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Egg production and hatching success of *Temora longicornis* (Copepoda, Calanoida) in the southern Gulf of St. Lawrence

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ABSTRACT: Egg production rate (EPR) and subsequent egg-hatching success of *Temora longicornis* from the southern Gulf of St. Lawrence were measured in the laboratory and at sea during 2 cruises in late June and early July of 2000 and 2001. A quantitative, functional Ivlev relationship between EPR, food concentration (µg C l^{-1}) and temperature was fit to the laboratory results. This relationship can serve as a template for expressing environmental control of *T. longicornis* egg production in models of the species population dynamics. Among the findings was a very low EPR at high temperature (18°C) when food was limiting (<200 µg C l^{-1}). The EPR of *T. longicornis* in the southern Gulf of St. Lawrence in early summer varied as a function of chlorophyll *a* concentration (integrated 0 to 50 m), and corresponded well with the functional laboratory relationship using a carbon/chlorophyll *a* conversion factor of 80. Mean hatching success in the laboratory was 42.8% for experimental temperatures <14°C, but declined dramatically to 7.5% at temperatures over 14°C. No relationship between hatching success and food concentration was observed. In the southern Gulf of St. Lawrence in late June, hatching success varied between 0 and 56% for mean temperatures between 3.3 and 10.9°C (median 6.6°C). While the presence of resting eggs at this time of year is the most probable explanation of our observations of low hatching success, other factors that may inhibit egg hatching, including methodology, insufficient fertilization and food quality, may also be implicated. We conclude that for *T. longicornis*, EPR is food-limited in early summer in this region. Comparison with other studies indicated that environmental controls on fecundity of *T. longicornis* may differ among regions where this species is the dominant copepod.

KEY WORDS: Copepod · *Temora longicornis* · Egg production rate · Hatching success · St. Lawrence

INTRODUCTION

The neritic copepod *Temora longicornis* is an important component of the mesozooplankton in the shallow southern Gulf of St. Lawrence (Lacroix 1967, Lacroix & Filteau 1971). *T. longicornis* is frequently the numerically dominant copepod in early summer (Castonguay et al. 1998) and can maintain very high abundances well into autumn (Roy et al. 2000). *T. longicornis* is prominent in the southern Gulf during early development of Atlantic mackerel and other fish species, for which its naupliar stages constitute a significant portion of the larval diet (Laroche 1982, Peterson & Ausubel 1984, Ringuette et al. 2002).

The egg production rate (EPR) and subsequent egg hatching success of *Temora longicornis* are fundamental not only for the estimation of the species' contribution to prey for fish larvae in the southern Gulf, but also for the accurate characterization of *T. longicornis* population dynamics. Spatially explicit, coupled, physical-biological models that include populaton dynamics of key species in the food web will be useful in the diag-

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nosis and prediction of fish habitat quality forced by climate-induced physical and ecological changes in the region (Runge et al. in press).

Food and temperature are well known as the main factors driving copepod fecundity (e.g. Poulet et al. 1995, Calbet & Agusti 1999). Studies of egg production of *Temora longicornis* in coastal environments (Peterson 1985, Kiørboe & Johansen 1986, Peterson & Bellantoni 1987, Fransz et al. 1989, Dam & Peterson 1991, Peterson et al. 1991, Peterson & Kimmerer 1994, Halsband & Hirche 2001) have shown that mean EPR of *T. longicornis* populations fluctuate between 0 and 55 eggs female^{-1} d^{-1}. While some studies indicate that these fluctuations are generally related to changes in food concentration, as estimated by chlorophyll *a* (chl *a*) (in particular the >10 µm size fraction) (Long Island Sound: Peterson & Bellantoni 1987), other studies have concluded that temperature controls egg production by influencing adult body size and that food is not limiting (North Sea: Halsband & Hirche 2001). It thus appears that environmental controls of *T. longicornis* fecundity differ among regions where *T. longicornis* is present, i.e. from the Gulf of Gascoigne in the SE Atlantic to the Gulf of St. Lawrence in the NW Atlantic. However additional interannual differences in control within regions cannot be ruled out.

The timing and success of hatching of *Temora longicornis* eggs are equally important for the accurate assessment of population growth rate and abundance of nauplii, which comprise food for early life stages of fishes. *T. longicornis* is known to produce both subitaneous eggs and resting eggs. The latter may remain dormant on the sediment surface for long periods, and are presumably stimulated to hatch by environmental conditions propitious for nauplii survival in the water column (Lindley 1990, Castellani & Lucas 2003). Other environmental influences on hatching success may include food quality, which can influence egg viability. Maternal assimilation of aldehydes in diatoms (Miralto et al. 1999), or a deficit of fatty acids or other nutritive material in the maternal diet (Jonasdottir et al. 1998), could affect embryogenesis. Although field observations have revealed no relation between diatom concentration and hatching success (Irigoien et al. 2002), there is still no satisfactory explanation for the discrepancy between field and laboratory results (e.g. Paffenhöfer 2002), which include inhibition of hatching by the congener *T. stylifera* (Ianora & Poulet 1993).

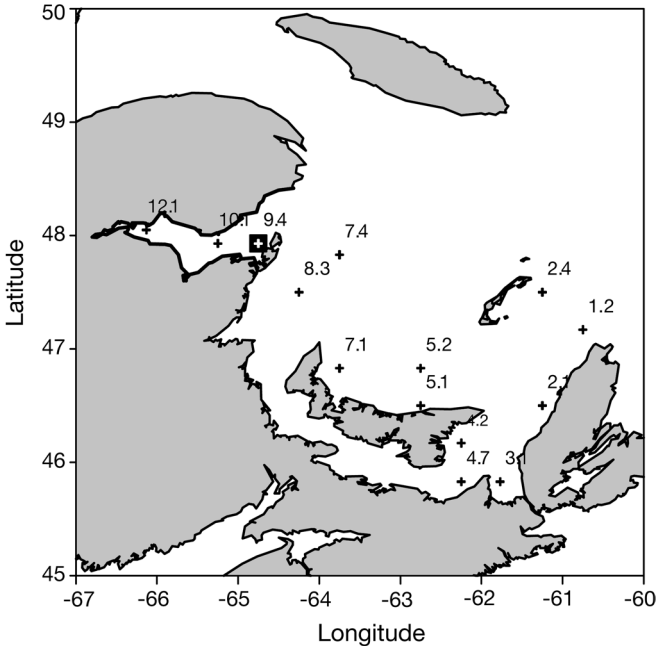

Fig. 1. Stations in southern Gulf of St. Lawrence sampled for *Temora longicornis* used in laboratory (✚, Baie des Chaleurs) and shipboard (+) experiments

Until the present study, egg production and hatching success of *Temora longicornis* had not been studied in the southern Gulf of St. Lawrence, a subarctic, seasonally ice-covered sea with strong vertical gradients in temperature. As part of an investigation into the ecological role and population dynamics of *T. longicornis* in this region, we herein characterize the effects of regional environmental variables on *T. longicornis* fecundity. We present the results of laboratory experiments showing effects of food and temperature on EPR and egg hatching success. We use the laboratory data to establish a quantitative relationship between food concentration, temperature and EPR that can serve in model descriptions of *T. longicornis* in the Gulf of St. Lawrence and as a template for expressing environmental control of *T. longicornis* in other regions. Finally, we present measurements of EPR and hatching success of *T. longicornis* at several stations in the southern Gulf of St. Lawrence in early summer and apply the laboratory-derived relationships to investigate whether food limitation of EPR is an important factor controlling production in this species in early summer in this region.

MATERIALS AND METHODS

Laboratory experiments

Experiments took place at the 'Aquarium and Marine Center' of Shippagan, New Brunswick, Canada. Live copepods were collected at a near shore station (Fig. 1) in the Baie des Chaleurs, Canada (latitude 47° 93′, longitude: –64° 75′, 17 m depth) on May 2, 2001, using a 1 m diameter, 158 µm-mesh plankton net gently towed from the bottom to the surface. The net catch was diluted in a 50 l cooler filled with surface

water. Several hundred adult *Temora longicornis* were sorted during the 2 d following collection; the experiment was performed using individuals originating from a single catch. The copepods were placed in groups of 5 individuals at 2°C (temperature during sampling) in Petri dishes (50 ml) containing filtered seawater and the dinoflagellate *Oxyrrhis marina* at approximately 100 cells ml^{-1}. Females and males were then acclimated separately for 1 wk prior to the experiment, during which time they were acclimated (4°C d^{-1}) to their assigned temperature in the presence of food (~100 cells *O. marina* ml^{-1}).

We conducted cross-incubation experiments at 4 food concentration levels (500, 1000, 2000 cells ml^{-1} and a maximum comprising undiluted cultures of *Oxyrrhis marina* that varied between 2500 and 4000 cells ml^{-1}) and 5 temperatures (2, 6, 10, 14 and 18°C). The experimental temperatures covered the range in spring/summer in the southern Gulf of St. Lawrence, i.e. 2 to 18°C (Koutitonsky & Bugden 1991). To avoid large temperature variations, the incubation containers were placed on a temperature-controlled aluminum plate immediately after removal from the incubator.

Each experiment was conducted in an 'egg separator', a clear PVC tube closed at one end by a 250 µm Nitex screen and immersed in a 2 l beaker to avoid egg cannibalism (Runge & Roff 2000). Each separator contained 900 ml seawater, into which 10 female and 10 male *Temora longicornis* were transferred. The addition of males allowed re-mating (Ianora et al. 1989). There was 1 experimental chamber (i.e. 'separator') for each treatment (total of 20 chambers).

The heterotrophic dinoflagellate *Oxyrrhis marina* was used as food for *Temora longicornis*. *O. marina* is a motile dinoflagellate of high nutritional value for copepods (Klein Breteler 1980, 1990, Klein Breteler et al. 1999), and can be maintained at an almost homogeneous concentration in experimental containers. The strain used was provided by the Bigelow Laboratory Center for the Culture of Marine Phytoplankton (Boothbay Harbor, Maine, USA) and grown in the presence of the flagellate *Isochrysis galbana* (also from Bigelow), as described by Pelegri et al. (1999). The concentration of algae in the main culture tank (both *O. marina* and *I. galbana*) was checked daily using a Coulter Counter particle analyzer. Dilutions were prepared to provide nominal food concentrations of 500, 1000, and 2000 cells ml^{-1}, as well as a maximum (undiluted culture) concentration varying between 2500 and 4000 cells ml^{-1}. The maximum experimental cell concentrations were similar to *in situ* phytoplankton cell concentrations encountered in highly productive areas (Levasseur et al. 1992, Ohman & Runge 1994). Mean algal concentrations during incubations were calculated with the equations of Frost (1972). We used the conversion factor (196×10^{-6} µg C $cell^{-1}$) of Pelegri et al. (1999) to convert cell numbers to carbon concentration. Maximum carbon concentration was maintained at about 500 µg C ml^{-1}.

The acclimatization period was long enough for females to spawn any residual fertilized eggs present at the time of capture. The experiment began with the addition of males to incubation chambers containing females to initiate fecundation and subsequent egg laying. The incubations lasted 7 d. Copepod mortality was checked daily. To maintain a sex ratio of 1:1, if 1 or more females had died an equivalent number of males were removed. If 1 or more males had died, however, an equivalent number of new males were transferred to the experimental chamber from a separate pool of males maintained with food at the relevant experimental temperature. To correct calculations of EPR, we assumed that individuals found dead had died half way through the time period between checks. After quickly transferring copepods to a new medium, the eggs in the original medium were gently filtered onto a 50 µm Nitex screen, counted, and then incubated in 5 ml Petri dishes at the same experimental temperature. The eggs have a diameter of 70 to 80 µm, are dark brown to black in color and often adhere together at the bottom of the Petri dish. Incubation duration varied according to the experimental temperature, following the equation of McLaren (1978) for mean hatching time. To end an experiment, white vinegar was added to the chamber and the fixed nauplii were counted using a Wild stereomicroscope. Acetic acid was used instead of formaldehyde because it darkens nauplii, making them easier to count, and is not toxic to humans.

In the data analyses, temperature was a fixed variable, and precautions were taken to minimize variation to <2°C during manipulation. However, the food supply, defined as *Oxyrrhis marina* carbon concentration, varied from day to day with the daily change in the incubation medium (Table 1). Since *Temora longicornis* can assimilate food over short time scales (<24 h) (Smith & Hall 1980, Tester & Turner 1990), food concentration was considered as a continuous variable rather than being partitioned into the 4 initial nominal concentrations (500, 1000, 2000, and 2500 to 4000 cells ml^{-1}).

Shipboard experiments

Temora longicornis EPR was measured in the SW Gulf of St. Lawrence (Fig. 1) in late June and early July of 2000 and 2001 during the annual mackerel stock assessment cruise on the CCGS 'Martha L. Black'. Zoo-

Table 1. Variation (daily mean ± SD, µg C l^{-1}) of food concentrations during laboratory incubation experiments for each treatment during the 4 d (Days 3 to 6) selected for statistical analyses, calculated by equations of Frost (1972). Max.: 2500 to 4000; 1/2: 2000; 1/4: 1000; and 1/8: 500 cells ml^{-1}

Food treatment	Temperature (°C) 2	6	10	14	18
Max.	332.6 ± 153.4	225.1 ± 85.4	320.3 ± 136.5	302.0 ± 81.2	429.3 ± 108.2
1/2	208.8 ± 23.2	162.1 ± 23.5	269.8 ± 61.8	264.7 ± 52.7	342.3 ± 39.9
1/4	100.4 ± 11.5	89.1 ± 13.6	112.9 ± 36.0	175.8 ± 58.5	211.5 ± 31.7
1/8	55.2 ± 14.2	52.8 ± 11.4	70.5 ± 13.7	81.0 ± 16.4	119.9 ± 32.1

plankton was collected with a gentle vertical net tow (158 µm mesh) from depth (varying from near 150 m for a few stations to <20 m). We immediately sorted 30 female *T. longicornis* which were individually incubated for 24 h in filtered seawater (FSW) on 9 occasions in 2000 (in 20 ml vials) and on 8 occasions in 2001 (in 50 ml Petri dishes). Incubation temperature was 11°C in 2000 and 8°C in 2001, in accordance with *in situ* temperature profiles obtained at the beginning of each cruise. After 24 h, females were removed from the containers and, for some observations (Table 2), prosome length was measured. Eggs were counted in the container (i.e. without manipulation) and subsequently maintained in the same container at the incubation temperature for 4 to 6 d to measure hatching success. We also recorded several environmental characteristics at each station with a CTD rosette. Water samples for chlorophyll analysis were taken at depths of 0, 5, 15, 25 and 50 m (the latter near the sea bottom). Chl *a* concentration was determined by the method of Welschmeyer (1994). Integrated values used hereafter are limited to depths above 50 m, since deeper stations were rare and since Lacroix & Filteau (1971) showed that *T. longicornis* concentrates above this depth.

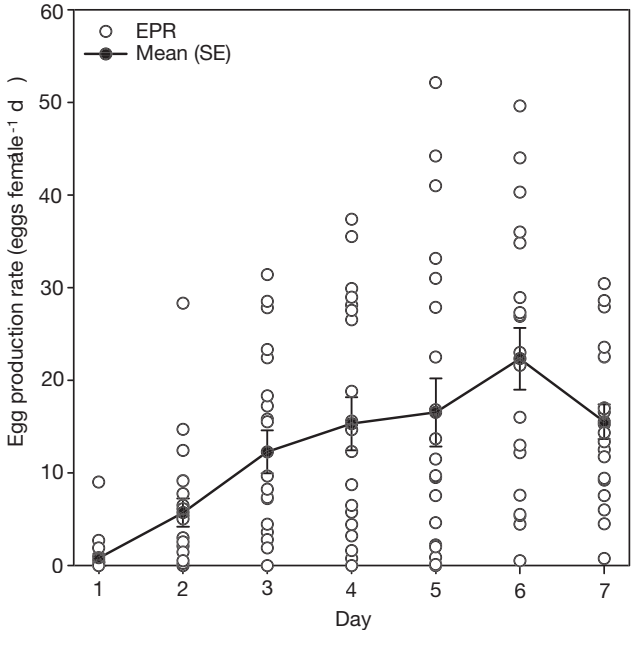

Fig. 2. *Temora longicornis*. Time course of egg production rates (EPR) during laboratory incubation experiments; all temperature and food treatments pooled

RESULTS

Laboratory studies

There was a temporal pattern in daily egg production over the 7 d experiment (repeated-measures ANOVA, $p < 0.0001$). Fig. 2 shows increasing means from Days 1 to 3, followed by more constant levels between Days 3 and 7. This suggests a period of acclimatization followed by a period of optimal production under the experimental conditions. An ANCOVA (EPR against day of experiment, with carbon food concentration as covariate) showed time to be an insignificant factor ($p = 0.32$) over 4 consecutive days (Days 3 to 6). Variations in EPR during this 4 d period were explained by daily variations in carbon concentration ($R^2 = 0.40$, $p < 0.0001$). Mortality of experimental females was substantially higher and EPR lower on Day 7 of the experiment, especially at 14 and 18°C. We attributed this result to the onset of senescence in some females, and therefore did not include Day 7 results in subsequent analyses. We

Table 2. *Temora longicornis*. Mean prosome length (PL, mm) of females in laboratory and *in situ* incubation experiments. Stations numbered as in Fig. 1

Stn	Sampling date (dd/mm/yy)	N	Mean PL	SD
Laboratory				
9.4	02/05/2001	40	1.012	0.051
In situ				
1.2	28/06/2000	12	1.021	0.124
3.1	29/06/2000	12	0.837	0.112
7.4	01/07/2000	12	0.972	0.097
2.1	13/06/2001	29	0.944	0.085
2.4	13/06/2001	55	0.920	0.084
4.1	14/06/2001	29	0.982	0.083
4.2	14/06/2001	59	0.984	0.068
5.1	14/06/2001	28	0.893	0.103
8.3	16/06/2001	58	0.947	0.082
9.4	17/06/2001	60	0.820	0.083
10.1	17/06/2001	26	0.844	0.076

assume that the variance resulting from repeated measurements of the same individuals over time is very similar to the variance that would be obtained using replicates containing different individuals measured on the same date (e.g. Razouls et al. 1986, Peterson 1988, J. A. Runge pers. obs.).

The relationship between EPR and mean food concentration for all temperatures combined was highly variable (Fig. 3). When EPR is examined in relation to food at each experimental temperature separately (Fig. 3), however, a substantial portion of the variability in the overall relationship (Fig. 3) is revealed. At 2°C (Fig. 3), there was no significant relationship between carbon concentration and EPR, which rarely exceeded 10 eggs female^{-1} d^{-1}, even for food concentrations >100 µg C l^{-1}. At 6 and 10°C, the data follow an Ivlev relationship (Parsons et al. 1967). At higher temperatures, we did not capture the actual maximum EPR within the range of experimental carbon concentrations. There was a tendency (starting at 2°C) for maximum EPR (EPR_{max}) and the food concentration at which EPR is 90% of EPR_{max} to increase with increasing temperature.

To model the response of *Temora longicornis* EPR to variations in food concentration and temperature, we followed the method of Thébault (1985). We used an Ivlev equation as a template, whose parameters were functions of temperature:

$$EPR(C,\theta) = \mu(\theta) \times (1 - \exp\{-\alpha(\theta) \times [C - C_0(\theta)]\})$$

where C is food concentration (here µg C l^{-1}), C_0 is a scaling factor, representing the threshold food level at which egg production commences; the relationships of the 3 parameters to temperature, θ, are shown in Fig. 4.

For 14 and 18°C we made the assumption that µ is represented by the mean maximum EPR_{max} observed in our experiments at these temperatures. We fixed the threshold parameter (C_0) at zero at 14°C, as there was no statistical justification for making it different from zero. Comparison with the regression lines fitted to the data is presented in Fig. 3.

For the 5 experimental temperature treatments, the Ivlev regression at 18°C was the only relationship with a threshold concentration significantly greater than zero. The experimental data for the 18°C treatment fall into 2 groups (Fig. 3f): (1) at food concentrations <250 µg C l^{-1}, EPR were even lower than at 2°C; (2) at food concentrations >250 µg C l^{-1}, EPR were high (mean = 36.32 eggs female^{-1} d^{-1}) and comparable to the EPR_{max} observed at 10 and 14°C.

Hatching success in the laboratory experiments was variable. Mean hatching success varied significantly between days (repeated-measures ANOVA: $p = 0.0387$), but there was no significant pattern (first- and second-order polynomial tests $p = 0.0833$ and $p = 0.5621$, respectively). There was no linear or non-linear relationship between hatching success and the food concentration fed to adults (Fig. 5). Hatching success across experimental temperatures was similar (Fig. 5), except at 18°C, at which temperature hatching was very low (7.5%) and significantly different from our other observations (Tukey's HSD-test). The overall mean and median hatching success across all days of the experiment, excluding data at 18°C, was 42.8 and 44.7%, respectively.

In situ observations

The EPR and hatching success of *Temora longicornis* were measured in the southern Gulf of St. Lawrence, during late June and early July (Table 3). EPR ranged from 3.3 to 22.2 eggs female^{-1} d^{-1} (mean = 11.8). Hatching success was zero during 2000, but ranged from 31 to 56% (mean = 44.6%) in 2001. EPR in coastal areas of the eastern southern Gulf and around the Magdalen Islands were 2 times higher than rates observed in the central southern Gulf and inside the Baie des Chaleurs, where the lowest EPR was measured. The spatial distribution of hatching success was more homogeneous.

Integrated temperature and chl *a* concentration were insufficient, separately or together, to explain variations in EPR. However a simple plot of *in situ* EPR against chl *a* concentration revealed a highly influencing outlier. This point was a station (Stn 12.1; Fig. 1) in the most western part of the Baie des Chaleurs, at the mouth of the Restigouche River. With the lowest salinity (25.4 psu) and a high temperature (with stratification), this station was indicative of a true estuarine environment, whereas all other stations represented coastal or oceanic water. We therefore decided to remove this station from further analyses, as it was ecologically apart from the other stations. Chl *a* concentration was then significant by itself ($R^2 = 0.28$, $p < 0.0001$) in explaining variations in EPR. Integrated temperature, however, still had an insignificant effect on EPR. An Ivlev equation did not provide a better fit ($R^2 = 0.27$) of the EPR–chl *a* relationship, indicating that a maximal EPR was not achieved and implying that the observed *in situ* EPR values were food limited.

Comparison between *in situ* and laboratory results

To compare *in situ* and laboratory results, we converted *in situ* pigment concentrations to carbon concentrations. This is problematic when measurements are made over a wide study area such as the present one, where phytoplankton composition is likely to vary (Bérard-Therriault et al. 1999). Classically, a carbon:

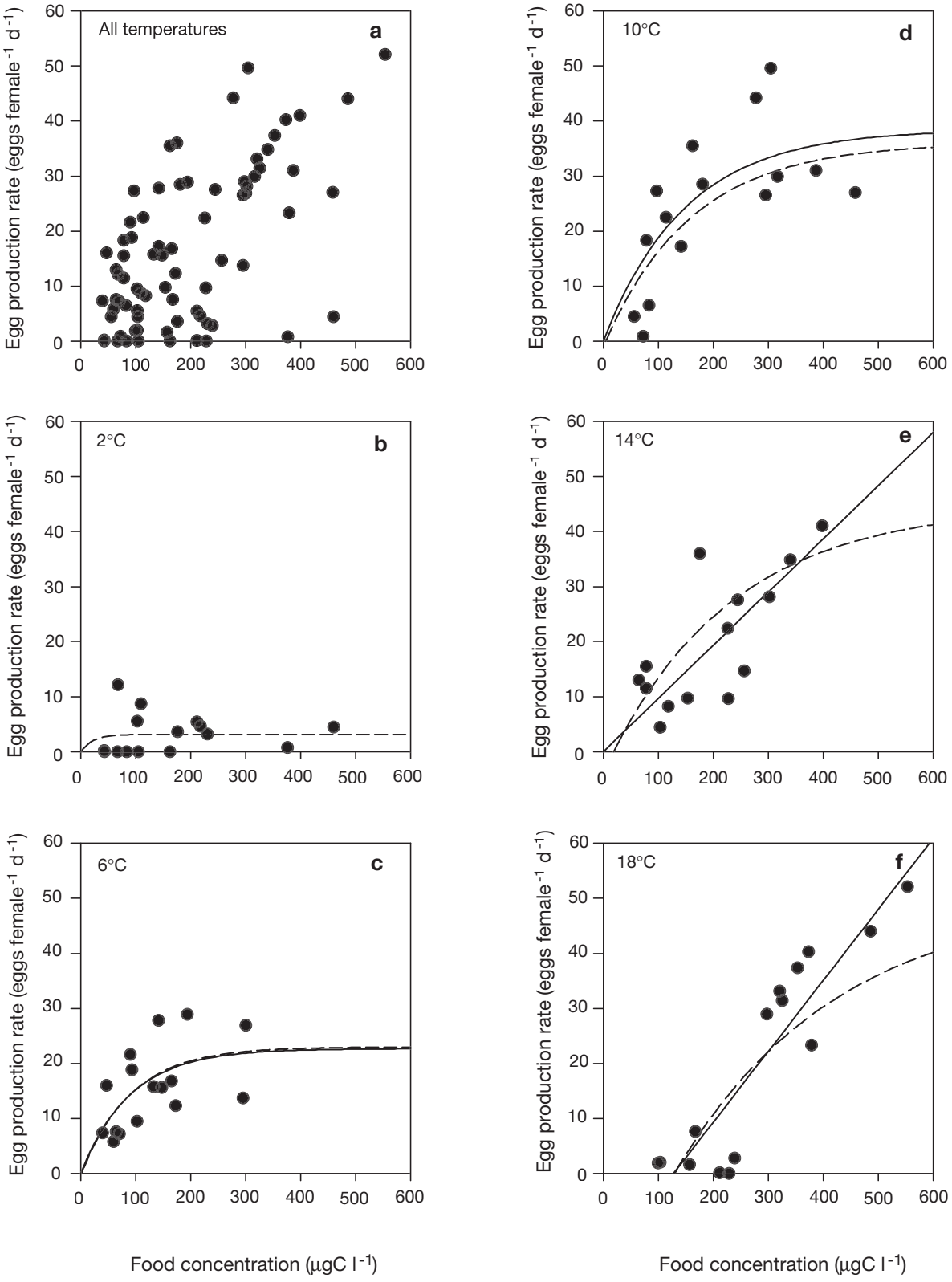

Fig. 3. *Temora longicornis*. Relationship between food concentration and laboratory EPR. Continuous lines are regression fits: 6°C, EPR = 22.67(1 – exp[–0.011*C*]), R^2 = 0.35; 10°C, EPR = 38.48(1 – exp[–0.007*C*]), R^2 = 0.58; 14°C, EPR = 0.097*C* (R^2 = 0.54, $p < 0.0001$); 18°C, EPR = 0.129*C* – 16.5 (R^2 = 0.82, $p < 0.0001$), where *C* = food concentration. Dotted lines are Ivlev model fits, using parameter relationships in Fig. 4

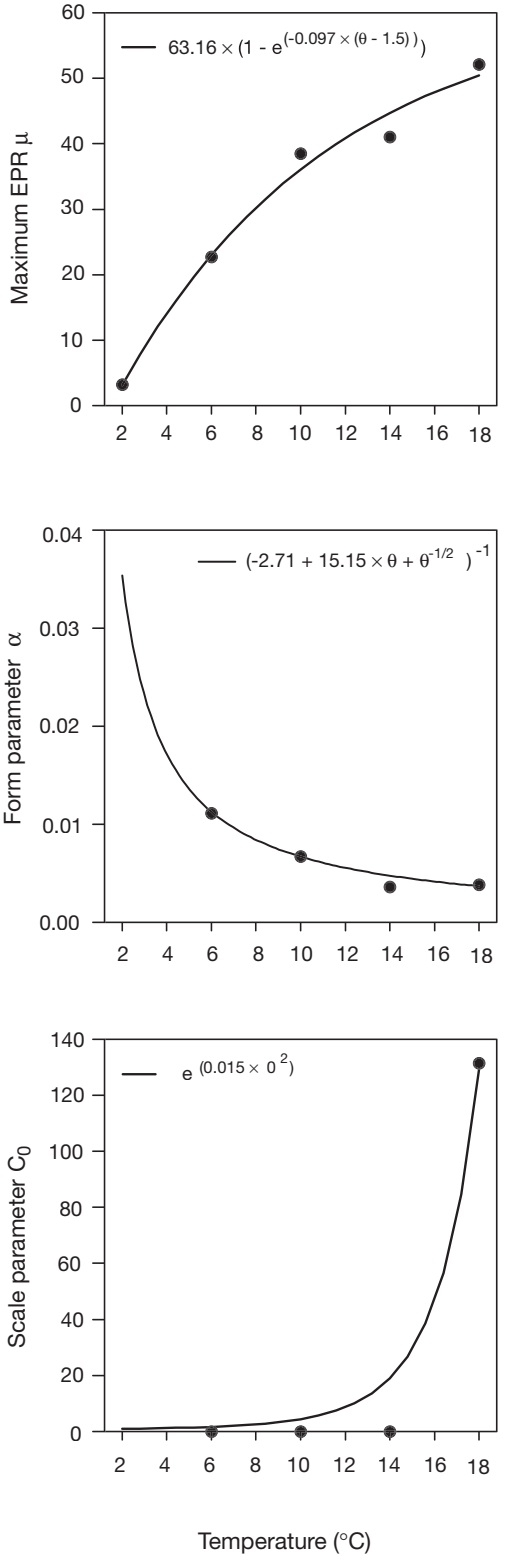

Fig. 4. *Temora longicornis*. Temperature dependence of parameters in modified Ivlev model of EPR as function of food and temperature, where scaling factor C_0 represents food threshold at which egg production begins. Data points represent best parameter fits to data at each temperature

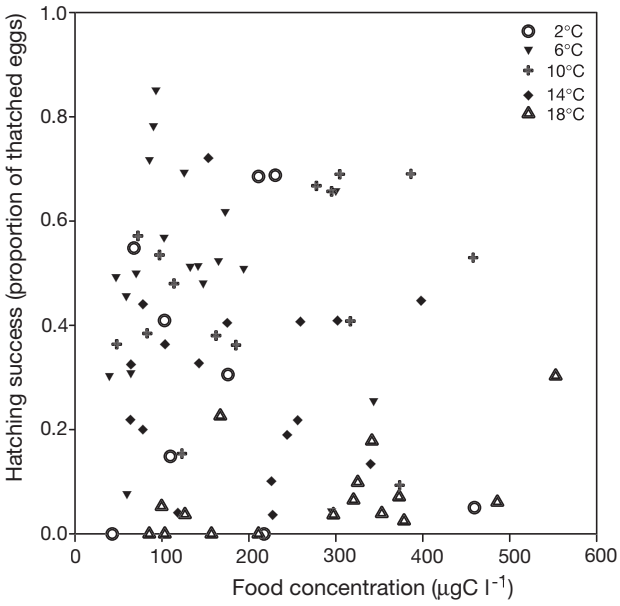

Fig. 5. *Temora longicornis*. Relationship between food concentration and hatching success in laboratory experiment. Hatching success of eggs produced by females incubated at different temperatures is represented by different symbols

chl *a* ratio of 50 is characteristic of a diatom bloom, whereas a conversion factor of 100 is representative of an environment dominated by smaller phytoplankton cells. We used the conversion factor of 80 employed by Roy et al. (2000) during summer cruises in the southern Gulf of St. Lawrence to compare *in situ* and laboratory

Table 3. *Temora longicornis*. *In situ* mean egg production rate (EPR, eggs female^{-1} d^{-1}) and hatching success (HS, %). No standard deviations for HS as eggs were pooled; HS was zero in 2000

Stn	Sampling date (dd/mm/yy)	N	EPR	SD	HS
1.2	28/06/2000	30	10.6	8.6	–
2.1	13/06/2001	27	12.6	12.6	41
2.4	28/06/2000	30	21.5	16.2	–
2.4	13/06/2001	30	22.2	23.2	49
3.1	29/06/2000	29	13.2	11.5	–
4.1	14/06/2001	29	18.5	15.5	56
4.2	29/06/2000	30	14.3	18.6	–
4.2	14/06/2001	29	15.9	17.3	50
5.1	14/06/2001	30	13.8	17.8	48
5.2	30/06/2000	30	3.3	6.5	–
7.1	01/07/2000	30	4.3	8.5	–
7.4	01/07/2000	30	4.5	7.7	–
8.3	16/06/2001	28	8.2	13.1	31
9.4	02/07/2000	30	12.7	16.5	–
10.1	17/06/2001	26	6.5	9.3	37
12.1	02/07/2000	30	7.3	9.4	–

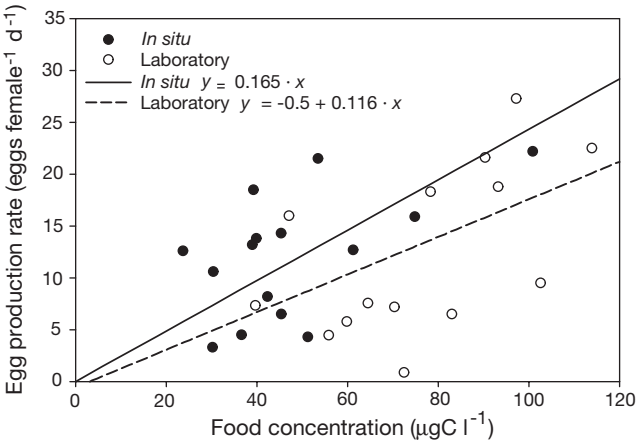

Fig. 6. *Temora longicornis*. Comparison of relationships between *in situ* and laboratory egg production rate and carbon concentration. *In situ* chlorophyll *a* values converted to carbon values using carbon:chlorophyll *a* ratio of 80

results. The range of available *in situ* food using this conversion factor was 23 to 100 µg C l^{-1} (mean concentrations over the top 50 m of the water column). To obtain similar variances for the environmental conditions in early summer in the southern Gulf, we drew from the laboratory results for carbon concentrations <120 µg C l^{-1} and for temperatures of 6 and 10°C.

In this range of food concentrations and temperatures, *Temora longicornis* EPR, both *in situ* and in the laboratory, fell within the linear part of the observed relationship to food concentration. Fitted Ivlev equations were not more significant than the linear regressions. The effect of carbon concentration on EPR always remained statistically discernible ($p < 0.0001$). Although the *in situ* and laboratory carbon concentration range did not perfectly overlap, Fig. 6 shows that the results were in good agreement. We did not pursue the statistical analysis further, since the experimental methodologies in the laboratory (10 pooled females) and *in situ* (individual incubations) measurements differed.

The *in situ* hatching success data were too sparse to allow a complete statistical analysis. The median laboratory and *in situ* results for 2001 (49.3 and 48%, respectively) were similar.

DISCUSSION

Egg production rate as a function of food and temperature

Our laboratory results indicate that from the moment they encounter mating partners and a high food supply, *Temora longicornis* females require an acclimatization period of approximately 3 d to achieve temperature-specific egg production (Fig. 2). This is consistent with laboratory experiments by Razouls et al. (1986), who found that egg production of female *T. stylifera* increased over a period of several days when they were transferred from a sparse to an abundant food medium. We interpret the lag observed herein to time needed for maturation of developing oocytes and consequently for the gonad state to equilibrate with the new food conditions (e.g. Plourde & Runge 1993). However, following this initial acclimatization period, we assumed (based on Smith & Hall 1980), a more rapid response of EPR to daily fluctuations in the nominal concentrations of the various food treatments (Table 1).

The modeled EPR using parameter-temperature relationships (Fig. 4) replicate the laboratory observations of egg production reasonably well (Fig. 3). As we did not observe a saturation effect for EPR in the range of food concentration provided at 14 and 18°C, the values of µ used to fit the model equation are fixed to the actual maximum value of the EPR distribution at these temperatures. This approach improves our capacity to generalize the results by means of numerical modeling. It provides a unique formulation which is able to handle the boundary effects while exploring the whole range of environmental conditions (i.e. temperature and food concentration) encountered by these copepods. Further study of EPR_{max} would, however, be needed to adjust or confirm parameterization to accurately predict µ at very high ambient temperatures.

When food concentration is lower than the critical (i.e. limiting) concentration, our results indicate that a temperature increase between ca. 3 and 13°C does not automatically augment egg production of *Temora longicornis*. At limiting food concentrations, any increase in ingestion rate with increasing temperature is likely to be used to meet energetic requirements rather than in the production of new material, including eggs (Ikeda et al. 2001). At high temperatures (beginning at around 14°C for *T. longicornis*) and low food supply, the relationship between egg production and food concentration in the southern Gulf appears to undergo a transition phase, during which the investment of ingested material in metabolism increases to the detriment of reproduction. At 18°C and at food concentrations ≲200 µg C l^{-1}, egg production ceases. This suggests that under these environmental conditions, food intake is used only for metabolism (Fig. 3). Under low ambient food conditions, an increase in temperature will have a negligible or negative influence on *T. longicornis* egg production. Food supply is generally limited in natural environments (Hirst & Lampitt 1998), and such a relationship has already been observed for other small-sized species (e.g. *T. stylifera* in Ianora et al. 1989, *Acartia bifilosa* in Koski & Kuosa 1999). However, the optimal temperature for egg production and

the range within which temperature has a reduced influence on EPR are particular to each species. The dramatic fall in the EPR during low food and high temperature conditions could explain why (unless there is a phytoplankton bloom) egg production of *T. longicornis* from Long Island Sound sharply decreases in summer when the temperature exceeds 17°C (Peterson 1985, Dam & Peterson 1993, Peterson & Kimmerer 1994).

Egg production rate in late June and early July in the southern Gulf of St. Lawrence

We first address a potential source of error in measurement of *in situ* EPR of *Temora longicornis* in the southern Gulf, which are based on 24 h incubations in filtered seawater. Saiz et al. (1997) have shown that food conditions during incubation (i.e. filtered seawater, surface seawater or seawater sampled at the chl *a* maximum) influence estimates of *in situ* egg production in a number of small, neritic copepods from the NW Mediterranean, including *T. stylifera*. In their study, the effect was much more marked at 23°C than at 13°C, the lowest temperature. This result may reflect the physiological effects of increased metabolism at higher temperatures. The potential exists, therefore, for our incubation method to have underestimated the actual *in situ* rates of females feeding in higher ambient food conditions. This possible source of error is also present in other published studies of egg production of *T. longicornis*. Bautista et al. (1994), using filtered seawater as the incubation medium, observed a range of EPR from 0 to 21 eggs female^{-1} d^{-1}, very similar to values we measured in the southern Gulf of St. Lawrence. Halsband & Hirche (2001) incubated *T. longicornis* females individually in cell wells filled with 3 ml of 50 µm-screened seawater; as females are capable of clearing a volume of water 1 order of magnitude greater than this in 24 h, these incubation conditions were closer to filtered seawater than to ambient food conditions. They measured rates of <10 to 30 eggs female^{-1} d^{-1} in June and July. Peterson & Bellantoni (1987) incubated individual *T. longicornis* females from Long Island Sound in 1 l bottles filled with 64 µm-screened seawater, and van Rijswijk et al. (1989) incubated approximately 10 females from the Oosterschelde Estuary (Southern Bight of the North Sea) in 1 l bottles of 300 µm-screened seawater, both for 24 h periods; the conditions in these 2 studies may have more closely replicated the ambient food environment than in the present study. EPR in Long Island Sound (New York, USA) reached a maximum of >50 eggs female^{-1} d^{-1} in March during the spring diatom bloom (similar to the maximum rates observed by Halsband & Hirche 2001) and ranged from approximately 5 to 30 eggs female^{-1} d^{-1} in June (Peterson & Bellantoni 1987). In the Oosterschelde Estuary, EPR ranged from 1 to 25 eggs female^{-1} d^{-1} over the 3 yr study of van Rijswijk et al. (1989). Hence, EPR measured in filtered seawater (Bautista et al. 1994, this study) or in conditions of low food concentrations (Halsband & Hirche 2001) are of the same magnitude as rates measured in conditions closer to those *in situ*. Since ambient temperatures (0 to 20°C) in the biogeographic area of *T. longicornis* are usually considerably lower than temperatures in the NW Mediterranean, it may be that the effect of food conditions on the production of eggs during short-term incubations is reduced. While we recommend that future *in situ* incubation studies of *T. longicornis* investigate the effect on egg production of food conditions during incubation, we believe that the use of filtered seawater does not invalidate the application of *in situ* measurements in the interpretation of *T. longicornis*' response to food conditions in the southern Gulf of St. Lawrence.

The similarity between the laboratory and field observations of egg production (Fig. 6) provides further evidence that the measurements at sea represent *in situ* processes. Although carbon concentration is merely an index representing a complexity of factors that together constitute food quality (e.g. Anderson & Hessen 1995, Kleppel et al. 1998, Guisande et al. 2000), the good agreement with the application of a high carbon:chl *a* ratio ($R_{c:chl}$ = 80) corresponds to an environment in which flagellates and ciliates dominate the diet of *Temora longicornis*, as observed in the southern Gulf of St. Lawrence in summer (Vandevelde et al. 1987, de Lafontaine et al. 1991). The estimates of *in situ* carbon were within the limiting range observed in the laboratory experiments. The *in situ* estimates of EPR increased significantly with increasing carbon concentration, indicating that EPR of *T. longicornis* in the southern Gulf were food limited in the early summer of 2000 and 2001.

The relationship of EPR to chl*a* concentration and the conclusion that egg production is food limited are in general agreement with studies of *Temora longicornis* fecundity in Long Island Sound (Peterson & Bellantoni 1987), the Skagerrak (Peterson et al. 1991) and the English Channel (Bautista et al. 1994). In all cases, the threshold concentration at which egg production approached zero was on the order of 0.5 µg chl l^{-1}. Peterson & Bellantoni (1987) found a significant Ivlev relationship of EPR with the >10 µm fraction of chl *a*, with a critical concentration on the order of 5 µg chl l^{-1}; data in the other studies were insufficient for determination of the critical concentration.

The results of our studies contrast with those of Halsband & Hirche (2001) for the southern North Sea, who

concluded that female body size, as a function of temperature during development, rather than present food conditions, was the primary factor controlling egg production of *Temora longicornis* during the spring and early summer. This conclusion was based on correlation analyses that showed a significant relationship between the annual cycle of fecundity and prosome length, but weak and insignificant correlations between EPR and estimated food abundance. While the study of Halsband & Hirche (2001) took seasonal changes in female body size into account (this was not the case in the studies in Long Island Sound and the English Channel: Peterson & Bellantoni 1987 and Bautista et a. 1994, respectively), it did not provide a detailed analysis of the functional relationship between EPR and estimated food abundance. Such analysis might have revealed an Ivlev relationship that would obscure simple correlations between food and EPR. Future investigation of factors influencing *T. longicornis* fecundity will require rigorous analysis of the interaction between temperature, body size and food conditions to accurately evaluate the hypothesis that environmental control of egg production differs among regions of *T. longicornis* presence.

Hatching success

We observed zero hatching success during a 5 d period in late June and early July 2000 in the southern Gulf. Hatching was recorded in 2001, but was still low relative to that of other species (see Irigoien et al. 2002) during field observations conducted during a 5 d period in mid-June 2001 (2 wk earlier than in 2000). Other studies have also found low hatching success in this species. Castellani & Lucas (2003) observed seasonally variable hatching success during a 3 yr study of *Temora longicornis* in the Menai Strait (eastern Irish Sea). They found hatching success minima of 10 to 50% in May to July of each year, and very high (90 to 100%) rates during winter. Using scanning electron microscopy to investigate egg membrane morphology, they confirmed that the low hatching success in May to July was the result of the production of mainly resting eggs during this period, at a time when *T. longicornis* population abundance was highest and the abundance of a major predator, *Pleurobrachia pileus*, was increasing. They found that temperature, photoperiod, or an internal clock were more likely to trigger production of resting eggs than phytoplankton concentration. Other studies, in both the laboratory and field, have also observed low (15 to 45%) mean hatching success (Irigoien et al. 2002, Dam & Lopes 2003), although Tang et al. (1998) found mean hatching success of 70 to 90% for *T. longicornis* in Long Island Sound in March and June.

While the predominance of resting egg production in our study is a reasonable explanation for low hatching success of *Temora longicornis* from the southern Gulf in May and June, such explanation is not unequivocal. At present, the distinction between resting and subitaneous eggs requires examination under a scanning electron microscope (Castellani & Lucas 2003). Other possible causes of low hatching success, either as alternative or confounding sources of variability, need to be considered: (1) there are possible sources of error in methodology. In our study and in the laboratory study of Dam & Lopes (2003) (although not in the study of Castellani & Lucas 2003), gentle wet-sieving was involved in the preparation of eggs for hatching success incubations; this process might have damaged membranes of some eggs used in the incubations and hence have contributed to the non-hatching proportion of our results. (2) We are also uncertain about the quality of the incubation water drawn from the ship's plumbing system in June 2000, which might have contributed to the absence of hatching in that year. (3) Problems with the fertilization of females might have contributed to the low hatching success, since unfertilized eggs were laid in substantial proportions by females of the congener species *T. stylifera* throughout the whole year (Ianora et al. 1989). There is lack of information about male reproductive physiology and behavior, which can influence hatching success (Maly & Maly 1998, Weissburg et al. 1998, Yen et al. 1998, Ianora et al. 1999). (4) Poor food quality may have contributed to low hatching success, although there is no evidence that *in situ* food quality differed between 2000 and 2001. Clearly, more research effort needs to be directed toward examining hatching success in *T. longicornis*, as this has important implications for the species' life cycle. Effective modeling of *T. longicornis* population dynamics will require knowledge of the functional relationships between egg hatching success (viability and production of resting eggs) and environmental conditions and cues.

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