Vol. 462: 51–66, 2012
doi: 10.3354/meps09830

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published August 21

Seasonal dynamics of fecundity and recruitment of *Temora longicornis* in the Baltic Sea

J. Dutz[1,3,*], J. E. E. van Beusekom[2], R. Hinrichs[1]

[1]Leibniz Institute for Baltic Sea Research Warnemünde, Seestrasse 15, 18119 Rostock, Germany
[2]Alfred-Wegener-Institute for Polar and Marine Research, Wadden Sea Station Sylt, Hafenstrasse 43, 25992 List/Sylt, Germany
[3]*Present address:* Technical University of Denmark, National Institute of Aquatic Resources, Kavalergården 6, 2920 Charlottenlund, Denmark

ABSTRACT: The seasonal cycle of reproduction in *Temora longicornis* was investigated in the Bornholm Basin, Baltic Sea, from March 2002 to May 2003. Variations in egg production of the population (EPR) and spawning females (sfEPR, ~ clutch size), proportion of spawning females (%FS), egg hatching success (HS), female prosome length (PL) and weight-specific egg production (spEPR) were compared with the seasonal variations in temperature, salinity, and food concentration and composition. Females reproduced year round with maxima of 9.8 to 12.3 eggs female^{-1} d^{-1} in spring and low to moderate egg production during the remaining seasons. PL was maximal during spring, and %FS, sfEPR and spEPR paralleled egg production. HS was low during winter and increased in spring. The statistical analyses showed that mean egg production correlated with both sfEPR and %FS. While %FS was significantly related to food concentration, sfEPR was dependent on both food availability and PL, which in turn was inversely related to temperature. Salinity had no effect on the seasonal variation in egg production because females maintained their vertical position in water with low seasonal amplitudes in salinity and temperature, presumably to avoid high energetic costs due to osmoregulation under fluctuating salinity. Nevertheless, the costs due to osmoregulation during development likely resulted in small female PL, and thus indirectly affected reproduction. Using empirical non-linear regression, 80% of the seasonal variation in egg production of *T. longicornis* was explained by female length and food concentration. However, despite the pronounced seasonal variation in egg production, the recruitment of nauplii was continuously high except throughout the productive season, indicating that a low reproductive success was offset by female abundance.

KEY WORDS: Fecundity · Hatching success · *Temora longicornis* · Baltic Sea · Food · Temperature · Body mass

INTRODUCTION

In the temperate ocean, calanoid copepods show a pronounced seasonal variation in population abundance, which is controlled by offspring recruitment and mortality (Kiørboe & Nielsen 1994, Peterson & Kimmerer 1994). Female egg production and egg viability constitute the initial steps in the recruitment process and essentially initiate population growth (Kiørboe & Nielsen 1994, Peterson & Kimmerer 1994). Numerous laboratory and field studies have identified the variables that control copepod reproductive rates, which can fluctuate widely on a daily to seasonal basis. Water temperature and food concentration are the principal determinants of copepod fecundity, either directly or indirectly via their effect on female body size (Landry 1978, Runge 1985, Durbin et al. 1992, Kiørboe & Nielsen 1994), but various other factors are known to affect egg production, such as phytoplankton cell size (Dam & Peterson

*Email: jdu@aqua.dtu.dk

1991, Kiørboe & Nielsen 1994), food quality in terms of mineral or biochemical composition (Jónasdóttir et al. 1995, Peters et al. 2007) or presence of noxious species (Van Rijswijk et al. 1989, Devreker et al. 2005) and suspended sediments (Castellani & Altunbaş 2006). In contrast, the variation in egg viability and egg hatching success is largely related to maternal effects such as female nutrition or resting egg production (Castellani & Lucas 2003, Paffenhöfer et al. 2005).

While the variables determining egg production and egg viability are generally well understood, our knowledge on the control of reproduction and recruitment of a species in specific environments is incomplete. Temperate copepod species often display a wide geographical distribution, and the relative importance of the variables controlling reproductive success and recruitment likely differ over the distribution range, depending on regional conditions. This information is pivotal for understanding the effect of climate variability and change on copepod recruitment and population dynamics, and its linkage to higher trophic levels in the coastal ocean.

In the present study, we investigated the reproductive biology of *Temora longicornis* in the Baltic Sea. This species has a wide geographical distribution, ranging from sub-tropical to sub-polar marine shelf waters on both sides of the North Atlantic (e.g. CPR Survey Team 2004). The reproductive biology of *T. longicornis* has been subject to several investigations, but the period of observation and the number of explored variables have often been limited (e.g. Arendt et al. 2005, Wesche et al. 2007). Recent studies conducted over the complete seasonal cycle suggest that the regulation of the reproductive success of *T. longicornis* is rather complex, but is nevertheless primarily controlled by the seasonally variable body mass of females (Halsband & Hirche 2001, Devreker et al. 2005, Castellani & Altunbaş 2006). This contrasts with results from earlier investigations in which food availability was identified to govern egg production (Kiørboe & Nielsen 1994, Peterson & Kimmerer 1994).

Apart from a description of the seasonal variation in egg production (Hansen et al. 2006), the environmental control of reproductive success and recruitment of *Temora longicornis* in the Baltic Sea is unknown. Analyses of inter-annual variation in the abundance and biomass of this species suggest that abiotic variables exert a strong control on the population dynamics, presumably due to the effects of reduced salinity of the brackish water and the pronounced amplitude of seasonal temperature variation on the vital rates of *T. longicornis* (Dippner et al. 2000, Möllmann & Köster 2002, Hänninen et al. 2003). Here we aimed to compare the respective importance of abiotic and biotic variables in controlling the reproductive success of *T. longicornis* in the Bornholm Basin, a deep basin (~100 m) in the western Baltic Sea. In particular, we wanted to (1) describe in detail the seasonal variation in egg production and egg hatching success of the species, (2) identify the relative significance of temperature, salinity, body mass and food availability in the regulation of the seasonal variation in egg production, and (3) estimate to what extent the seasonal recruitment of nauplii is controlled by variations in reproductive success.

MATERIALS AND METHODS

Sampling

Plankton was collected during a series of 15 cruises to the Bornholm Basin, central Baltic Sea, between March 2002 and May 2003 at a centrally located station (55° 17.5′ N, 15° 45′ E, 95 m depth, Fig. 1). Additional stations north and south from the central station were irregularly sampled during some months. Copepods were collected by vertical net tows of a WP-2 net equipped with a non-filtering cod end (200 µm mesh size, towing speed 0.2 m s^{-1}) from 50 m to the surface. The catch was carefully diluted into a large bucket containing unfiltered seawater from the surface (during autumn to spring) or from below the thermocline (during summer) and brought into a

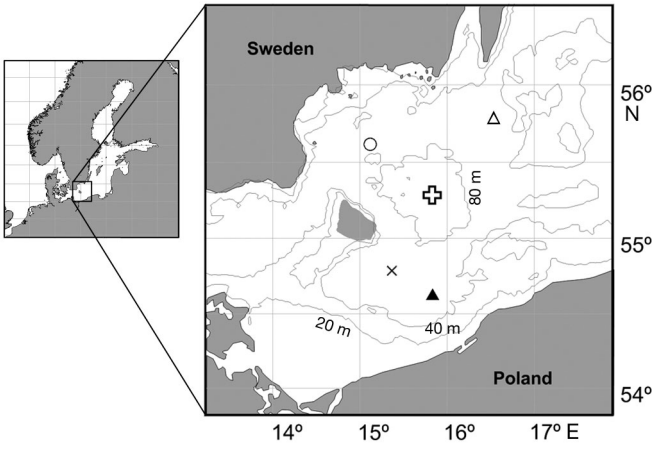

Fig. 1. Study area and sampling stations for *Temora longicornis* egg production experiments in the Bornholm Basin, Baltic Sea; open cross: central station for the seasonal study of reproduction in individual incubations; circle, triangles and cross indicate additional, irregularly sampled stations

temperature-controlled walk-in chamber set to ambient water temperatures. Females of *Temora longicornis* were sorted within 10 to 30 min after collection.

At each station, a standard CTD probe (SeaBird 911+ or ADM) was lowered from the surface to close to the seabed to obtain vertical profiles of temperature (T, °C) and salinity (S, as measured on the practical salinity scale). Microplankton samples were collected with a rosette of Niskin bottles from 5 to 10 discrete water depths, depending on the stratification pattern, and fixed with acidic Lugol's solution (2% final concentration). Sampling was conducted from March 2002 to April 2003. The microplankton taxonomic composition and biomass were analysed as described in detail by Van Beusekom et al. (2009). In short, after concentration in settling chambers, phyto- and microzooplankton were counted with an inverted microscope at 200× to 400× magnification and then classified into taxonomic categories. Cell dimensions of each category were measured, and cell volume was converted to carbon biomass (Edler 1979, Putt & Stoecker 1989). Samples to estimate standing stocks of nauplii and copepodites were taken by vertical tows of a Multinet (0.25 m^2, 50 µm mesh size, Hydrobios, towing speed 0.1 m s^{-1}) and double oblique tows with a Bongo net (0.12 m^2, 150 µm mesh size, towing speed 0.5 m s^{-1}), respectively. The details of the sampling grid, subsequent analytical procedures and the seasonal variation in stock composition were reported by Dutz et al. (2010).

Egg production

Between 25 and 35 actively swimming females were randomly selected from each catch. Single females were kept in 200 ml spawning chambers, containing an inner compartment of 100 ml with a bottom made of 100 µm mesh gauze to prevent copepods from feeding on their eggs. The chambers were filled with ambient seawater that was screened through a 48 µm sieve to remove any eggs. During autumn, winter and spring, the seawater was collected at 5, 10 and 15 m depth with Niskin bottles and mixed in equal shares. During summer, when the seasonal thermocline had formed, the seawater was taken at 2 depths below the thermocline (10 and 15 m) because females generally occurred below the warm upper layer. The chambers were kept for 24 h in a temperature-controlled water bath at the ambient water temperatures (±0.2°C), under dim light with natural light/dark regimes. Incubations were stopped by removing the females with the inner compartment. The content of the spawning chambers was carefully concentrated on a 20 µm sieve and flushed into dishes. The eggs were counted with a dissecting microscope at dim, cool light; empty egg shells were included in the egg counts. Afterwards, eggs were pooled and transferred to 275 ml glass bottles containing GF/F filtered seawater and incubated at ambient temperature for the determination of hatching success (HS). In addition, some eggs were incubated in parallel in Petri dishes containing GF/F filtered sea water, to determine the hatching time. The hatching incubations were stopped when the eggs in the Petri dishes had hatched. The incubation time ranged from 3 d (August to September) to 13 d (December to February). Bottle contents were concentrated, and remaining eggs, empty egg shells and hatched nauplii were fixed in Lugol's solution (2% final concentration) and counted in the laboratory.

The condition of females was visually inspected; incubations with dead females were not included in the calculation of the egg production rate (EPR). The prosome length (PL) of all live females was measured under a dissecting microscope at 60× magnification (resolution: 15 µm). The carbon weight of females was calculated using a length–weight conversion factor established by Köster (2003). Egg volume was determined from the diameter of at least 30 eggs per experiment, and egg carbon was estimated by applying a conversion factor of 0.31×10^{-6} µg C $µm^{-3}$ (Dutz et al. 2008; egg diameter 81 µm). During winter, eggs were scarce and data were pooled from several cruises (November to February). Weight-specific egg production rates (spEPR) were calculated as egg carbon produced per day divided by female carbon. The percentage of females spawning (%FS) out of all females was calculated as the ratio between the numbers of females that produced eggs and the total number of incubated individuals. Spawning female egg production rate (sfEPR) represents the EPR of only those females that spawned and is equivalent to the sum of egg clutches laid within a day.

In order to estimate the contribution of *in situ* egg production to the seasonal recruitment, we compared the stocks of eggs and nauplii. For this, the daily egg production of the *Temora longicornis* population (popEPR) was estimated from the mean egg production rate and the mean integrated abundance of females in the Bornholm Basin. Assuming a steady state, the egg stock (eggs m^{-2}) was calculated by multiplying popEPR by embryonic development time, which was estimated from the Bělehrádek function given by Corkett & McLaren (1970). In order to calcu-

late the standing stock of nauplius stage 1 (N1) from the total nauplii stock (N, nauplii m^{-2}), which was not stage separated, we assumed an exponential decrease in abundance with a seasonally constant instantaneous mortality rate (μ) of stages (*i*) N1 to N5 of 0.15 d^{-1} (Kiørboe & Nielsen 1994) and a seasonal stage duration (*t*, d) of nauplii given by Dutz et al. (2010, see their Table 2) according to:

$$N1 = \frac{N}{\sum_{i=0}^{5}(e^{-i\mu t})} \quad (1)$$

Data analysis

Relationships between environmental (temperature, salinity, concentration of different food items and total food) and biological variables (PL, mean EPR, mean sfEPR, %FS, HS) were first tested with Spearman rank order correlation analysis. Linear or non-linear regressions were then used to establish empirical relationships between the pairs of variables that were significantly correlated, using environmental variables as independent and biological variables as dependent variables. Linear functions were used to relate PL to environmental factors (Checkley 1980), while exponential and Ivlev functions were used to investigate the relation of egg production (mean EPR, sfEPR) to PL and food concentration, respectively, in non-linear regressions (Durbin et al. 1992). When the relationship was unknown, functions providing the best fit were used.

Temora longicornis females displayed a variable depth distribution with a seasonal submergence below the warm surface layer and diel vertical migration during the stratification period (Dutz et al. 2010). Therefore, the weighted means of *T* and *S* (WM_T and WM_S) were determined over the depth range of the female distribution according to:

$$WM_T = \frac{\sum n_i T_i}{\sum n} \quad (2)$$

where n_i is the abundance of each stage *i* (ind. m^{-3}) in each depth stratum with a mean *T* of T_i (similar for *S*). Averages of day and night WM_T and WM_S were used for analyses of reproductive data. Regarding food, we used the day/night means of the average concentration of various protist groups over the depth range of the occurrence of females. For the regression of female PL with *T*, *S* and food stock (integrated over 0 to 50 m) were averaged over the period of cohort development, which was estimated from the stage durations (see Dutz et al. 2010 and Table 1 for details). The statistical analyses were carried out using the means of PL, EPR and sfEPR of each experiment because the data for single females failed the constant variance tests. All statistical analyses were performed with the Sigma Plot 11.0 and SPSS 11.5 statistical packages (Systat Software).

RESULTS

Environmental conditions

Characteristic of the hydrographical conditions in the Bornholm Basin was a brackish water layer with <8 salinity extending to depths of 40 to 50 m which overlaid a bottom layer of higher salinity (8–15, Fig. 2a). In the brackish layer, a seasonal thermocline formed from May until October, which separated the warm surface layer (10–21°C) from the colder inter-

Table 1. *Temora longicornis*. Generations and averaged environmental conditions during cohort development (June 2002 to April 2003). *T*: temperature, *S*: salinity and food stock in the upper 50 m of the water column (ciliates, dinoflagellates, flagellates, diatoms, other, and total). See 'Materials and methods' for further explanations

Month	Generation	*T* (°C)	*S*	Food stock (g C m^{-2})					
				Ciliates	Dinofl.	Flag.	Diatom	Other	Total
June 2002	G 1	7.9	7.2	1.94	0.98	0.72	0.08	0.49	4.21
July 2002	G 2	10.9	7.1	0.68	0.30	1.15	0.20	1.90	4.23
August 2002	G 3	9.6	7.1	0.52	0.55	1.12	0.11	0.81	3.11
September 2002	G 3	8.4	7.2	0.90	0.46	0.47	0.08	0.53	2.44
October 2002	G 4	11.4	7.4	1.59	0.27	0.52	0.03	0.60	3.12
November 2002	G 5	11.0	7.3	0.55	0.14	0.14	0.03	0.47	1.38
January 2003	G 5/6	8.0	7.3	0.39	0.10	0.14	0.03	0.33	0.90
February 2003	G 5/6	6.4	7.4	0.42	0.13	0.15	0.04	0.28	1.00
March 2003	G 5/6	4.2	7.4	0.47	0.12	0.13	0.31	0.07	1.10
April 2003	G 5/6	2.9	7.4	0.89	0.32	0.25	0.29	0.07	1.82

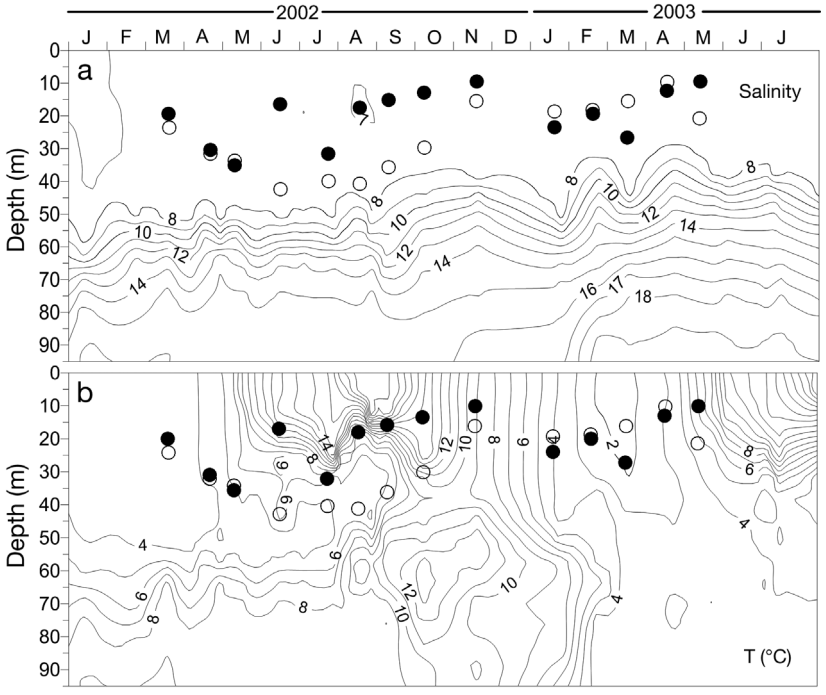

Fig. 2. Seasonal and vertical variation in (a) salinity and (b) temperature at the central station in the Bornholm Basin during January 2002 to August 2003. Circles denote the weighted mean depth of *Temora longicornis* females during day (open) and night (filled)

mediate layer (4–10°C, Fig. 2b). Several saline water inflows at depths >60 m occurred from September 2002 to February 2003 (see Mohrholz et al. 2006 for details), which increased the salinity in the bottom layer to >18. Temperature at depth increased to 10–11°C due to a relatively warm inflow in September 2002 and remained high until December 2002, but decreased below 4°C with a cold water inflow in January 2003. Due to the uplifting of the bottom water, the intermediate layer was eroded from September 2002 onwards.

Temora longicornis females were generally distributed in the brackish water at depths of 0 to 50 m (see details in Dutz et al. 2010). As indicated by the seasonal variation in the weighted mean depth at daytime (Fig. 2), females occurred in the upper mixed layer from November to April and in the intermediate water from May to October. Due to this seasonal submergence into the colder intermediate layer, the temperature amplitude experienced by females (weighted mean: 2.2–12.9°C) was generally less than the seasonal variation in surface water temperature (1.8–21.3°C; Fig. 3a). Until August 2002, females occurred in rather cold water (3.4–7.9°C), only interrupted by the migration into the warm surface at night (10.3°C) in June 2002. From September to November 2002, vertical migration and also the erosion of the cold intermediate water by the warm water inflows increased the environmental temperature to 9.1–12.9°C. In winter, the temperatures decreased again to 2.2–6.1°C until May 2003. In contrast to temperature, the salinity experienced by females changed little (7.4–8.4, Fig. 3b). In June 2002, however, larger day/night differences of 7.2 to 9.5 occurred due to the deep residence depth of females during the day.

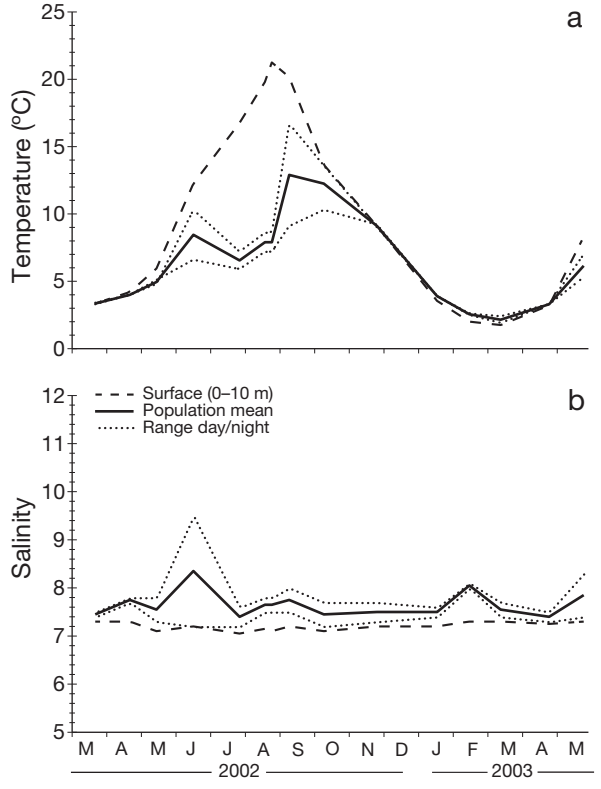

Fig. 3. Weighted mean (a) temperature and (b) salinity experienced by the female *Temora longicornis* population in the Bornholm Basin during March 2002 to August 2003 (solid line). Dotted lines give the day/night range of the weighted mean caused by diurnal vertical migration, and the dashed lines give the seasonal variation in surface temperature and salinity

The concentration and composition of protists showed a pronounced seasonal variation (Fig. 4a,b). Due to the seasonal submergence and diel vertical migration, the food concentration experienced by females during May/July to September was generally lower than food availability in the surface 30 m of the water column. Total food biomass increased from approximately 60 µg C l^{-1} in March in both years to 518 and 158 µg C l^{-1} in April 2002 and 2003, respectively. Ciliates and dinoflagellates almost exclusively accounted for the protists; diatoms contributed considerably to total protists only in March 2003. From May onwards, food biomass experienced by the females generally fluctuated from 57 to 91 µg C l^{-1} until October, with a minimum of 22 µg C l^{-1} in July 2002. Flagellates and 'other' (Table 1), which was dominated by cyanobacteria, were most abundant during the summer. They were replaced by ciliates in September/October 2002. The winter biomass was low and did not exceed 20 µg C l^{-1}. Flagellates and ciliates (*Mesodinium rubrum*) accounted for most of the food available in winter.

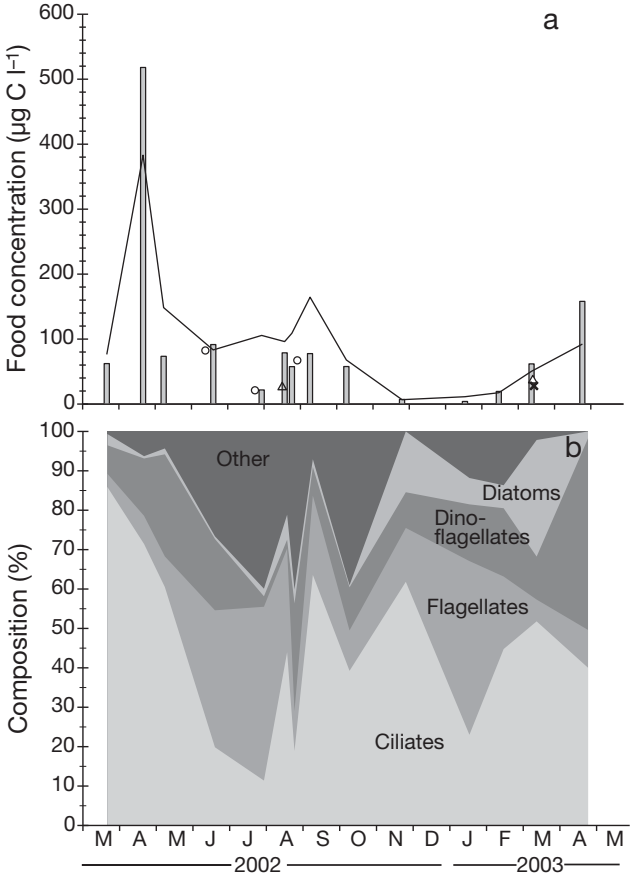

Fig. 4. Seasonal variation in (a) food concentration (grey bars, in µg C l^{-1}) and (b) composition (%) over the distribution range of *Temora longicornis* females at the central station of the Bornholm Basin during March 2002 to August 2003. The solid line in (a) represents the food concentration at the surface (0–30 m), and symbols represent supplemental stations as denoted in Fig. 1

Reproductive cycle of *Temora longicornis*

Females reproduced throughout the year, but mean EPR varied considerably depending on the season (Fig. 5a). It was high in April in both years, with a mean (±SE) daily rate of 12.3 ± 1.8 and 9.8 ± 1.7 eggs $female^{-1}$ (hereafter eggs fem^{-1}) for 2002 and 2003, respectively. Moderate mean EPR ranging from 4.2 ± 0.7 to 6.8 ± 1.1 eggs fem^{-1} d^{-1} was observed in March and May 2002/2003 and in October 2002. Egg production was low during summer and winter (0.4 ± 0.1 to 2.0 ± 1.4 eggs fem^{-1} d^{-1}). The %FS and their sfEPR mirrored the mean EPR (Fig. 5b,c). %FS was generally high in spring (53–73%) and autumn (73–80%), while mean sfEPR was maximal only in April 2002/2003 (~18 eggs fem^{-1} d^{-1}). HS was variable (range: 35–96%) and, with the exception of 3 sampling points in April and November 2002 and January 2003 (20–40%), mostly >63% (Fig. 5d). The calculated mean spEPR was maximal in spring and autumn, similar to EPR (Fig. 5e). The reproductive indices of females caught at the periphery of the Bornholm Basin generally resembled those at the central station (Fig. 5a–d). Female abundance increased substantially from 2×10^3 to 156×10^3 ind. m^{-2} during May 2002 and decreased again during August and September 2002 to a low overwintering stock (5×10^3 to 8×10^3 ind. m^{-2}, Fig. 5f). The ratio in female/male abundance fluctuated around 1, with values varying from 0.6 to 1.3 (Fig. 5f). A low female/male ratio was observed in summer 2002 and spring 2003.

The mean PL (±SE) of females varied seasonally (Fig. 6). It was maximal during March to May (822 ± 12 to 869 ± 14 µm) and minimal during July to October (748 ± 10 to 793 ± 15 µm). The length frequency distribution indicated that PL was very variable at each sampling date; small and large females were present throughout the study, but their proportions changed seasonally.

Factors controlling reproduction

Mean egg production of females correlated significantly with the mean sfEPR, %FS, mean PL and, among the environmental variables, with the concen-

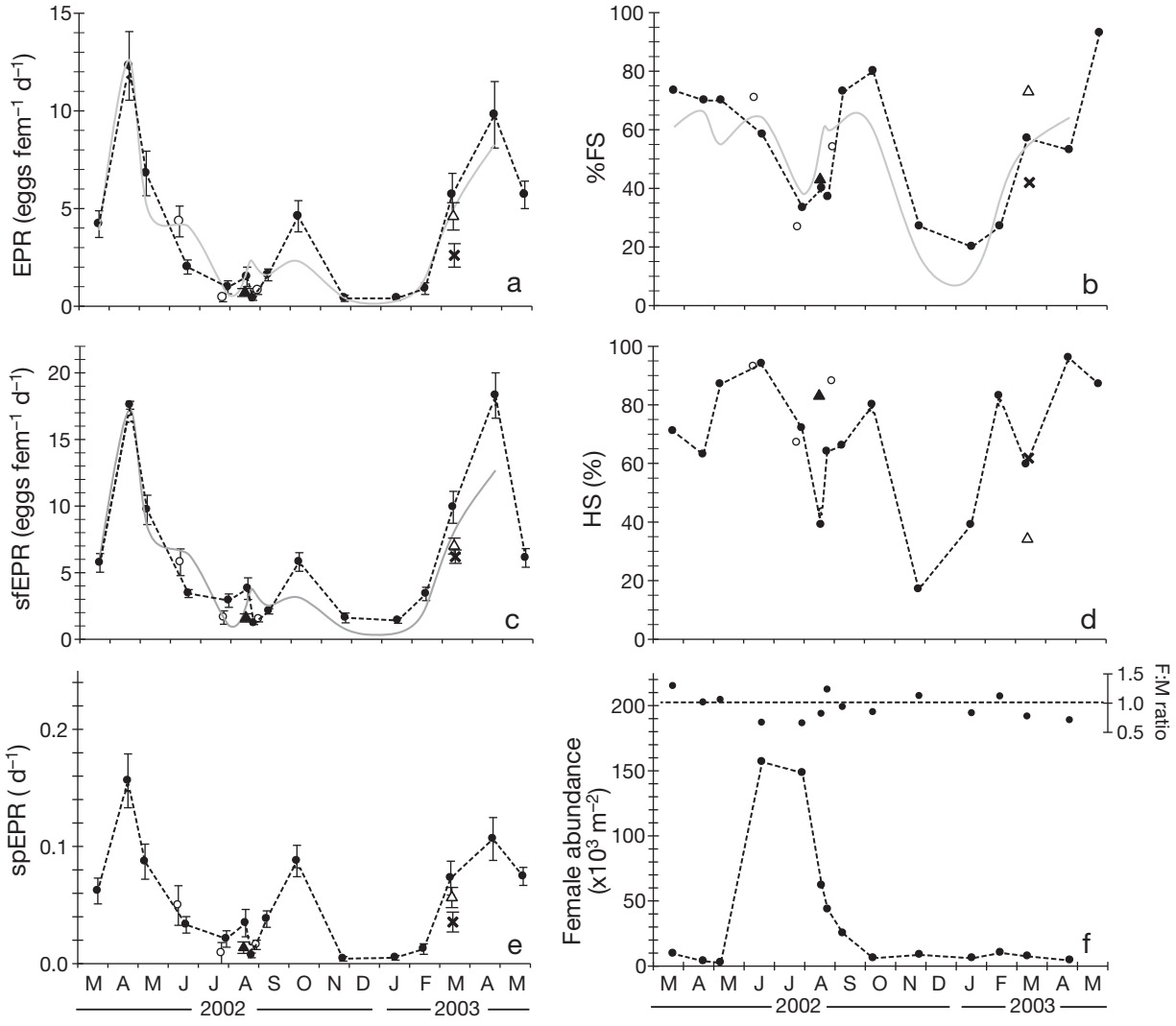

Fig. 5. *Temora longicornis*. Seasonal variation in (a) mean (±SE) egg production (EPR), (b) spawning frequency (%FS), (c) mean (±SE) spawning female egg production (sfEPR), (d) egg hatching success (HS), (e) mean (±SE) specific egg production (spEPR) and (f) female abundance and female:male ratio (F:M) at the central station (filled circles) and supplemental stations (denoted as in Fig. 1) in the Bornholm Basin during March 2002 to August 2003. Grey lines show the model predictions for (a) mean EPR, (b) %FS and (c) mean sfEPR (see Table 4)

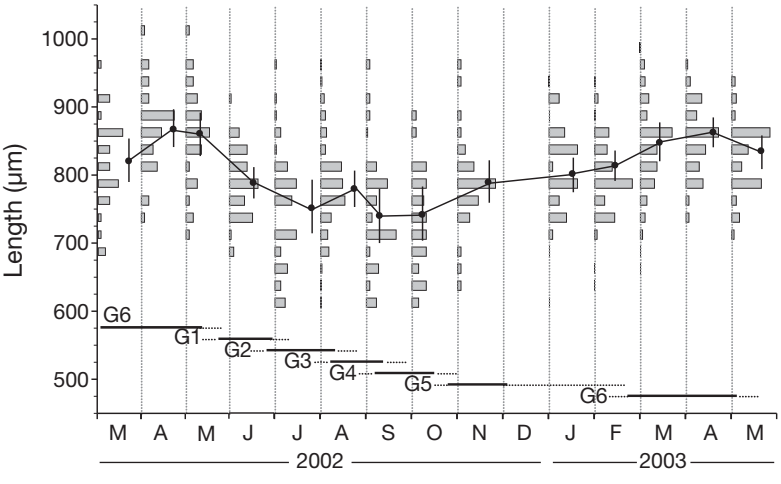

Fig. 6. *Temora longicornis*. Seasonal variation in length (solid line) and length frequency (bars) of females at the central station in the Bornholm Basin during March 2002 to August 2003. The horizontal lines at the bottom of the figure indicate succession of female generations as described by Dutz et al. (2010)

Table 2. *Temora longicornis*. Spearman rank order correlation coefficients between biological and environmental variables in the Bornholm Basin, Baltic Sea, during March 2002 to April 2003 (number of observations: 20). Note that for mean prosome length (PL) the averaged environmental conditions during cohort development instead of instantaneous conditions were used for correlation analysis (see 'Materials and methods'; number of observations: 17). EPR: mean egg production rate; sfEPR: mean EPR of spawning females, %FS: proportion of females spawning, HS: hatching success, *T*: temperature, *S*: salinity, Cil: biomass of ciliates, Dino: biomass of dinoflagellates, Flag: biomass of flagellates, Diat: biomass of diatoms, Other: biomass of non-specified protists, TF: total food (= biomass of protists). Significance levels: $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$

	sfEPR	%FS	HS	PL	*T*	*S*	Cil	Dino	Flag	Other	Diat	TF
EPR	0.958***	0.715***	0.191	0.540*	−0.323	0.016	0.800***	0.503**	0.427	0.071	0.069	0.643**
sfEPR		0.541*	0.085	0.591**	−0.459*	−0.073	0.734***	0.352	0.297	0.144	−0.104	0.518*
%FS			0.085	0.191	0.139	0.197	0.709***	0.541**	0.409	0.069	0.298	0.691***
HS				−0.124	0.250	0.259	−0.035	0.599**	0.379	0.331	−0.457*	0.275
PL					−0.685**	0.851***	−0.430	−0.539	−0.709**	−0.915***	0.091	−0.685*

tration of ciliates (Cil), dinoflagellates (Dino) and total food (TF, Table 2). SfEPR and %FS were also correlated with each other, reflecting the tendency that when a high proportion of females spawned, egg production was also high. SfEPR correlated significantly with PL, Cil and TF, and negatively with *T*, while %FS was highly correlated only with food (Cil, Dino, TF). Hatching success was positively correlated with the concentration of dinoflagellates and negatively with that of diatoms. Mean PL correlated negatively with *T* and the stocks of flagellates, 'other' and TF and positively with *S* in the period June 2002 to April 2003.

Linear functions gave the best fit for the relation of mean EPR with mean sfEPR and %FS (Fig. 7a,b). The

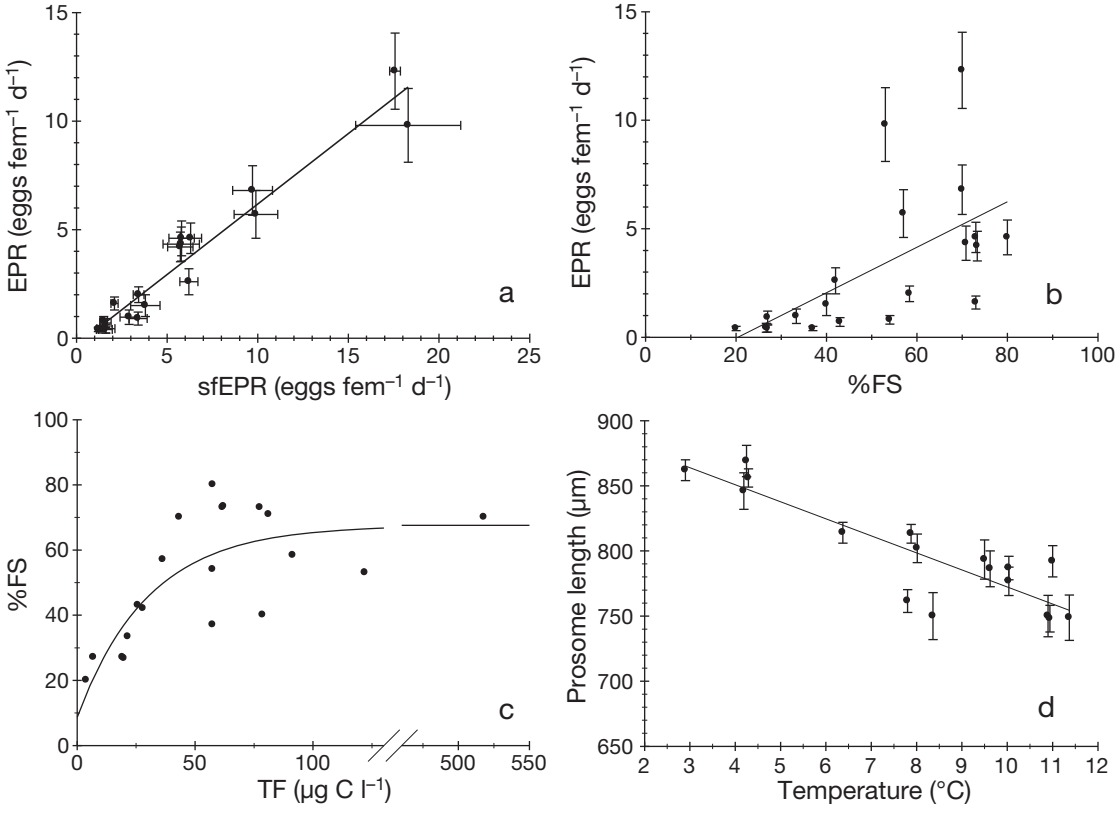

Fig. 7. *Temora longicornis*. Relationships of (a) mean (±SE) egg production (EPR) to mean (±SE) spawning female egg production (sfEPR), (b) mean EPR (±SE) to spawning frequency (%FS), (c) %FS to total food concentration (TF) and (d) mean (±SE) prosome length (PL) to temperature (°C). Regressions are (a) EPR = −0.31 + 0.65 sfEPR (df = 19, $r^2 = 0.94$, $F = 289.9$, $p < 0.001$) and (b) EPR = −2.1 + 0.11 %FS (df = 19, $r^2 = 0.36$, $F = 10.2$, $p = 0.005$); for (c) and (d) see 'Results: Factors controlling reproduction' and Tables 3 & 4

relationship of both variables to correlating environmental variables was therefore investigated separately. An exponential function and an Ivlev function were chosen to investigate sfEPR in relation to PL and TF concentration, respectively, using non-linear regression (Checkley 1980, Durbin et al. 1992). The non-linear regression gave significant results for both variables. PL and TF alone explained 62 and 48% in the variation of sfEPR, respectively, and a combination of both increased the explanatory power of the non-linear model to 74% (Table 3). SfEPR also showed a negative correlation with *T* (Table 2). Adding *T* to the regression using an exponential function (Sekiguchi et al. 1980, Durbin et al. 1992) did not produce significant results, but removed the significance of PL as variable (results not shown). The relationship of %FS and TF has previously not been described. Of various functions tested, only the Ivlev function produced significant results (Fig. 7c). Using this function, TF explained 61% of the variation of %FS (Table 3). Finally, mean EPR was significantly related to PL (exponential function) and TF (Ivlev function) using a non-linear model (Table 3). PL and TF alone explained 61 and 57% of seasonal variation in EPR, respectively, but combined both variables explained 80% of the variation in EPR.

The relationship of PL to environmental factors was investigated using linear functions (Checkley 1980). A multiple linear regression using *T*, *S* and TF only gave a significant negative relationship to *T* (Table 4, Fig. 7d). The model coefficient suggested a decrease of 13 µm in length with an increase of 1°C in temperature.

Recruitment

With the exception of winter (November to February), daily egg production of females and female abundance were inversely related to each other during the seasonal cycle (Fig. 5a,f). Accordingly, the calculated stock of eggs and viable eggs showed relatively little seasonal variation (Fig. 8). The egg stock for summer/autumn (206×10^3 to 1980×10^3 eggs m^{-2}) was in a similar range as that calculated for the period of maximal egg production in spring (March to May, 119×10^3 to 1593×10^3 eggs m^{-2}). Recruitment was low only in winter (35×10^3 eggs m^{-2}). Except June 2002 and winter (November to February), the calculated standing stock of nauplius stage N1 was high ($>1.6 \times 10^4$ m^{-2}) during the seasonal cycle and largely mirrored the seasonal variation in the stock of eggs (Fig. 8).

Table 3. *Temora longicornis*. Non-linear regression of mean spawning female egg production (sfEPR, eggs fem^{-1} d^{-1}), the proportion of spawning females (%FS) or mean female egg production (EPR, eggs fem^{-1} d^{-1}) as a function of mean female prosome length (PL, µm) and/or total food concentration (TF, µg C l^{-1}). Significance levels: $^{**}p < 0.05$, $^{***}p < 0.01$. Number of observations was 20 for all models

Estimated model	df	a	b	c	*F*	R^2	p
$sfEPR = a \exp^{(bPL)}$	1, 18	$5.5\ 10^{-7} \pm 2.1\ 10^{-6}$	$0.019 \pm 0.004^{***}$	–	30.1	0.62	$<0.0001^{***}$
$sfEPR = a\ (1-e^{-bTF})$	1, 18	$18.8 \pm 4.8^{***}$	$0.006 \pm 0.002^{**}$	–	16.4	0.48	$<0.001^{***}$
$sfEPR = a \exp^{(bPL)}\ (1-e^{-cTF})$	2, 17	$9.4\ 10^{-5} \pm 3.1\ 10^{-4}$	$0.014 \pm 0.003^{***}$	$0.019 \pm 0.006^{***}$	24.4	0.74	$<0.0001^{***}$
$\%FS = a + b\ (1-e^{-cTF})$	2, 17	8.7 ± 13.1	$65.9 \pm 5.8^{***}$	$0.041 \pm 0.012^{**}$	13.1	0.61	$<0.0001^{***}$
$EPR = a \exp^{(bPL)}$	1, 18	$6.0\ 10^{-9} \pm 3.3\ 10^{-8}$	$0.024 \pm 0.006^{***}$	–	28.1	0.61	$<0.0001^{***}$
$EPR = a\ (1-e^{-bTF})$	1, 18	$13.2 \pm 3.5^{***}$	$0.005 \pm 0.002^{**}$	–	20.2	0.53	$<0.001^{***}$
$EPR = a \exp^{(bPL)}\ (1-e^{-cTF})$	2, 17	$5.5\ 10^{-5} \pm 2.1\ 10^{-4}$	$0.014 \pm 0.004^{***}$	$0.015 \pm 0.005^{***}$	31.8	0.80	$<0.0001^{***}$

Table 4. *Temora longicornis*. Multiple linear regression of mean prosome length (PL, µm) as a function of temperature (*T*, °C), salinity (*S*) and total food (TF, g C m^{-2}). Coefficients and significance are the best fit for a stepwise backward regression. Significance levels: $^{***}p < 0.001$. n: number of observations

Estimated model	Coefficient	Value	SE	*F* (to remove)	*F* (to enter)	p
$PL = a + b\,T + c\,S + d\,TF$	a	903.1	15.6			
n = 17, df = 1, 15	b	−13.1	1.8	50.658		$<0.001^{***}$
$R^2 = 0.77$	c				0.467	0.505
Adj. $R^2 = 0.76$	d				2.871	0.111

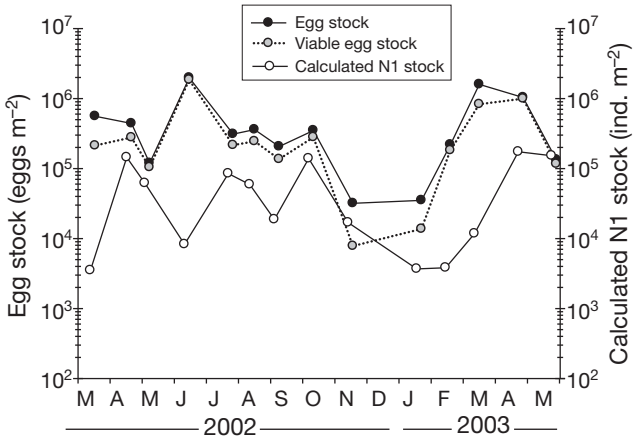

Fig. 8. *Temora longicornis*. Seasonal variation in mean (±SE) egg stock (eggs m^{-2}), mean (±SE) viable egg stock (eggs m^{-2}) and calculated nauplii stage 1 (N1) stock (ind. m^{-2}) in the Bornholm Basin during March 2002 to August 2003

DISCUSSION

In the western regions and central basins of the brackish Baltic Sea, *Temora longicornis* is a key species and forms an important diet for pelagic fish (Flinkman et al. 1998, Möllmann & Köster 2002). Long-term studies suggested a strong link of vital rates, including egg production, and biomass of the species to the climatically driven variation in surface seawater temperature and salinity (Dippner et al. 2000, Möllmann & Köster 2002, Hänninen et al. 2003), but the underlying mechanisms remain unresolved as the population dynamics and its governing variables are insufficiently understood. In this context, our investigation provides the first analysis of the seasonal variation and control of reproductive success of *T. longicornis* in the Baltic Sea. Below we discuss the seasonal variation in the reproductive parameters of *T. longicornis*, its control by environmental factors in the Baltic Sea, how this compares to other regions of the species occurrence and the contribution of individual egg production to the recruitment of nauplii.

Reproductive success of *Temora longicornis* in the Baltic Sea

The seasonal variation in the reproductive success of *Temora longicornis* in the brackish Bornholm Basin largely resembled that in marine areas. Similar to *T. longicornis* in the North Sea, the Kattegat or the Irish Sea (e.g. Kiørboe & Nielsen 1994, Halsband & Hirche 2001, Castellani & Altunbaş 2006), reproduction continued throughout the year, with a minimum during winter, a pronounced increase in spring and subsequent peaks in egg production, which is typical for seasonally variable environments. However, compared to marine studies, the maximal EPR of Baltic females under surplus food was considerably reduced. Rates of 7 to 12 eggs fem^{-1} d^{-1} in spring in the Bornholm Basin compare well with earlier results from the same area (Hansen et al. 2006), but are much lower than the rates of >40 to 50 eggs fem^{-1} d^{-1} observed in spring in marine areas (Peterson & Bellantoni 1987, Kiørboe & Nielsen 1994, Halsband & Hirche 2001, Castellani & Altunbaş 2006). This indicates that the brackish conditions influence the reproductive performance of *T. longicornis* (see below: 'Factors controlling egg production').

The seasonal variation in %FS is poorly studied in *Temora longicornis*. The proportion was very variable and particularly low during winter and early summer, which is consistent with observations from the North Sea (Halsband & Hirche 2001, Wesche et al. 2007), whereas a continuously high frequency was observed in the English Channel (Devreker et al. 2005).

HS was also variable, but generally >60% throughout the productive season. This is in agreement with various other marine studies (Tang et al. 1998, Devreker et al. 2005, Wesche et al. 2007). A pronounced switch from high to low HS during spring associated with resting egg production as reported by Castellani & Lucas (2003) was not observed in our study. Instead, HS increased during the winter to spring transition. The correlation analysis suggested a negative relationship of HS with the presence of diatoms and a positive relationship with the abundance of dinoflagellates. This is consistent with an adverse effect of diatoms on copepod reproduction (Ianora et al. 2003, Paffenhöfer et al. 2005, Dutz et al. 2008). However, food concentrations were very low during winter time (<20 µg C l^{-1}) and also in July 2002, during which diatoms were nearly absent and hatching was also low. Therefore, the general physiological condition of females might have been poor at these times and may have caused a decrease in HS.

Factors controlling egg production

In previous field investigations, egg production of *Temora longicornis* and other copepods has mainly been related to temperature, chlorophyll *a* concentration and female size (e.g. Landry 1978, Checkley 1980, Runge 1985, Durbin et al. 1992, Kiørboe &

Nielsen 1994). Since these factors often vary on different timescales in seasonally variable environments and partly affect egg production in different ways, the regulation of the reproductive cycle is rather complex (Durbin et al. 1992, Devreker et al. 2005, Castellani & Altunbaş 2006). In brackish environments, salinity is an additional factor affecting reproduction in copepods (Ambler 1985, Devreker et al. 2009).

Salinity

Salinity is known to exert a strong effect on egg production of copepods of brackish (Ambler 1985, Devreker et al. 2009) or marine origin (Calliari et al. 2008, Holste et al. 2009). Copepods adjust their bodily free amino acid and ionic concentrations upon osmotic stress, which can be energetically costly under a fluctuating or sub-optimal salinity (Farmer & Reeve 1978, Goolish & Burton 1989). Accordingly, in a recent study with cultures of *Temora longicornis*, a decrease in egg production with decreasing salinity (26 to 8) was attributed to the costs of ionic regulation (Holste et al. 2009).

The seasonal cycle of the reproductive success of *Temora longicornis* in the Bornholm Sea revealed no relationship with salinity, likely due to the minor fluctuations in the depth range at which the species resided. Nevertheless, the considerably lower maximal egg production under optimal food conditions in spring compared to those reported from the marine environment likely indicate a strong environmental constraint by the brackish water conditions. Our results, however, suggest that the small size of Baltic females rather than costs of osmoregulation primarily limit egg production in the field. The maximal egg production of *T. longicornis* is generally related to its size/body mass (Arendt et al. 2005, Castellani & Altunbaş 2006, this study), and females in the Bornholm Basin were considerably smaller (maximum 869 µm) compared to those in marine water (maximum >1200 µm, Halsband & Hirche 2001, Arendt et al. 2005), which is consistent with a dependence of copepod body length on environmental salinity (Gaudy et al. 1988, Miliou 1996). The calculated weight-specific egg production, in contrast, was similar to marine studies. Considering that we used a 2.3 times higher factor for the conversion of egg volume to egg carbon (consistent with Dam & Lopes 2003) than older studies, maximal weight-specific rates of 0.11 to 0.16 d^{-1} for all females or 0.19 to 0.22 d^{-1} for spawning females (to account for a low spawning frequency in our study) compare well with those of 0.05 to 0.09 d^{-1} (corrected by 2.3: 0.12 to 0.21 d^{-1}) observed in marine field and laboratory studies (Kleppel et al. 1991, Kiørboe & Nielsen 1994, Koski et al. 2005). If energetic costs related to osmoregulation were high in females (Holste et al. 2009), a lower weight-specific egg production would be expected. This is consistent with low maintenance costs for osmoregulation in euryhaline *Acartia* spp. under hypo-osmotic conditions (Goolish & Burton 1989, Calliari et al. 2006). The small size of Baltic females, however, suggests that growth of development stages is more negatively affected by salinity stress than egg production is. This could be explained by the proportionally higher energetic expenditures in smaller juvenile stages compared to larger adults as ionic turnover rates have been related to size (Brand & Bayly 1971). The costs related to osmoregulation in different developmental stages of *Temora longicornis* and their influence on production therefore require further investigation.

Throughout the year, females were typically distributed in the surface and intermediate water with a reduced salinity and avoided entering the more saline bottom water. Moreover, females migrated below the warm surface layer after onset of the seasonal stratification. As a consequence, the seasonal amplitude in temperature (2 to 13°C) and in salinity (7.4 to 8.4) experienced by females was generally low. This behaviour might reflect the strategy of females to minimize environmental stress and to optimize energy allocation for egg production. Under food-limiting conditions, Maps et al. (2005) observed that at temperatures higher than 14°C the metabolic needs of females increase to the detriment of egg production. Thus, females apparently stayed in a temperature window optimal for egg production at low food conditions during summer. Instantaneous changes in salinity are also known to negatively affect egg production, development and survival of brackish and marine copepods (Cervetto et al. 1999, Lee & Petersen 2003, Calliari et al. 2008, Devreker et al. 2009), presumably because the up- or down-regulation of the osmotic potential following a hyper- or hypo-osmotic shock is energetically expensive (Farmer & Reeve 1978, Goolish & Burton 1989). This can be substantially amplified by increasing temperature (Gaudy et al. 2000). In contrast, maintenance costs for osmoregulation under uniform conditions are low (Farmer & Reeve 1978, Goolish & Burton 1989, Calliari et al. 2006) and could explain the habitat preference of females for the brackish water layer.

Female size, temperature and food

Female size, temperature and food concentration, although not always simultaneously measured, have been identified as the major variables determining the seasonal variation in egg production of pelagic copepods, including *Temora longicornis* (e.g. Runge 1985, Durbin et al. 1992, Castellani & Altunbaş 2006). In our study, we analysed environmental effects on sfEPR and %FS separately, because both variables correlated highly with egg production of *T. longicornis*. sfEPR in the Bornholm Sea was largely determined by variation in female body length and available food concentration, while the %FS was related to food concentration only. Empirical models based on non-linear regression of both variables explained 74 and 59% of the variation in sfEPR and %FS, respectively, and projected their seasonal variation well (Table 4; Fig. 5b,c).

The variables determining sfEPR have rarely been studied in *Temora longicornis*. A general positive scaling of egg production with the size of *T. longicornis* is known from the North Sea and Irish Sea (Devreker et al. 2005, Castellani & Altunbaş 2006). This scaling is likely related to the reproductive biology and gonad development, in which oocytes mature synchronously and are deposited as eggs in 1 clutch, similar to *Calanus* (Niehoff 2007). In *Calanus* spp., clutch size is related to gonad size, which, in turn, depends on female size and food concentration (Runge 1984, Hirche et al. 1997, Plourde & Joly 2008). A significant correlation of clutch size with female length and phytoplankton carbon has been observed for *T. longicornis* in the North Sea, but the correlation of clutch size with egg production was not investigated (Halsband & Hirche 2001). Strictly speaking, sfEPR in our study cannot be interpreted as clutch size, because *Temora* is known to produce more than 1 clutch d^{-1} (Ianora et al. 1989). However, this might particularly occur at conditions of food saturation and high temperature (see Ianora et al. 1989). The significant relationship of sfEPR with female length and food concentration in our study might therefore similarly reflect the effect on gonad development. The body length of *T. longicornis* was further negatively related to environmental temperature. This agrees with investigations in the North Sea and the laboratory (Evans 1981, Klein Breteler & Gonzalez 1988, Devreker et al. 2005), but, in contrast to these studies, we did not observe a positive scaling of length with food concentration. Thus, temperature was an important variable indirectly controlling the seasonal variation in egg production via its effect on body size.

%FS also determined egg production in this population of *Temora longicornis*. Food concentration was the only significant variable explaining the seasonal variation in %FS. This contrasts with a correlation of %FS with temperature for the period February to July in the English Channel (Devreker et al. 2005). The %FS of a copepod population likely depends on a combination of various intrinsic factors affecting the maturity of females, such as fertilisation, presence of premature females or senescence (e.g. Parrish & Wilson 1978, Ianora et al. 1989), and environmental variables that effect the rate of clutch production of mature females (Runge 1984, Hirche et al. 1997). Intrinsic factors are difficult to evaluate in field studies and were not specifically studied by us. However, they are unlikely to show a hyperbolic response with regard to food concentration as observed for *T. longicornis*. In addition, females were found to be continuously replenished from younger stages throughout most of the year (Dutz et al. 2010), while the ratio of females to males was largely constant and egg production increased in spring despite continuously low numbers of females and males. Thus, intrinsic variables are unlikely to primarily account for the observed variation in %FS.

The rate of clutch production per day (spawning frequency), however, depends both on temperature and food availability (Runge 1984, Hirche et al. 1997). Both variables control the metabolic activity and the rate at which nutritious compounds are transferred to gonads, and thus contribute to %FS. Regarding food, a hyperbolic response of %FS was previously observed in *Calanus* spp. (Uye & Murase 1997, Plourde & Joly 2008). However, the spawning frequency describes clutch production rates in spawning females only. With regard to the very low food concentrations (<20 µg C l^{-1}) in winter and in July 2002, the minimal %FS at these times could also reflect the proportion of females staying immature due to sub-optimal food conditions. Thus, the state of maturity and spawning frequency might both contribute to the variation in %FS, which needs further investigation.

Temperature is well known to positively affect egg production in copepods up to its optimum (Ianora 1998, Maps et al. 2005), presumably by its effects on spawning frequency, which was the main mechanism for the regulation of egg production in *Calanus* spp. (Runge 1984, Hirche et al. 1997). In contrast to food, we could not detect an influence of temperature on the proportion of spawning females (%FS). Egg production in *Temora longicornis* was already high at temperatures below 5°C, and a potential increase in

spawning frequency due to warming might have been offset by declining food levels. However, food explained only 59% of the variation in %FS. Thus, undetected temperature effects or intrinsic factors could account for the remaining variation.

PL, which was largely determined by temperature, and food concentration were the main variables controlling the daily egg production of *Temora longicornis* (Table 3). Both variables accounted for a similar proportion of its variance (61 and 53%) and together explained 80% of the variation in EPR of the population. Regarding food, egg production followed the seasonal abundance of dinoflagellates and ciliates. However, we interpret this as the general dependence of egg production on food concentration instead of the importance of specific protist groups, because the ephemeral diatom bloom in the Baltic occurring in March and April 2003 was simply missed in our investigation (see Dutz et al. 2010).

The control of egg production by a combination of body size and food concentration in the Baltic contrasts with previous investigations. The importance of food availability for egg production of *Temora longicornis* has been stressed in studies from the Kattegat and Long Island Sound (Peterson & Bellantoni 1987, Kiørboe & Nielsen 1994). Egg production showed a high correlation with food abundance and was apparently food limited after the spring phytoplankton bloom. Body length, however, was not determined in these studies. This contrasts with studies from the English Channel, the German Bight and the Irish Sea, in which seasonal variation in egg production of *T. longicornis* was mainly controlled by body weight and its relationship to environmental temperature (Halsband & Hirche 2001, Devreker et al. 2005, Castellani & Altunbaş 2006). The striking difference among studies is likely explained by differences in the hydrographical regimes of the investigated areas. The Bornholm Basin, Long Island Sound and Kattegat are characterised by large thermal amplitudes associated with seasonal stratification and, as a consequence, also larger variations in available food concentration and particle size (Peterson & Bellantoni 1987, Kiørboe & Nielsen 1994, this study). Female size typically displays less pronounced fluctuations with an increase in winter/spring and a gradual decrease during the seasonal warming. Since feeding is largely related to food availability rather than to body size under such conditions (Dam & Peterson 1991), food concentration controls egg production in combination with body size in the Baltic Sea. The studies at the coastal English Channel, the German Bight and the Irish Sea, in contrast, were conducted in shallow, well mixed areas, with high food levels frequently exceeding limitation during spring and summer (Halsband & Hirche 2001, Devreker et al. 2005, Castellani & Altunbaş 2006). Under such unlimited food conditions, egg production is expected to be more frequently controlled by size, which determines the maximal reproductive rate. A similar dependence of the controlling factors on the hydrographical regime has been observed for several other, but not all, copepod species (Durbin et al. 1983, 1992, Runge 1985, Peterson & Bellantoni 1987).

Temora longicornis recruitment

In comparison to the numerous investigations on egg production and the variables controlling its seasonal variation, only little is known about the importance of *in situ* egg production for nauplii recruitment. In pelagic copepods, peaks in egg production associated with phytoplankton blooms and low egg mortality are considered to be key factors controlling the seasonal recruitment and copepod population dynamics (Kiørboe & Nielsen 1994, Peterson & Kimmerer 1994). We compared nauplii recruitment using egg production, egg hatching and female abundance with nauplii abundances observed in the field (Fig. 8). The results need to be interpreted with care because nauplii were not separated by stage in field samples, and the constant mortality among all nauplii stages used to calculate N1 abundance does not necessarily concur with the dynamic nature of copepod populations in the field. However, the estimated egg mortality based on the calculated egg and N1 stocks ranges from 0.7 to 6.5 and compares well with published rates for the species (Peterson & Kimmerer 1994). Thus, calculated N1 stocks appear reasonable.

The comparison of egg and calculated N1 stocks suggests that peak egg production is not a prerequisite for cohort development. Although the EPR varied seasonally and decreased strongly following the vernal bloom, population egg production and recruitment of nauplii was continuously high until October, which compares well with the similarly constant abundance of nauplii over the productive season. This continuous high recruitment is achieved by the alternation of peak egg production of a low female stock during the spring bloom with the low egg production of abundant females in succeeding generations. Despite the continuously high population egg production and recruitment, the numbers of females declined strongly from August onwards. This

suggests that population dynamics of *Temora longicornis* in autumn are determined by intense mortality of offspring.

CONCLUSIONS

In conclusion, we have shown that the seasonal variation in egg production of *Temora longicornis* in the Baltic Sea can be understood by separately analysing the effects of environmental variables on the sfEPR and the %FS. PL was the main variable together with food concentration explaining the seasonal variation in sfEPR. In turn, PL was largely determined by the seasonal variation in temperature, and, on a more general scale, by salinity, which appeared to limit size due to energetic constraints. The %FS was mainly dependent on food concentration. However, food explained only about half of the seasonal variation in %FS. Various other undetected factors such as maturation state, female age or spawning frequency likely determine %FS and should be the subject of future studies in order to provide a mechanistic understanding of the environmental control of %FS.

While the small size of females emphasizes a considerable constraint by the brackish conditions in the Baltic Sea, no direct effects of salinity or temperature on reproduction were detected. This is likely related to the behavioural adaptation of *Temora longicornis* to avoid energetic constraints due to suboptimal temperature conditions and a fluctuating salinity by staying in the cold intermediate water layer, which apparently constitutes a refuge and explains the species' success in the Baltic Sea. Nevertheless, any direct effects of salinity or temperature may also be undetected in field studies because they co-vary with the relevant variables such as size or food availability.

The importance of female length and food availability as main factors controlling the seasonal variation in egg production contrast with suggestions for a stimulation of reproduction by climate-driven changes in surface water temperature as a mechanism behind the observed increase in *Temora longicornis* stocks in the Baltic Sea (Dippner et al. 2000, Möllmann & Köster 2002). Our results suggest instead that any stimulation of egg production by temperature will likely be compensated by its negative effects on female size. Moreover, rising spring temperatures likely affect the conditions of the intermediate water layer and increase the environmental stress for egg production of *T. longicornis*. How the observed recruitment pattern of *T. longicornis* in the Baltic Sea changes in response to the environmental pressure should therefore be the subject of future studies.

Acknowledgements. The study was funded by the German Federal Ministry for Education and Research within the GLOBEC GERMANY project (03F0418C). We thank the crews and scientific parties of the RVs 'Heincke', 'Alkor' and 'Alexander von Humboldt' for excellent support during the study. We are grateful to M. Koski, E. Durbin and 3 anonymous reviewers for valuable comments on earlier versions of the manuscript.

LITERATURE CITED

Ambler JW (1985) Seasonal factors affecting egg production and viability of eggs of *Acartia tonsa* Dana from East Lagoon, Galveston, Texas. Estuar Coast Shelf Sci 20: 743–760

Arendt KE, Jónasdóttir SH, Hansen PJ, Gärtner S (2005) Effects of dietary fatty acids on the reproductive success of the calanoid copepod *Temora longicornis.* Mar Biol 146:513–530

Brand GW, Bayly IAE (1971) A comparative study of osmotic regulation in four species of calanoid copepod. Comp Biochem Physiol B Comp Biochem 38:361–371

Calliari D, Andersen CM, Thor P, Gorokhova E, Tiselius P (2006) Salinity modulates the energy balance and reproductive success of co-occurring copepods *Acartia tonsa* and *A. clausi* in different ways. Mar Ecol Prog Ser 312: 177–188

Calliari D, Andersen CM, Thor P, Gorokhova E, Tiselius P (2008) Instantaneous salinity reductions affect the survival and feeding rates of the co-occurring copepods *Acartia tonsa* and *A. clausi* differently. J Exp Mar Biol Ecol 362:18–25

Castellani C, Altunbaş Y (2006) Factors controlling the temporal dynamics of egg production in the copepod *Temora longicornis.* Mar Ecol Prog Ser 308:143–153

Castellani C, Lucas IAN (2003) Seasonal variation in egg morphology and hatching success in the calanoid copepods *Temora longicornis, Acartia clausi* and *Centropages hamatus.* J Plankton Res 25:527–537

Cervetto G, Gaudy R, Pagano M (1999) Influence of salinity on the distribution of *Acartia tonsa* (Copepoda, Calanoida). J Exp Mar Biol Ecol 239:33–45

Checkley DM (1980) Food limitation of egg production by a marine, planktonic copepod in the sea off southern California. Limnol Oceanogr 25:991–998

Corkett CJ, McLaren IA (1970) Relationship between development rate of eggs and older stages of copepods. J Mar Biol Assoc UK 50:161–168

CPR (Continuous Plankton Recorder) Survey Team (2004) Continuous Plankton Records: Plankton atlas of the North Atlantic Ocean 1958–1999. II. Biogeographical charts. Mar Ecol Prog Ser Suppl 2004:11–75

Dam HG, Lopes RM (2003) Omnivory in the calanoid copepod *Temora longicornis*: feeding, egg production and egg hatching success. J Exp Mar Biol Ecol 292:119–137

Dam HG, Peterson WT (1991) *In situ* feeding behavior of the copepod *Temora longicornis*: effects of seasonal changes

in chlorophyll size fractions and female size. Mar Ecol Prog Ser 71:113–123

Devreker D, Souissi S, Seuront L (2005) Effects of chlorophyll concentration and temperature variation on the reproduction and survival of *Temora longicornis* (Copepoda, Calanoida) in the Eastern English Channel. J Exp Mar Biol Ecol 318:145–162

Devreker D, Souissi S, Winkler G, Forget-Leray J, Leboulenger F (2009) Effects of salinity, temperature and individual variability on the reproduction of *Eurytemora affinis* (Copepoda; Calanoida) from the Seine estuary: a laboratory study. J Exp Mar Biol Ecol 368:113–123

Dippner JW, Kornilovs G, Sidrevics L (2000) Long-term variability of zooplankton in the Central Baltic Sea. J Mar Syst 25:23–31

Durbin EG, Smayda TJ, Verity PG (1983) Food limitation of production by adult *Acartia tonsa* in Narragansett Bay, Rhode Island. Limnol Oceanogr 28:1199–1213

Durbin EG, Durbin AG, Campbell R (1992) Body size and egg production in the marine copepod *Acartia hudsonica* during a winter-spring bloom in Narragansett Bay. Limnol Oceanogr 37:342–360

Dutz J, Koski M, Jónasdóttir SH (2008) Copepod reproduction is unaffected by diatom aldehydes or lipid composition. Limnol Oceanogr 53:225–235

Dutz J, Mohrholz V, van Beusekom JEE (2010) Life cycle and spring phenology of *Temora longicornis* in the Baltic Sea. Mar Ecol Prog Ser 406:223–238

Edler L (1979) Recommendations on methods for marine biological studies in the Baltic Sea. Phytoplankton and chlorophyll. Balt Mar Biol 5:1–38

Evans F (1981) An investigation into the relationship of sea temperature and food supply to the size of the planktonic copepod *Temora longicornis* Müller in the North Sea. Estuar Coast Shelf Sci 13:145–158

Farmer L, Reeve MR (1978) Role of the free amino acid pool of the copepod *Acartia tonsa* in adjustment to salinity change. Mar Biol 48:311–316

Flinkman J, Aro E, Vuorinen I, Viitasalo M (1998) Changes in northern Baltic zooplankton and herring nutrition from 1980s to 1990s: top-down and bottom-up processes at work. Mar Ecol Prog Ser 165:127–136

Gaudy R, Moraitou Apostolopoulou M, Pagano M, Saint Jean L, Verriopoulos G (1988) Salinity as a decisive factor in the length of cephalothorax of *Acartia clausi* from three different areas (Greece and Ivory Coast). Rapp P-V Comm Int Explor Sci Mer Mediterr 31:233

Gaudy R, Cervetto G, Pagano M (2000) Comparison of the metabolism of *Acartia tonsa* and *A. clausi*: influence of temperature and salinity. J Exp Mar Biol Ecol 247: 51–65

Goolish EM, Burton RS (1989) Energetics of osmoregulation in an intertidal copepod: effects of anoxia and lipid reserves on the pattern of free amino acid accumulation. Funct Ecol 3:81–89

Halsband C, Hirche H (2001) Reproductive cycles of dominant calanoid copepods in the North Sea. Mar Ecol Prog Ser 209:219–229

Hänninen J, Vuorinen I, Hjelt P (2003) Atlantic climatic factors control decadal dynamics of a Baltic Sea copepod *Temora longicornis.* Ecography 26:672–678

Hansen FC, Möllmann C, Schütz U, Neumann T (2006) Spatio-temporal distribution and production of calanoid copepods in the central Baltic Sea. J Plankton Res 28: 39–54

Hirche HJ, Meyer U, Niehoff B (1997) Egg production of *Calanus finmarchicus*: effect of temperature, food and season. Mar Biol 127:609–620

Holste L, St. John MA, Peck MA (2009) The effects of temperature and salinity on reproductive success of *Temora longicornis* in the Baltic Sea: a copepod coping with a tough situation. Mar Biol 156:527–540

Ianora A (1998) Copepod life history traits in subtemperate regions. J Mar Syst 15:337–349

Ianora A, Scotto di Carlo B, Mascellaro P (1989) Reproductive biology of the planktonic copepod *Temora stylifera.* Mar Biol 101:187–194

Ianora A, Miralto A, Poulet SA (2003) The effects of diatoms on copepod reproduction: a review. Phycologia 42: 351–363

Jónasdóttir SH, Fields D, Pantoja S (1995) Copepod egg production in Long Island Sound, USA, as a function of the chemical composition of seston. Mar Ecol Prog Ser 119: 87–98

Kiørboe T, Nielsen TG (1994) Regulation of zooplankton biomass and production in a temperate, coastal ecosystem. Limnol Oceanogr 39:493–507

Klein Breteler WCM, Gonzales SR (1988) Influence of temperature and food concentration on body size, weight and lipid content of two calanoid copepod species. Hydrobiologia 167-168:201–210

Kleppel GS, Holliday DV, Pieper RE (1991) Trophic interactions between copepods and microplankton: a question about the role of diatoms. Limnol Oceanogr 36: 172–178

Koski M, Dutz J, Klein Breteler WCM (2005) Selective grazing of *Temora longicornis* in different stages of a *Phaeocystis globosa* bloom — a mesocosm study. Harmful Algae 4:915–927

Köster P (2003) Körpermaße und Kohlenstoffgehalte dominanter Zooplanktonarten der Ostsee in Abhängigkeit von Salzgehalt, Ernährungszustand und Temperatur. MS thesis, University of Rostock

Landry MR (1978) Population dynamics of a planktonic marine copepod, *Acartia clausii*, in a small temperate lagoon on San Juan Island, Washington. Int Rev Ges Hydrobiol 63:77–119

Lee CE, Petersen CH (2003) Effects of developmental acclimation on adult salinity tolerance in the freshwater-invading copepod *Eurytemora affinis.* Physiol Biochem Zool 76:296–301

Maps F, Runge JA, Zakardjian B, Joly P (2005) Egg production and hatching success of *Temora longicornis* (Copepoda, Calanoida) in the southern Gulf of St. Lawrence. Mar Ecol Prog Ser 285:117–128

Miliou H (1996) The effect of temperature, salinity and diet on final size of female *Tisbe holothuriae* (Copepoda, Harpacticoida). Crustaceana 69:742–754

Mohrholz V, Dutz J, Kraus G (2006) The impact of exceptionally warm summer inflow events on the environmental conditions in the Bornholm Basin. J Mar Syst 60: 285–301

Möllmann C, Köster FW (2002) Population dynamics of calanoid copepods and the implications of their predation by clupeid fish in the Central Baltic Sea. J Plankton Res 24:959–977

Niehoff B (2007) Life history strategies in zooplankton communities: the significance of female gonad morphology and maturation types for the reproductive biology of marine calanoid copepods. Prog Oceanogr 74:1–47

Paffenhöfer GA, Ianora A, Miralto A, Turner JT and others (2005) Colloquium on diatom–copepod interactions. Mar Ecol Prog Ser 286:293–305

Parrish KK, Wilson DR (1978) Fecundity studies on *Acartia tonsa* (Copepoda: Calanoida) in standardized culture. Mar Biol 46:65–81

Peters J, Dutz J, Hagen W (2007) Role of essential fatty acids on the reproductive success of the copepod *Temora longicornis* in the North Sea. Mar Ecol Prog Ser 341: 153–163

Peterson WT, Bellantoni DC (1987) Relationships between water-column stratification, phytoplankton cell size and copepod fecundity in Long Island Sound and off central Chile. S Afr J Mar Sci 5:411–421

Peterson WT, Kimmerer W (1994) Processes controlling recruitment of the marine calanoid copepod *Temora longicornis* in Long Island Sound: egg production, egg mortality and cohort survival rates. Limnol Oceanogr 39: 1594–1605

Plourde S, Joly P (2008) Comparison of *in situ* egg production rate in *Calanus finmarchicus* and *Metridia longa*: discriminating between methodological and species-specific effects. Mar Ecol Prog Ser 353:165–175

Putt M, Stoecker DK (1989) An experimentally determined carbon:volume ratio for marine 'oligotrichous' ciliates from estuarine and coastal waters. Limnol Oceanogr 34: 1097–1103

Runge JA (1984) Egg production of the marine, planktonic copepod, *Calanus pacificus* Brodsky: laboratory observations. J Exp Mar Biol Ecol 74:53–66

Runge JA (1985) Relationship of egg production of *Calanus pacificus* to seasonal changes in phytoplankton availability in Puget Sound, Washington. Limnol Oceanogr 30: 382–396

Sekiguchi H, McLaren IA, Corkett CJ (1980) Relationship between growth rate and egg production in the copepod *Acartia clausi hudsonica.* Mar Biol 58:133–138

Tang KW, Dam HG, Feinberg LR (1998) The relative importance of egg production rate, hatching success, hatching duration and egg sinking in population recruitment of two species of marine copepods. J Plankton Res 20: 1971–1987

Uye SI, Murase A (1997) Relationship of egg production rates of the planktonic copepod *Calanus sinicus* to phytoplankton availability in the Inland Sea of Japan. Plankton Biol Ecol 44:3–11

Van Beusekom JEE, Mengedoht D, Augustin CB, Schilling M, Boersma M (2009) Phytoplankton, protozooplankton and nutrient dynamics in the Bornholm Basin (Baltic Sea) in 2002–2003 during the German GLOBEC Project. Int J Earth Sci 98:251–260

Van Rijswijk P, Bakker C, Vink M (1989) Daily fecundity of *Temora longicornis* (Copepoda Calanoida) in the Oosterschelde estuary (SW Netherlands). Neth J Sea Res 23: 293–303

Wesche A, Wiltshire KH, Hirche HJ (2007) Overwintering strategies of dominant calanoid copepods in the German Bight, southern North Sea. Mar Biol 151:1309–1320

Editorial responsibility: Edward Durbin, Narragansett, Rhode Island, USA

Submitted: July 18, 2011; Accepted: May 22, 2012
Proofs received from author(s): August 2, 2012