the highest recorded for *T. longicornis*. This study, conducted for the first time in the Eastern English Channel, showed high levels of productivity of *T. longicornis* despite a decrease of egg production during a *Phaeocystis* sp. dominated bloom in April.

Keywords: Chlorophyll concentration; Eastern English Channel; Egg production; Hatching success; *Temora longicornis*; Temperature

* Corresponding author. Tel.: +33 321 992 908; fax: +33 321 992 901.
E-mail address: Sami.Souissi@univ-lille1.fr (S. Souissi).

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doi:10.1016/j.jembe.2004.12.011

1. Introduction

Copepods are the most important secondary producers of the world ocean. They represent an important link between phytoplankton, microzooplankton and higher trophic levels such as fish (Fockedey and Mees, 1999; Kleppel, 1993; Zismann et al., 1974). With regard to their role in marine food webs, it is important to know how environmental variation affect their production. Several studies have shown that food concentration and temperature are the main factors that control copepod egg production and egg viability in the field (Ambler, 1985; Ianora et al., 1992; Smith and Lane, 1985). Food can have limiting effects on reproductive parameters either quantitatively (Beckman and Peterson, 1986; Dagg, 1978) or qualitatively (Alonzo et al., 2001; Hopp et al., 1997; Koski et al., 1999a). Other studies have suggested that temperature could affect reproductive parameters by controlling metabolic activity (Hirche et al., 1997; Razoul, 1975). The combination of these factors can have direct or indirect effect on reproductive activity. Firstly, the maximum number of clutches produced during the complete lifespan of a female copepod is affected by both temperature and food, since adult longevity depends on these two parameters (Carotenuto et al., 2002; Hall and Burns, 2002; Klein Breteler and Gonzalez, 1984; Makino and Ban, 2000; Poli and Castel, 1983). The number of clutches also varies as function of the rate of egg production, which can fluctuate during the lifespan of a female (Ianora and Poulet, 1993). Secondly, egg production can be affected by female size (Hirche, 1992), depending on both food availability (Mullin and Brooks, 1970) and temperature (Burdloff et al., 2002; Gillooly et al., 2001). As a consequence, copepod reproductive responses exhibit variable patterns of response to the wide ranges of food quantity and temperature encountered during different seasons (Ambler, 1985; Castellani and Lucas, 2003; Halsband-Lenk et al., 2001).

In northern temperate coastal ecosystems, the calanoid copepod *Temora longicornis* is one of the most abundant copepod species, where it can represent 35–70% of the total copepod population (Daan, 1989). It has been shown to be able to remove up to 49% of the daily primary production (Dam and Peterson, 1993). Effects of food quantity and temperature fluctuations on the reproduction of *T. longicornis* have mainly been studied in the North Sea and in the coastal areas of the North Atlantic Ocean (Castellani and Lucas, 2003; Fransz et al., 1992; Halsband and Hirche, 2001; Klein Breteler et al., 1982; Peterson and Kimmerer, 1994; Van Rijswijk et al., 1989). These studies have shown that in situ egg production increases with temperature and food quantity, particularly during phytoplankton blooms (Fransz et al., 1992; Peterson and Kimmerer, 1994). The maximum egg production rate of *T. longicornis* is highly variable, from 6 to 60 eggs female^{-1} day^{-1}, varying as a function of season and geographical location (Halsband-Lenk et al., 2001). The impact of food quality has been discussed in more detail, especially with regard to diatoms, which may be responsible for in situ egg production and hatching success limitations (Ianora et al., 2003; Laabir et al., 1995) or improvements (Dam and Lopes, 2003) or could have no particular effect on reproduction (Irigoien et al., 2002). However diatoms are not the only algae that may affect copepod reproduction and viability. Some prymnesiophyceae such as *Prymnesium patelliferum* have been classified as potentially toxic algae for copepods (Koski et al., 1999b) particularly during bloom conditions. In the coastal waters of the Southern Bight of the North Sea and the Eastern English Channel, the spring phytoplankton blooms are often dominated by another prymnesiophyceae, *Phaeocystis* sp. (Hansen and van Boekel, 1991; Van Rijswijk et al., 1989) and often coincide with maximal abundance of the copepod *T. longicornis* (Fransz et al., 1992).

In the Eastern English Channel, *T. longicornis* is of great ecological significance and dominates the zooplankton assemblages during the phytoplankton spring bloom (Brylinski et al., 1984, 1988). However, its reproductive biology has never been studied in this area, where temperature may vary from 3 °C to 20 °C and where the combination of high nutrient concentration and high mixing rates leads to intense spring phytoplankton blooms (Seuront et al., 2002). *Phaeocystis* sp. can reach very high concentrations during blooms, up to 10^7 cells l^{-1} (Seuront and Souissi, 2002). Previous studies have shown that this type of phytoplankton bloom affects

copepod ingestion by changing its selectivity (e.g. Cotonnec et al., 2001, 2003). A debate as to whether or not *Phaeocystis* sp. is ingested by copepods (i.e. *T. longicornis*) is present in the literature (Bautista et al., 1992; Breton et al., 1999; Gasparini et al., 2000; Hamm and Rousseau, 2003; Turner et al., 2002). Most methods used in these studies have indirectly detected the presence of fatty acids or pigments in the guts of copepods during *Phaeocystis*-dominated blooms (Cotonnec et al., 2001; Hamm and Rousseau, 2003). Nevertheless, until now the egg production of *T. longicornis*, which is often directly affected by its ingestion (Peterson and Dam, 1996), has been poorly studied in the Eastern English Channel.

The aim of this paper is thus to understand the effects of food quantity and temperature variation on the egg production, hatching success, hatching time, percentage of spawning females, female mortality and female body size of *T. longicornis* in the Eastern English Channel. We investigate the temporal variability of reproductive parameters before, during and after the spring phytoplankton bloom largely dominated by *Phaeocystis* sp. The results obtained here are compared to other similar studies conducted in the North Atlantic Ocean and the North Sea.

2. Materials and methods

2.1. Sampling and animal acclimatization

Zooplankton were collected weekly before, during and after the *Phaeocyctis* sp. bloom in the Eastern English Channel from February to July 2003, at the inshore station (50°40′75″N, 1°31′17″E) of the SOMLIT network (Service d'Observation du Milieu Littoral) at high tide (Fig. 1). Copepods were collected using a WP2 net (200 μm mesh size) and specimens were stored in 30 l isotherm tanks and transported within 1 h to the laboratory where adult females of *T. longicornis* were immediately sorted for experiments. Females were progressively acclimated from seawater to experimental temperature in few hours as function of the difference of temperature.

Water temperature (°C) profiles from the surface to bottom were measured using a Seabird SBE 19 or Seabird SBE 25 Sealogger CTD at each sampling date. The maximum depth never exceeded 25 m. Water samples were taken from sub-surface, intermediate and bottom waters using 5 l Niskin bottles for chlorophyll *a* determination (Chl. *a*, μg l^{-1}). Chlorophyll *a* concentration was determined by fluorometric analysis in methanol extracts: 250 ml to 1 l of seawater were filtered on a glass fibre filter (Whatman

Fig. 1. Location of the two sampling sites (asterisk) at the inshore (I) and the offshore (O) stations of the SOMLIT (Service d'Observation du Milieu Littoral) network near Boulogne sur Mer in the Eastern English Channel (E: England; B: Belgium; N: Netherlands).

GF/C 47 mm, porosity 0.45 μm). Immediately after filtration, the filter was transferred to plastic tubes containing 5 ml of 100% methanol. The tubes were plugged and placed in the dark at 4 °C until they were stored in the laboratory in the dark at −20 °C; no difference could be observed between the results with and without grinding in methanol, agreeing with conclusions by Holm-Hansen and Riemann (1978). Before fluorescence measurements, the tubes were shaken gently and fluorescence was measured directly in glass test tubes with a Turner 450 fluorometer. Correction for phaeopigments was made by acidification (Holm-Hansen et al., 1965), by addition of 50 μl HCl 0.5 N. Calibration of the fluorometer was made with pure Chl. *a* (*Anacystis nidulans* extract; Sigma Chemicals) in pure methanol with its concentration first measured on a spectrophotometer.

2.2. Egg production and hatching rate

Egg production and hatching rate measurements were conducted in cold rooms at 10 °C (±1 °C), corresponding to the upper value of the optimal temperature range of in situ maximum reproductive activity (Halsband-Lenk, 2001; Van Rijswijk et al., 1989). Experimental temperature was maintained constant to ensure that the variability in our results is due to environmental variations rather than experimental variations. We kept 15 to 23 females individually in 60 ml beakers equipped with 200 μm mesh chambers filled with 50 ml of filtered seawater (GF/C Whatman, 0.45 μm porosity). The inner chamber was used for separating eggs and females, and thus prevented the predation of females on eggs, which could lead to an underestimation of egg production. Beakers were inspected every 6 or 12 h by removing the inner chamber. Eggs were counted using a binocular microscope and transferred into 40 ml beakers for incubation in order to survey the hatching rate. Eggs were carefully removed once or twice a week in new 40 ml beakers to prevent bacterial proliferation. All experiments were performed under a light cycle representative of field conditions.

Laabir et al. (1995) showed that egg production from the first 24 h of incubation reflects the feeding history of females in the field. To verify the applicability of this concept egg production was always observed during 72 h in this study. Egg production was expressed as mean egg production of all females (spawning or not) during 24 h of incubation (eggs female^{-1}) and compare with the egg production of the same females during 72 h of incubation. Egg production from 48 to 72 h of incubation was negligible. Consequently, only the hatching success and hatching time from eggs produced during the first 24 h were considered.

The number of spawning females is given as the percentage of females that laid eggs during the experiments. In addition, individual observations allowed us to calculate the standard deviation (SD) for the egg production at each sampling date.

Hatching was monitored every 6–12 h to determine hatching success. Hatched eggs were counted when empty shells appeared in the 40 ml beaker. Hatching rate was controlled for 2 weeks in order to determine if eggs that did not hatch during the first days will degenerate as nonfertilized eggs. The hatching rate per clutch was calculated as a function of the total number of eggs of the clutch and the time when 50% of the eggs have hatched (i.e. embryonic development time in Halsband-Lenk et al., 2002).

2.3. Female survival and body length

Survival of starving females was investigated in all experiments. After the spawning period of 72 h females were observed one or two times a day until their death. Afterwards their prosomes were immediately measured using a micrometer eyepiece mounted on the binocular microscope. Female survival time was considered for each sampling date as the mean time of survival of all females from that sampling date. The SD was calculated for both parameters. As the age of the wild females is unknown, their mortality gives a general idea of the effect of the environmental factor on their viability but does not give a measure of the longevity of the adult stage.

2.4. Generation length

Generation lengths of *T. longicornis* as function of the semi-annual variation of temperature were calculated using the index of development *day-degrees* (Weltzien et al., 1999). The post-embryonic development time data found by Klein Breteler and Gonzalez

(1984) at four different temperatures (5, 10, 15 and 20 °C) were used.

2.5. Additional sampling and experiments

Three additional sampling were taken in mid-April, the end of May and at the beginning of July, at the offshore station of the SOMLIT network (50°40′75″ N, 1°24′60″ E) at a distance of 6 km from the coastal station (Fig. 1). The goal was to investigate the influence of the sampling location on the reproductive parameters of *T. longicornis*. Moreover, two experiments with females from the coastal station were performed at 15 °C at July 7 and July 18, 2003 and two other experiments at July 8 and July 19, 2004 at 13, 15 and 21 °C to investigate the effect of experimental conditions on the results.

2.6. Statistical analysis

Relationships between environmental factors (i.e. temperature and chlorophyll *a* concentration) and biological parameters are tested with Spearman rank correlation test (Scherrer, 1984). Nonparametric correlation was preferred to parametric correlation because parameters are different and the number of observations was variable and usually low.

Differences in biological parameters between offshore and inshore sampling stations and between the different experimental temperatures were tested with the nonparametric Mann–Whitney test (Scherrer, 1984). All statistical analyses were performed using the Statistica Software v5.5.

3. Results

3.1. Temperature and chlorophyll concentration

Temperature was constant over the whole water column and linearly increased from 5 °C to 20 °C during the study period (Fig. 2), in accordance with the seasonal temperature patterns observed in this area (Seuront, 1999).

Chlorophyll *a* concentration was highly variable (Fig. 2C) but showed no pronounced gradient throughout the water column except in July (Fig. 2). Chlorophyll concentration showed four peaks that appeared in February, March, May and July. Maximum concentrations reached during the three first peaks increased respectively from 15 μg l^{-1} to 25 μg l^{-1} and 35 μg l^{-1}. The last peak was 20 μg l^{-1}. The succession of the three first peaks was rapid and contrasting with a longer period (2 months) of relatively low chlorophyll concentration (10 μg l^{-1}) separating the last peak (Fig. 2C).

3.2. Reproductive parameters

Mean egg production of *T. longicornis* varied strongly over the study period. This parameter increased from February to March and reached the highest value of 75.5 eggs $female^{-1}$ on March 20 (Fig. 3A). The low mean egg production value on February 20 (17 eggs $female^{-1}$) coincided with a low percentage of spawning females of 40% (Fig. 4). A second peak of egg production occurred in May at 55.3 eggs $female^{-1}$. Between these two periods of high reproductive activity the egg production decreased to 18 eggs $female^{-1}$. After the second peak, the egg production decreased and reached the lowest value of the study (9.5 eggs $female^{-1}$) at the end of July. The highest individual egg production rate by a single female reached 161 eggs $female^{-1}$ on March 13. Temporal variation of the standard deviation (SD) followed the same pattern as mean egg production (Fig. 3A). It increased from February to March and reached a maximum at 57.4 eggs $female^{-1}$ on March 13, 1 week before the maximum mean egg production. During the second peak of egg production the SD was low (23.9 eggs $female^{-1}$) as compared to the first peak. The SD decreased between the two peaks of egg production and after the last peak, reaching a level of 6.8 eggs $female^{-1}$.

On the other hand, hatching success varied slightly during the study period and fluctuated around 75% (Fig. 3B). Minimum levels of hatching success occurred at the end of February and in April (63%). It reached a maximum of 84% at the beginning of July before decreasing rapidly to 43%. The hatching time showed higher variability (Fig. 3C). It decreased from 8 days in February to 2.5 days in March. From April to July hatching time varied between 2 and 4 days with a maximum of 7 days observed on April 25.

Temporal variation of the percentage of spawning females fluctuated strongly from one sampling date to

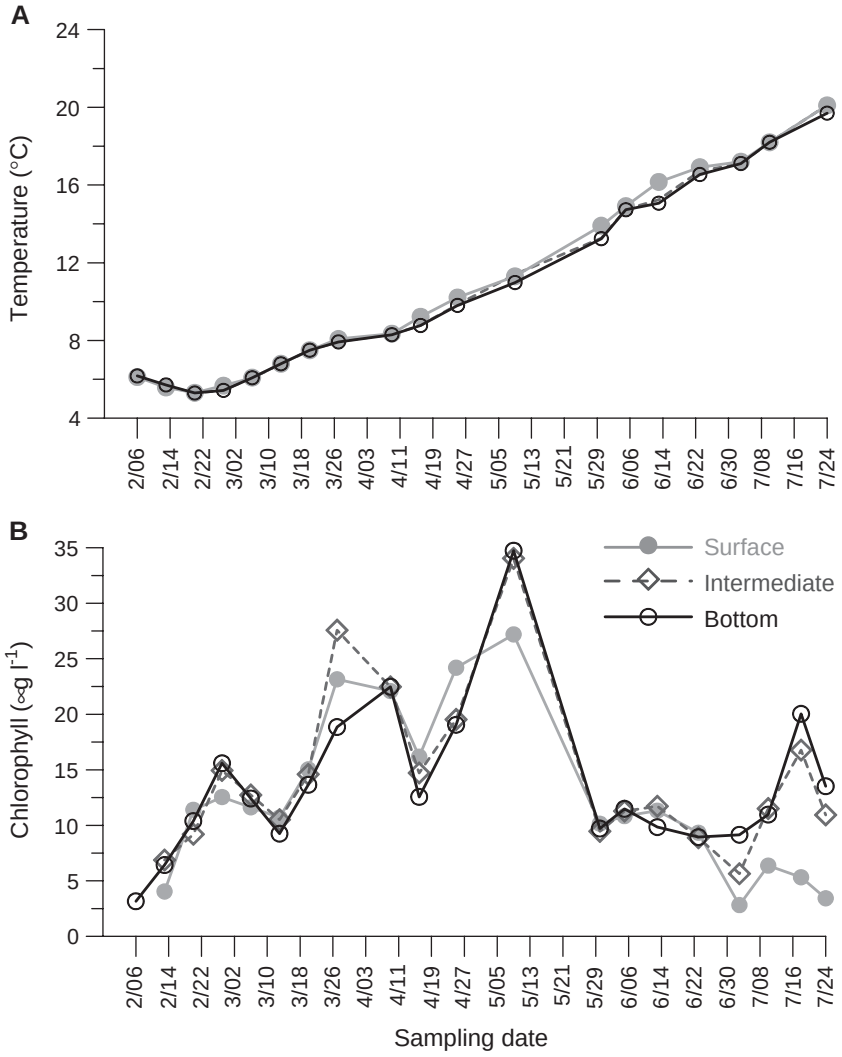

Fig. 2. Temporal change in (A) temperature and (B) chlorophyll concentration at three different depths from February 2003 to July 2003 at the inshore station.

another. It could increase or decrease by 30–40% in 1 week (Fig. 4). Nevertheless the general pattern of variation increased from February to July with a maximum of 100% on June 23. The lowest value of spawning females of 42% was recorded at the end of February (2/20).

3.3. Female survival and body size

Female survival time in filtered seawater was shortest (2 to 4 days) at the beginning of the study period and after the second peak of egg production (Fig. 5). Maximum values (ca. 9 days) were observed from March to April with a maximum of 10 days on March 20. A peak of survival time (7.5 days) occurred in June. The SD follows approximately the same pattern of variation as mean female survival. Nevertheless the SD remained constant, around 5 days, from February to March and after June 13. It increased up to 9 days during the period of maximum survival time (from March 27 to May 9) and during the peak of survival time in June.

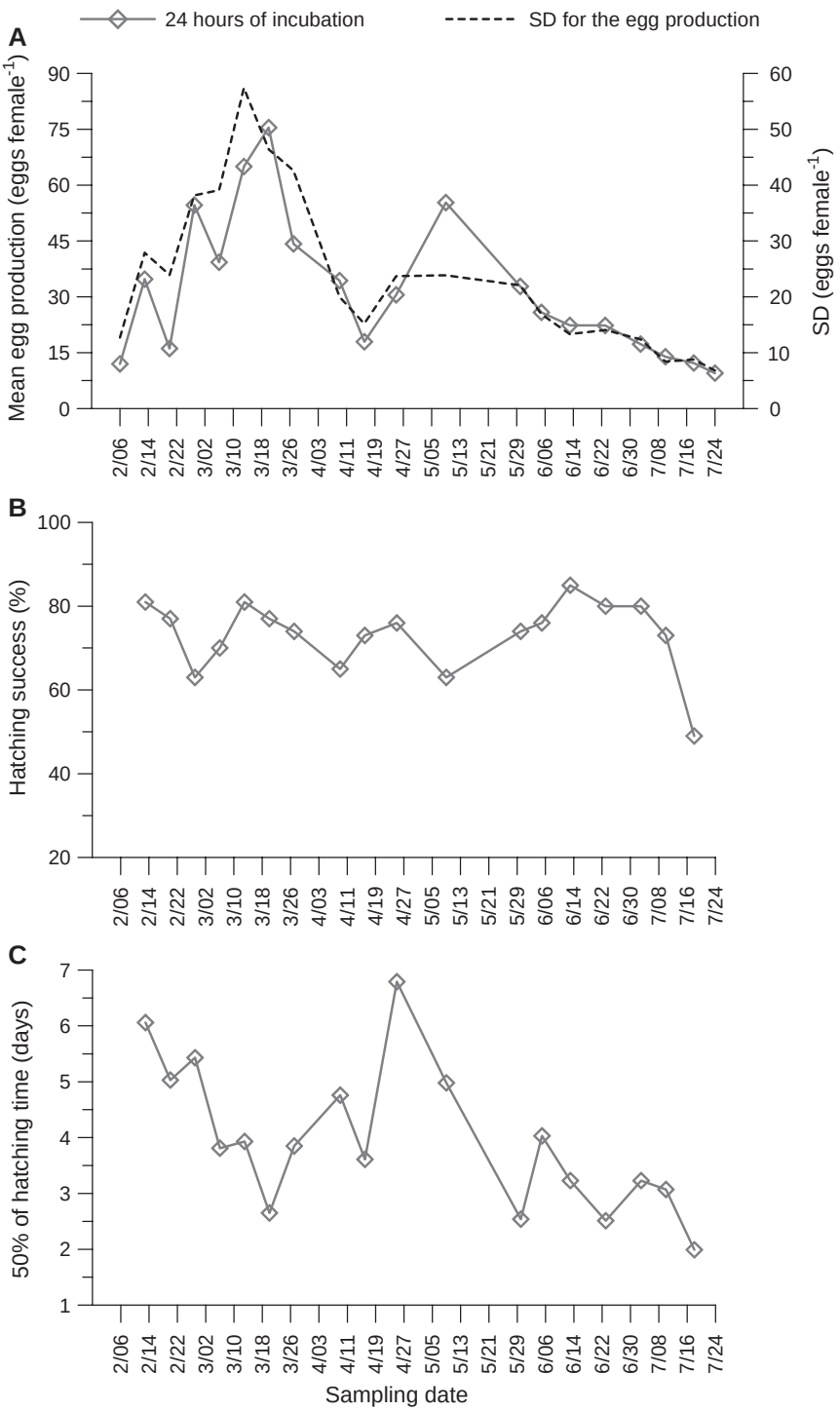

Fig. 3. Temporal changes in reproductive parameters of *T. longicornis* in the Eastern English Channel. (A) Egg production; (B) hatching success; (C) median hatching time. The three parameters are given for a period of 24 h of incubation. The production of eggs after 24 h was very low.

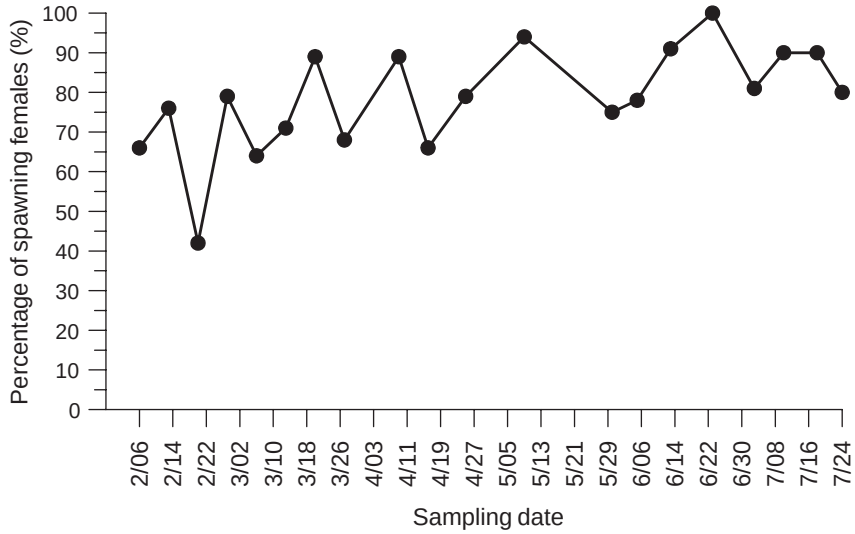

Fig. 4. Temporal variation of the percentage of spawning females, proportion of egg-laying female compared to all isolated females for each sampling date.

Female prosome length fluctuated between 820 and 1330 μm for individuals and between 997 μm and 1173 μm for mean values calculated at each sampling date (Fig. 6). A high proportion of small females were found in the population during the period of cold temperature in February 20. A relationship could exist with the lower value of percentage of spawning female (Fig. 4) and the low value of egg production (Fig. 3A) recorded at this date.

3.4. Effects of chlorophyll concentration and temperature

Egg production and chlorophyll concentration were slightly correlated during the entire study period (Table 1) with a strong correlation between egg production and surface chlorophyll concentration from April to July (Table 2). The absence of correlation from February to March was reflected by

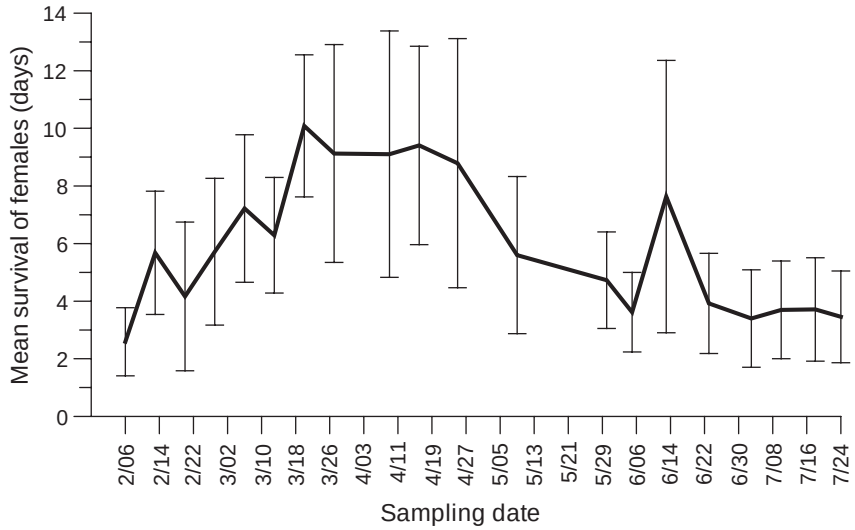

Fig. 5. Temporal variation in the mean mortality of females incubated at each sampling date; vertical bars correspond to standard deviation (SD).

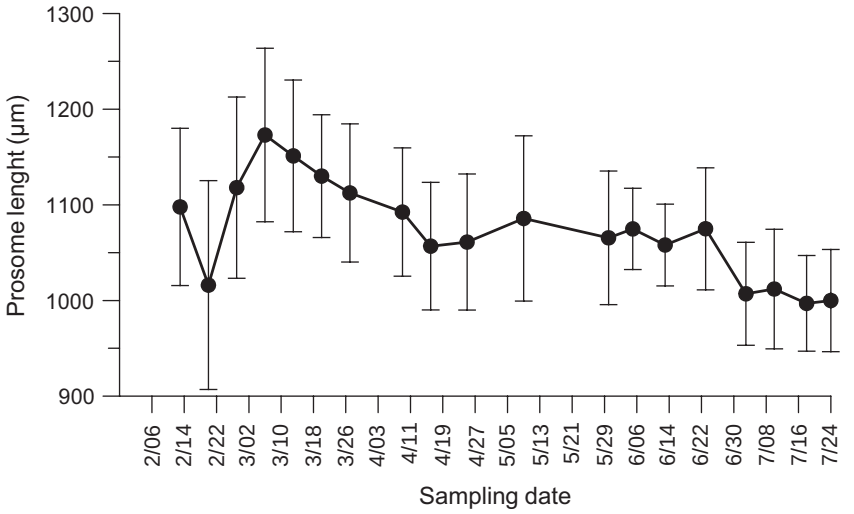

Fig. 6. Temporal variation in the prosome length of females incubated at each sampling date; vertical bars correspond to standard deviation (SD).

the lag observed between the second peak of chlorophyll concentration and the first peak of egg production in March (Figs. 2 and 3).

Female size and survival were also dependent on chlorophyll concentration. Female body size and female survival were not correlated to depth-averaged chlorophyll concentration during the entire study period (Table 1) but were significantly correlated with the chlorophyll surface concentration from April to July (Table 2). Body size and female survival were correlated (Table 1). The general pattern of mean survival (Fig. 5) and mean prosome length (Fig. 6) variation showed that large females survived longer than small females. The hatching time was significantly correlated with surface chlorophyll concentration only during the April–July period (Table 2).

Female survival and egg production were negatively correlated with temperature, particularly from April to July (Table 2). Female body size and temperature were negatively correlated (Table 1); the minimum and maximum size corresponded to the highest and lowest temperature, respectively. The percentage of spawning females increased and decreased with temperature, respectively (Table 1).

3.5. Effect of experimental temperature

Table 3 shows the effects of different experimental temperatures (10, 13, 15 and 21 °C) on the

Table 1
Spearman correlation coefficients (r) between all biological and environmental factors measured during the entire study period (from February to July) at the inshore station of SOMLIT network

	EP	HS	PL	SF	FS	HT	T	C
EP	1	0.178	0.896***	0.001	0.705***	0.330	−0.504*	0.520*
HS		1	0.239	−0.194	−0.083	−0.009	−0.205	−0.511*
PL			1	−0.263	0.609**	0.337	−0.712***	0.300
SF				1	−0.197	−0.300	0.650**	0.073
FS					1	0.413	−0.454*	0.699***
HT						1	−0.618**	0.300

Significance levels: *p<0.05; **p<0.01; ***p<0.001.
EP, egg production; HS, hatching success; PL, prosome length; SF, percentage of spawning female; FS, female survival; HT, hatching time; T, temperature; C, chlorophyll concentration.

Table 2
Spearman correlation coefficients (r) between chlorophyll concentration at three different depths and temperature versus egg production (EP), female survival (FS), prosome length (PL) and hatching time (HT) during (F-M) and after (A-J) the supposed *Phaeocystis* sp. dominated bloom

Chlorophyll	EP		FS		PL		HT	
	F-M	A-J	F-M	A-J	F-M	A-J	F-M	A-J
Surface	0.428	0.811***	0.570	0.818**	0.142	0.713**	−0.714	0.827**
Intermediate	0.535	0.433	0.500	0.734**	0.285	0.293	−0.571	0.590
Bottom	0.571	0.209	0.595	0.517	0.107	0.132	−0.535	0.563
Mean	0.598	0.591*	0.658	0.825***	0.126	0.447	−0.630	0.690*
T (°C)	0.476	−0.790**	0.690	−0.860***	0.428	−0.713**	−0.785*	−0.781**

Significance levels: *p<0.05; **p<0.01; ***p<0.001.

studied biological parameters. A variation of the experimental temperature clearly modifies the hatching success except at one date (July 8, 2004). The difference is more important in the second experiment at July 18, 2004 (30% of increase) and between 15 and 21 °C in July 19, 2004 than in the first one at July 10 (20% of increase). No variation of hatching success was observed between the three experimental temperatures at July 8, 2004. The apparent decrease in egg production and percentage of spawning female is not statistically significant (p>0.05). Female survival significantly decreased between 15 and 21 °C at July 8, 2004 and between 13 and 15 °C at July 19, 2004.

Fig. 7 shows that the difference between the in situ and the experimental temperature has no influence on the hatching success when keeping the same experimental temperature during the study. On the other hand, an effect of in situ temperature was observed only at the end of the study period (Fig. 3B) when the differences between experimental and in situ temperature were the highest. On the contrary, female survival tended to increase when experimental and in situ temperatures are close and decrease when this difference increases (Fig. 7).

4. Discussion

4.1. Effect of in situ chlorophyll concentration on T. longicornis reproduction

The increase of egg production and female survival as well as the decrease of hatching time during the first peak of chlorophyll concentration, while temperature remained low, indicates an increase in the food quality ingested by copepods. Similar responses of biological parameters to increases in chlorophyll concentration have been observed in several copepod species (Escaravage and Soetaert, 1995; Halsband and Hirche, 2001). Egg production and female survival continued to increase while the chlorophyll concen-

Table 3
Variation in environmental parameters (in situ and experimental temperatures and mean chlorophyll *a* concentration) and biological parameters (EP, HS, SF, PL and FS; see Table 1) as function of the experimental temperature (T_{exp}) at four different dates

Sampling date	July 10, 2003		July 18, 2003		July 8, 2004			July 19, 2004		
Chloro *a* (μg l^{-1})	9.6		14		3.5					
$T_{in\ situ}$ (°C)	18.2		19		17			17.5		
T_{exp} (°C)	10	15	10	15	13	15	21	13	15	21
EP (eggs female^{-1})	13.90	10.50	12.20	11.00	24.6	26.1	19.93	23.0	18.6	15.75
	(8.40)	(9.78)	(8.76)	(8.86)	(17.4)	(20.9)	(14.0)	(12.6)	(12.6)	(7.76)
SF	90%	75%	90%	75%	86.5%	72%	78%	93%	85%	91%
HS	62%	81%	43%	70%	95%	90%	95%	60%	40%	15.5%
PL (mm)	1.01	1.01	0.99	0.99	0.98	1.00	1.02	0.99	0.99	0.97
	(0.06)	(0.05)	(0.05)	(0.05)	(0.07)	(0.05)	(0.06)	(0.08)	(0.06)	(0.07)
FS (days)	3.33	2.40	3.50	3.21	4.58	4.90	1.85	4.67	2.99	1.90
	(1.69)	(1.24)	(1.80)	(1.88)	(3.35)	(4.34)	(1.17)	(2.75)	(2.61)	(1.38)

In parentheses: standard deviation. Significantly different groups are separated by underline type (Mann–Whitney test, α=5%).

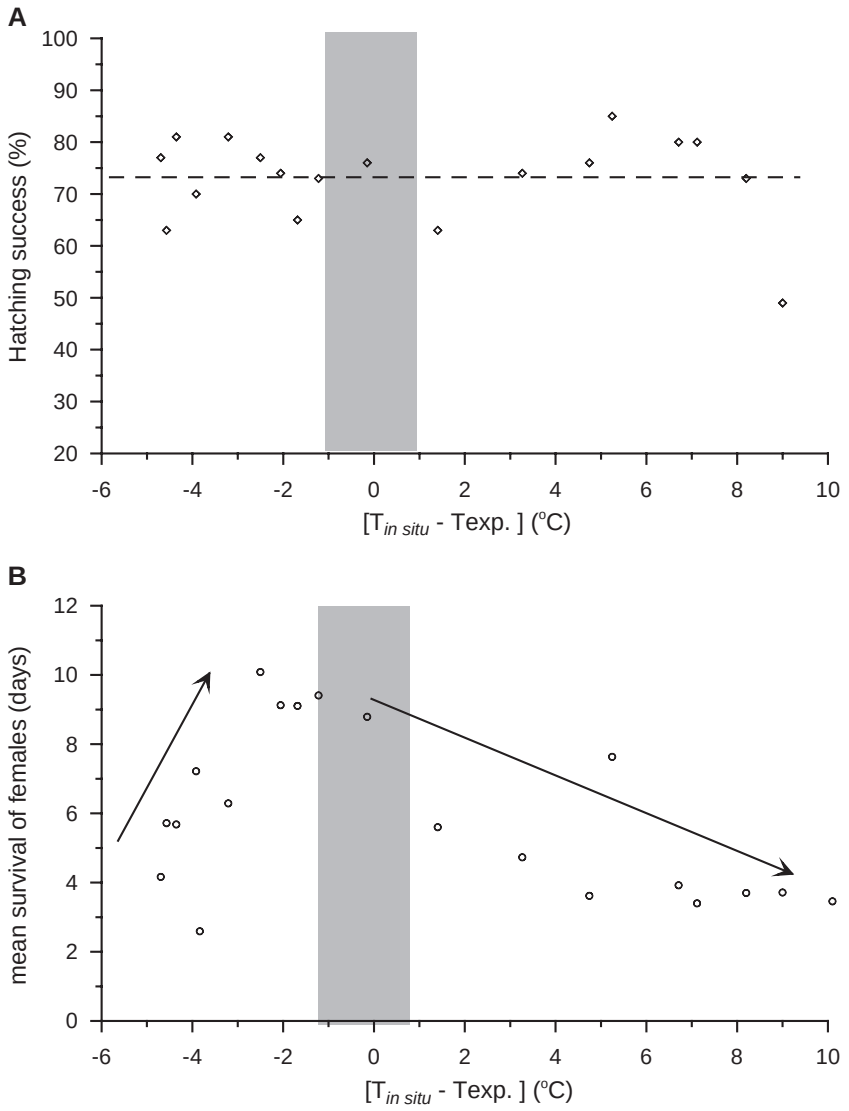

Fig. 7. Hatching success (A) and egg production (B) as function of the difference between the experimental temperature (10 °C) and the in situ temperature during the study period. Grey area shows the period when in situ and experimental temperatures are very close.

tration decreased at the end of February. Afterward, egg production decreased whereas the chlorophyll concentration strongly increased. From April to July most of the biological parameters investigated in this study closely followed the variations of surface chlorophyll concentration (Table 2), excepting the hatching success, which was not affected by chlorophyll concentration variation.

The observed pattern of variation in egg production and chlorophyll *a* concentration (Figs. 2C and 3A) as well as the low significance of the spearman coefficient of correlation (Table 2) indicate that only the second peak of chlorophyll had an impact on *T. longicornis* reproduction. One possible cause is a change in the algal composition (Hopp et al., 1997). The succession of phytoplankton species during the study period showed a bloom of diatoms from February to the beginning of March (Artigas, unpublished data). In March, solitary cells of *Phaeocystis* sp. dominated the phytoplankton community whereas

the proportion of colonies increases in April and May (Artigas, unpublished data). The abundance of diatoms was very low in March compared with *Phaeocystis* sp. but increased in April and May. In June, *Phaeocystis* sp. was essentially found as solitary cell. The presence of other algae has been reported, especially in February and May, such as Dinophyceae and Cryptophyceae, but in lesser proportion (Breton et al., 2000). As copepod ingestion is inherently linked to food quality (Paffenhofer and van Sant, 1985), variation in the relative abundance of different algae is likely to influence *T. longicornis* reproductive activity and survival (Klein Breteler et al., 1990). The decrease in egg production observed in March and April could be related to the dominance of *Phaeocystis* sp. colonies (Artigas, unpublished data). During the third peak of chlorophyll, when the concentration of diatoms has increased, the increase in egg production may suggest a shift in the diet of zooplankton. Egg production was finally independent of the last chlorophyll peak, which was associated with a local bloom of estuarine phytoplankton, brought offshore by tidal advection, and characterised by high sinking rates and poor physiological condition, indicated a chlorophyll increase from the surface to the bottom and a high proportion of phaeopigments, respectively (Seuront et al., unpublished data). It is thus likely that the increase of phytoplankton biomass could not be used by copepods as investment in egg production.

Several studies have shown that *T. longicornis* do not feed on *Phaeocystis* sp., even at high concentrations (Bautista et al., 1992; Hansen and van Boekel, 1991). Other studies showed that copepods grazed on *Phaeocystis* sp. but classified this alga as a poor food source (Cotonnec et al., 2001; Turner et al., 2002). A diet on *Phaeocystis* sp. decreased egg production but not survival and hatching success (Turner et al., 2002), matching our observations during the second peak of chlorophyll in March (Figs. 2C and 3A). Alternatively, Hamm and Rousseau (2003) showed that colonies of *Phaeocystis globosa* contained fatty acids with high nutritional value and are the major food source for copepods and decapods during *Phaeocystis* blooms. In addition, egg production of *T. longicornis* can increase during *Phaeocystis* blooms when *Phaeocystis* sp. is mixed with diatoms even when diatoms are in lesser concentration (Van Rijswijk et al., 1989). Thus, we conclude that the decrease in egg production at the end of March may correspond to an increase of solitary cells of *Phaeocystis* sp. at the beginning of the bloom, while the increase of egg production in late April could correspond to an increase in diatom abundance as well as the increase of colonial forms of *Phaeocystis* sp.

4.2. Effect of in situ temperature on T. longicornis reproduction

While food quantity and quality can affect copepod ingestion and, consequently, their reproductive biology, temperature may also affect metabolic processes like oxygen consumption (Roddie et al., 1984), development (Ban, 1994; Vijverberg, 1980) and reproduction (Abdullahi, 1990).

Seawater temperature increased continuously from 5 °C to 20 °C from February to July. Body size significantly decreased with increasing temperature, as in many ectotherms (Atkinson, 1994; Gillooly et al., 2002). Temperature controls body length through development speed; high temperatures decrease development time and thus reduce the final organism body size (Mauchline, 1998). Temperature also affected hatching time (embryonic development time) that decreased with increase in temperature in our study (Table 1). The observed variations in development time were similar to those found by Halsband-Lenk et al. (2002). They observed a hatching time ranging from 2 to 4 days at 10 °C, which is slightly faster than the values obtained at the same temperature in our study. Longer development times occurred at colder temperatures (6 days at 5 °C) and shorter development at warmer temperatures (2 days at 18–20 °C).

By controlling metabolic rate (Gillooly et al., 2001), temperature can increase reproductive activity up to an optimum (Atkinson, 1994; Ban, 1994). In our study, no clear relationship was found between temperature and reproductive parameters. According to Laabir et al. (1995) and Ianora et al. (1992), no effect of temperature variation was shown on hatching success of *Calanus helgolandicus* and *Centropages typicus*. The most significant correlations between the measured biological parameters and temperature were observed for prosome length (see Table 1). Temperature variations had a significant effect on egg

production from April to July (Table 2), showing a complex interaction between temperature, food availability, egg production and body size, as these two last biological parameters were also strongly correlated (Table 1).

Increasing temperature had a negative effect on *T. longicornis* survival in the Eastern English Channel, because it increased energetic cost. It is worth noting that the survival under starvation conditions is an indirect indication of their internal reserves and their physiological resistance to extreme conditions (Devreker et al., 2004). As a consequence, when the availability and/or quality of food decreased, female survival under starvation also decreased. Temperature and female survival were, however, not always correlated (Table 2). Survival increased in February, whereas temperature showed very little variation. Therefore, the better survival likely reflects better food conditions, a change in food composition or an effect due to the succession of copepod generations. Changes in body size due to temperature variation were also observed from one generation to the next one. Thus, as temperature, body size and female survival are all correlated, a link may exist between the succession of generations and the variation in female survival. Considering the post-embryonic development time found by Klein Breteler and Gonzalez (1984) at four different temperatures (5, 10, 15 and 20 °C), the number of generations occurring during our study period can be estimated. From a generation born at the beginning of our study, six successive generations of 49, 31, 24, 21, 19 and 17 days, respectively, could influence the female survival during the entire study period. However, as the reproduction of *T. longicornis* occurred continuously in Eastern English Channel, we may suspect a high number of cohorts developing over a seasonal cycle. The success of recruitment of these cohorts, depending on several factors controlling the population dynamics of *T. longicornis*, can determine the strength of generations sampled during our study.

4.3. Effect of experimental temperature and sampling location

In the Eastern English Channel temperature can be very variable at different spatial and temporal scales (Brylinski et al., 1984; Seuront et al., 1999). It is thus difficult to reproduce experimentally a seasonal cycle of biologically significant temperature, particularly when experiments overlap between them. As a consequence, in our study the experimental temperature was maintained at 10 °C whatever the in situ temperature. Alternatively, in many other studies females have been incubated at in situ temperature (Burdloff et al., 2002; Ianora et al., 1992; Peterson and Kimmerer, 1994; Van Rijswijk et al., 1989). The value of 10 °C, characteristic of spring conditions, was chosen. Moreover, during summer, when in situ temperature was at least 5 °C above the reference experimental temperature, additional experiments were conducted at 15 °C and 21 °C. We have shown that excepting the summer conditions where the differences between in situ and experimental temperature were above 9 °C, the use of constant temperature did not affect the hatching success. Temperature does not directly influence hatching success (Ban et al., 2000) but has an higher impact on embryonic development time as shown by the correlation between hatching time and temperature in our study (Tables 1 and 2). Copepod females can produce nonviable eggs when they are either not fertilized or when the food quality is very poor (Campbell and Head, 2000; Ceballos and Ianora, 2003). Our results confirmed that experimental temperature may induce serious biases when data of hatching success are compiled from several studies performed at different temperatures. A possible effect of temperature on the limits of tolerance of copepod species should be considered in future studies, particularly in the emerging framework of climatic warming (Halsband-Lenk et al., 2002).

In the Eastern English Channel temperature and chlorophyll *a* concentration usually showed a decreasing gradient from inshore to offshore waters (Brylinski et al., 1984). This gradient is particularly pronounced for chlorophyll *a* concentration (Table 4). On smaller spatial scales such as centimetres chlorophyll *a* concentration is highly variable (Seuront et al., 1999). As the Eastern English Channel is characterised by a megatidal regime with high turbulence and many mixing events (Seuront and Lagadeuc, 2001), copepods can encounter different environmental conditions and a patchy distribution of chlorophyll *a* at several scales during a day. This absence of homogeneity may be

Table 4
Spatial and temporal variation in environmental factors (temperature and mean chlorophyll *a* concentration) and biological parameters (EP, HS, SF, PL and FS; see Table 1) at three different dates during 2003 and between two sampling stations

Sampling date	April 16		May 30		July 3	
Sampling location	Offshore	Inshore	Offshore	Inshore	Offshore	Inshore
Temperature (°C)	8.47	8.92	12.60	13.50	16.70	17.15
Chl. *a* (μg l^{-1})	4.00	14.50	5.80	9.70	3.24	5.80
EP (eggs $female^{-1}$)	13.55 (13.3)	17.90 (15.2)	36.30 (19.7)	37.80 (22.1)	13.30 (8.04)	17.30 (12.4)
SF	70%	60%	85%	75%	85%	82%
HS	70%	65%	75%	75%	84%	83%
PL (mm)	1.05 (0.07)	1.06 (0.06)	1.06 (0.04)	1.06 (0.07)	0.99 (0.07)	1.00 (0.05)
FS (days)	13.30 (5.48)	9.41 (3.45)	6.10 (3.83)	4.73 (1.68)	4.17 (3.14)	3.40 (1.69)

The offshore station is distant from 6 km from our inshore station (see asterisk in Fig. 1). In brackets: standard deviation. Significantly different parameters between two stations are underlined (Mann–Whitney test, α=5%).

a cause for the absence of significant differences between biological parameters of copepods inshore and offshore (Table 4). Thus, a local sampling strategy often used in monitoring programmes is not adapted to quantify the level of heterogeneity and patchiness of chlorophyll *a* distribution, and the potential consequence on biological processes occurring at individual and population levels.

These comparisons show that local variability in chlorophyll *a* concentration has a relatively small impact at the population scale of *T. longicornis* (i.e. kilometres) in the Eastern English Channel. Comparison between many studies on *T. longicornis* reproduction at different geographical localisation (Bautista et al., 1994; Castellani and Lucas, 2003; Fransz et al., 1992; Halsband-Lenk et al., 2004; Van Rijswijk et al., 1989) showed strong variability at a higher spatial scale (100 km and more). Thus it is important to consider the populations of *T. longicornis* developing in the Eastern English Channel, which have not previous been compared to other populations, in the context of large spatial scale variations of copepod production.

4.4. Geographical variability in *T. longicornis* reproduction

The values of temperature during maximum egg production (referred as MEP hereafter) suggest that the optimal in situ temperature for *T. longicornis* reproduction ranges between 7 and 12 °C (Table 5). Compared to other geographical areas, *T. longicornis* in the Eastern English Channel showed the highest MEP; i.e. 75.5 eggs $female^{-1}$ (Table 5). Lowest MEP was found in the Oosterschelde estuary (25 eggs $female^{-1}$; (Van Rijswijk et al., 1989)) and at Plymouth (21 eggs $female^{-1}$; (Bautista et al., 1994)). Chlorophyll *a* concentrations during these MEP periods varied between 2 and 35 μg l^{-1} with minimum levels in the coastal waters off Plymouth

Table 5
Maximum egg production (MEP) of *T. longicornis* in different geographic areas

Geographical localisation	MEP (eggs $female^{-1}$ day^{-1})	*T* (°C)	Chlorophyll concentration	References
Eastern English Channel	75.5	8	15 μg l^{-1}	present study
Belgian Coast	42	7–8	5–10 μg l^{-1}	Antajan (unpublished data)
Oosterschelde estuary (Netherlands)	25	12	10–35 μg l^{-1}	Van Rijswijk et al., 1989
Wadden Sea (Netherlands)	60	7–8	>35 μg l^{-1}	Fransz et al., 1992
German Bight	65.1	7–8	350 μg C l^{-1}	Halsband-Lenk et al., 2004
Eastern Irish Sea	28.05	8	5–15 μg l^{-1}	Castellani and Lucas, 2003
Plymouth (Western English Channel)	21	10–11	2–3 μg l^{-1}	Bautista et al., 1994

Temperature (*T*, °C) and chlorophyll *a* concentration are given for the period of maximum egg production.
Chlorophyll concentration in Halsband-Lenk et al. (2004) is given as μg of carbon per litre.

(Bautista et al., 1994) and a maximum in the Wadden Sea (Fransz et al., 1992). A similar study conducted in the Southern Bight of the North Sea, the closest area to our sampling location, showed a peak of egg production in March as well as a decrease in egg production during the maximal chlorophyll concentration in April (Antajan, unpublished data). This peak was identified as the *Phaeocystis* sp. dominated bloom.

Variation of chlorophyll concentration and MEP between those different geographical localisations do not show any consistent pattern. However different reasons may explain the absence of relationship. First, chlorophyll concentration was significantly lower in the Southern Bight of the North Sea, representing lower resource availability. Second, the maximal chlorophyll concentration may be related to an increase in the concentration of algae with low nutritive value, such as *Phaeocystis* sp. in the single-celled state. As a consequence, high levels of reproductive activity are likely to occur before or after the maximum chlorophyll concentration when better food is available and/or more nutritive. Phytoplankton species composition can differ in each area and thus have different effects on *T. longicornis* reproduction even at similar concentrations. Finally, interannual differences between spring blooms can depend on large scale and local climatic conditions (Seuront and Souissi, 2002) as well as the level of eutrophication (Fransz et al., 1992). Future surveys devoted to the reproductive biology of *T. longicornis* should thus take into consideration both the quality and the quantity of phytoplankton assemblages.

5. Conclusion

This was the first study of *T. longicornis* egg production in the Eastern English Channel conducted during and after a phytoplankton spring bloom, and has shown that *T. longicornis* productivity is very high as compared to other geographical areas, where it is a dominant species. Its maximum levels of productivity occurred in the middle of March before the spring phytoplankton bloom was dominated by *Phaeocystis* sp. During this bloom, the chlorophyll concentration reached 35 μg l^{-1}, whereas the mean egg production decreased from 75.5 to 18 eggs $female^{-1}$ in mid-April. However, the *T. longicornis* population was not strongly negatively affected during this period, as the survival of females was maximal. Moreover, a second period of high productivity arose in May, when chlorophyll concentration was highest. The increase of temperature from February to July induced a decrease of female body size. Temperature affected hatching time (decreasing) and percentage of spawning female (increasing) only between April and July. Most of these biological parameters are influenced by both temperature and chlorophyll concentration and by other biological parameters (e.g. egg production versus body size). Consequently, it is difficult to distinguish the effect of each of these parameters from in situ studies. Experimental studies under controlled conditions are necessary to identify the effects of both temperature and food quantity and quality on *T. longicornis* in the Eastern English Channel, in order to improve biogeochemical models and the parameterisation of secondary production. Our study addressed the key question of the use of constant experimental temperature. As the temperature is one of the most significant external factors on several studies, both experimental and in situ temperatures and the experimental design should be presented carefully in future studies. We showed here that the highest differences between in situ and experimental temperature (around 10 °C) affected some reproductive parameters (i.e. hatching success). When this difference of temperature was low, copepods showed a high capacity for physiological adaptation. The study of the real patterns of temperature variation in the field, known to be very variable in megatidal seas (i.e. English channel), should also be considered in building future monitoring programmes.

Acknowledgements

This work is a contribution to programme CPER "Contrat Plan Etat Region" and PNEC "Chantier Manche Orientale et Sud mer du Nord". We thank C. Lachèze, G. Flamme and C. Carme for their contribution to additional experiments. Thanks are due to G. Leignel and C. Daullet, crew of the RV "Sepia II". We thank M. Priem, E. Lecuyer and D. Menu for their help during this study. We are grateful to Dr. G. Beaugrand for his comments, which improved the

manuscript. We thank Dr. F. Artigas for providing the necessary information on phytoplankton species succession. We also thank J.R. Seymour and Dr. R.L. Waters who kindly improved the English. Two anonymous reviewers are also acknowledged. **[SS]**

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