ORIGINAL PAPER

Environmental cues and constraints affecting the seasonality of dominant calanoid copepods in brackish, coastal waters: a case study of *Acartia*, *Temora* and *Eurytemora* species in the south-west Baltic

A. Berenike S. Diekmann · Catriona Clemmesen ·
Michael A. St. John · Matthias Paulsen ·
Myron A. Peck

Abstract Information on physiological rates and tolerances helps one gain a cause-and-effect understanding of the role that some environmental (bottom–up) factors play in regulating the seasonality and productivity of key species. We combined the results of laboratory experiments on reproductive success and field time series data on adult abundance to explore factors controlling the seasonality of *Acartia* spp., *Eurytemora affinis* and *Temora longicornis*, key copepods of brackish, coastal and temperate environments. Patterns in laboratory and field data were discussed using a metabolic framework that included the effects of 'controlling', 'masking' and 'directive' environmental factors. Over a 5-year period, changes in adult abundance within two south-west Baltic field sites (Kiel Fjord *Pier*, 54°19′89N, 10°09′06E, 12–21 psu, and North/Baltic Sea Canal *NOK*, 54°20′45N, 9°57′02E, 4–10 psu) were evaluated with respect to changes in temperature, salinity, day length and chlorophyll a concentration. *Acartia* spp. dominated the copepod assemblage at both sites (up to 16,764 and 21,771 females m^{-3} at *NOK* and *Pier*) and was 4 to 10 times more abundant than *E. affinis* (to 2,939 m^{-3} at *NOK*) and *T. longicornis* (to 1,959 m^{-3} at *Pier*), respectively. Species-specific salinity tolerance explains differences in adult abundance between sampling sites whereas phenological differences among species are best explained by the influence of species-specific thermal windows and prey requirements supporting survival and egg production. Multiple intrinsic and extrinsic (environmental) factors influence the production of different egg types (normal and resting), regulate life-history strategies and influence match–mismatch dynamics.

Introduction

Understanding the physiological-basis behind the distribution and productivity of marine organisms is important if we hope to increase our ability to predict how anthropogenic changes to environments will affect key species and the functioning of ecosystems (Pörtner and Farrell 2008; Pörtner and Peck 2010; Somero 2010). At the most basic level, suitable environments are those where organisms have excess energy available to fuel growth and other essential activities (e.g. Huey and Kingsolver 1993; Pörtner and Knust 2007). Changes in key environmental factors can affect the amounts of available energy and influence the seasonal timing and spatial extent of environments that are optimal for the productivity of predators and their prey, influencing match–mismatch dynamics and the functioning of marine systems (Rijnsdorp et al. 2009; Pörtner and Farrell 2008). Compared to deeper, marine habitats, estuaries and other shallow coastal zones can display relatively rapid changes in key abiotic factors (e.g. temperature, salinity and nutrient concentration). These rapid changes

A. B. S. Diekmann (✉) · M. A. St. John · M. A. Peck
Institute of Hydrobiology and Fisheries Science,
University of Hamburg, Olbersweg 24,
22767 Hamburg, Germany
e-mail: berenike.diekmann@uni-hamburg.de

C. Clemmesen · M. Paulsen
Leibniz Institut für Meereswissenschaften (IFM-GEOMAR),
Düsternbrooker Weg 20, 24105 Kiel, Germany

Present Address:
M. A. St. John
National Institute of Aquatic Resources (DTU-Aqua),
Technical University of Denmark, Jægersborg Allé 1,
2920 Charlottenlund, Denmark

place added physiological demands and constraints on local organisms.

Small-bodied copepods form the bulk of secondary production in coastal, estuarine environments, and in northern temperate latitudes, species are characterized by short generation times and overlapping broods (Conover 1988; Mauchline 1998). Calanoid species within the genera *Acartia*, *Temora* and *Eurytemora* dominate the copepod biomass of many estuaries (Mauchline 1998), and key species within the Baltic Sea include *Eurytemora affinis*, *Acartia tonsa*, *A. bifilosa*, *A. longiremis* and *Temora longicornis*. These species have local populations within shallow waters of Kiel Fjord and the Kiel Canal within the south-west Baltic Sea that display different phenologies due to species-specific differences in temperature optima as well as feeding strategies. For example, *E. affinis* dominates in the spring (to 15 °C) but is succeeded by *A. tonsa* in warmer periods (Hirche 1992 and references therein). *Acartia* spp. utilize raptorial and suspension feeding and ingest a wider size spectrum of food than *E. affinis* that only utilizes suspension feeding (Gyllenberg 1980; Adrian et al. 1999 and references therein). In late summer, large decreases in the copepod assemblage result from the intensive predation by fish and mysids (Adrian et al. 1999). Adrian et al. (1999) also reported a larger decline during winter in the biomass of *E. affinis* compared to *Acartia* spp. (here: *A. bifilosa* and *A. longiremis*), which was explained by the differences in feeding efficiency. In the winter, *A. tonsa* is reported to be absent (Christiansen 1988) but the other congeners (*A. bifilosa* and *A. longiremis*) can be found all year round with maximal abundances in nauplii in February/March and November (Hernroth and Ackefors 1979). Working in offshore areas of the Baltic Sea, Schulz et al. (2007) also demonstrated that populations of *A. longiremis* as well as *Temora longicornis* persisted throughout most of the year but that these species did not utilize the warmer, surface waters. In that study, *A. bifilosa* inhabited warm surface waters where its egg production rate was more controlled by food availability than temperature (Schulz et al. 2007).

In the following, we summarize present knowledge on how temperature, salinity, day length, phytoplankton production and the interactions among those factors affect reproductive success and population productivity of dominant calanoid copepods inhabiting coastal waters of the south-west Baltic Sea. Information from controlled laboratory studies was compared to site-specific changes in the abundance of adult *Acartia* spp., *T. longicornis* and *E. affinis* at the two field locations in the south-west Baltic Sea. Based upon the classification of Fry (1971), we distinguished among 'controlling' factors that govern metabolic rate by affecting molecular kinetics (e.g. temperature), 'masking' factors that modify the effect of other environmental factors by influencing energy allocation (e.g. salinity affecting osmoregulation) and 'directive' factors that cue some response affecting energy partitioning typically via hormone induction (e.g. day length on reproduction). Based upon previous research on these copepods, we hypothesize that (1) *Acartia* spp. should be found throughout the year (albeit as varying proportions of the three congeners), (2) temperatures should be suitable for *T. longicornis* and *E. affinis* throughout the year but that salinity will affect abundance since *T. longicornis* (*E. affinis*) is not adapted to low (high) salinities (Holste et al. 2009; Viitasalo et al. 1994), and (3) *E. affinis* will occur at highest abundance during spring and at lower abundance during the rest of the year. Unless otherwise stated, literature data summarized in subsequent sections were collected on south-west Baltic Sea populations of these copepods. We highlight differences in life cycle strategies and speculate on how potential climate-driven changes in key factors would influence the copepod community and lower trophic level match–mismatch dynamics in the south-west Baltic region.

Materials and methods

Laboratory data

Egg production rate (*EPR*; eggs female^{-1} day^{-1}) and hatching success (*HS*; %) were measured in a 16-day trial conducted with *A. tonsa*. The methods employed were the same as those discussed by Diekmann et al. (2009), examining different algal treatments on *EPR* except for the following changes. First, *EPR* and *HS* are presented from control groups of copepods—those fed with algae maintained in exponential growth-phase. Second, trials were conducted at each of two Baltic Sea salinities (8 and 18 psu), using a day length of 13 h and 16 °C water. Third, three different egg types were distinguished: subitaneous eggs (*SBE*) which rapidly hatched, resting eggs (*RE*) which neither hatched nor disintegrated within a 3-week incubation and dead eggs (*DE*) which did not hatch but disintegrated within this 3-week period. In terms of *RE*, we did not distinguish between diapause eggs that require an obligatory refractory phase before hatching and quiescence eggs that have a facultative pause in development under unfavourable conditions, but hatch as soon as conditions ameliorate.

Field data

From March 2005 until September 2010, a regular survey aimed at determining the abundance and species composition of zooplankton in relation to environmental data has

been performed at two sampling sites (Kiel Fjord (*Pier,* 54°19′89N, 10°09′06E) and the North/Baltic Sea Canal (*NOK*, 54°20′45 N, 09°57′02E), Fig. 1). For exact sampling periods, see Table 1. All samples were collected aboard the RV 'Polarfuchs'. For this study, temperature (*T*), salinity (*S*) and chlorophyll a (*Chl a*) and adult female copepod abundance data were utilized. Measurements of *T* and *S* were made at 7 m (WTW senor through 2006 then Sea and Sun Technology, CTD48M), and concentrations of *Chl a* were measured in water collected at 7 m using a 5L Nanson water sampler deployed at both sites. A 250-ml water sample was filtered through a GF/F glass fibre filter (25 mm diameter, Whatman), and *Chl a* was determined using the method of Jeffrey and Humphrey (1975). Copepods were sampled with a WP2 net (200-μm mesh size) hauled vertically from 3 m above the bottom to the surface. Contents were preserved with a 4 % formalin solution. In the laboratory, a plankton splitter was used to obtain a representative sub-sample that contained at least 100 individuals of the most abundant copepod species. The subsample counts were converted to total abundance (individuals m^{-3}). *Eurytemora* and *Temora* were identified to the species level (*E. affinis*; *T. longicornis*) and *Acartia* to the genus level. In a few instances (specific dates and species), we back-calculated the hatch date of adult females based upon previously published, species-specific, temperature-dependent development times (e.g. Ban 1994; Klein Breteler and Gonzalez 1982; Mauchline 1998). For these rough estimates, we assumed that females were 1-week-old when captured and that temperature changed in a linear fashion between (weekly) measurements.

Results

Literature and laboratory-based findings

Thermal windows

A summary of *EPR* measurements reported in various studies and at various study sites in the Baltic and North Sea suggest an optimum temperature (T_{opt}) for *A. tonsa* and *T. longicornis* at 23 and 17 °C, respectively (Fig. 2). Upper and lower 'pejus' temperatures were calculated to be equal to the points where *EPR* was 50 % than at T_{opt}. Temperatures between lower and upper pejus thresholds (T_P) can be considered to represent the window of optimal thermal conditions. When thermal windows were calculated in this manner, both *A. tonsa* and *T. longicornis* could be considered thermal generalists with the former slightly more stenothermal (12.5 °C; range between upper and lower T_P) compared to the latter (15 °C range). For *A. tonsa,* a lethal temperature of 34 °C has been reported.

Egg development/hatching

Hatching and/or development of the three different egg types was found to be influenced by day length and salinity (Fig. 3). The proportion of *SBE* increased with increasing day length but remained relatively unchanged at ≥16 h of light (Fig. 3a). A key difference between 8 and 18 psu was that the proportion of *RE* produced was significantly higher at the former versus the latter salinity (Kruskal–Wallis and Mann–Whitney; arcsine transformation; $p \leq 0.001$)

Fig. 1 Location of the two field sampling sites utilized in this study: North Sea and Baltic Canal (*NOK*, 54°20′45N, 9°57′02E) and Kiel Fjord (*Pier*, 54°19′89N, 10°09′06E), Baltic Sea, Germany. Note that the coordinates are given in decimals: *NOK* (latitude: 54.34; longitude: 9.96) and *Pier* (latitude: 54.33; longitude: 10.15)
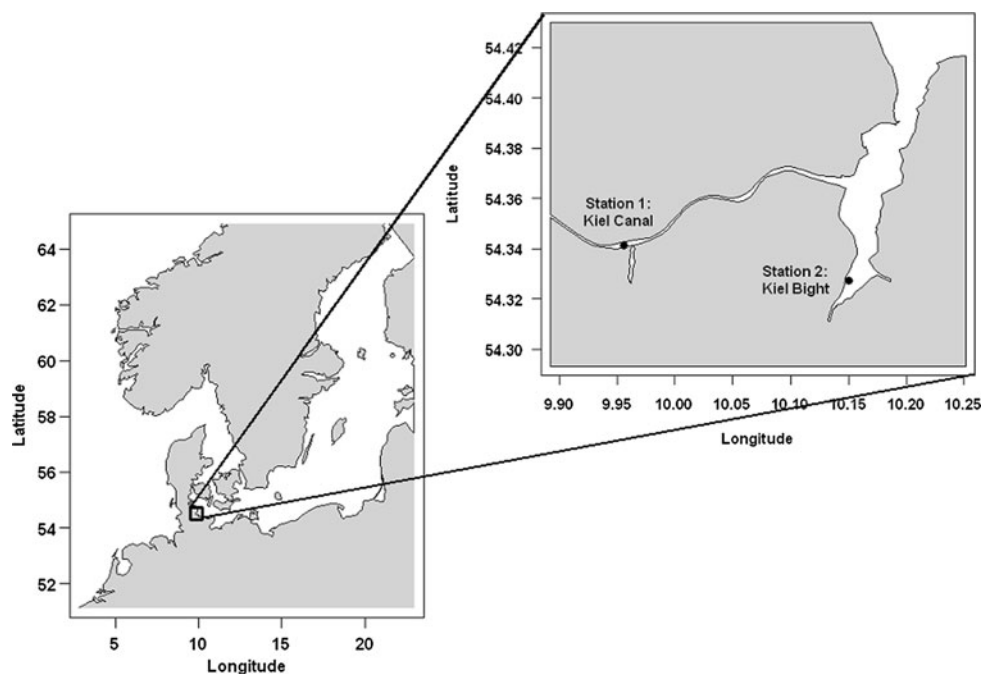
Table 1 Data set sampling periods per station and year in calendar week (CW) and month

	Dates of *Pier* sampling		Dates of *NOK* sampling	
	First (CW/month)	Last (CW/month)	First (CW/month)	Last (CW/month)
2005	13/March	51/December	–	–
2006	09/March	42/October	–	–
2007	01/January	51/December	17/April	39/September
2008	02/January	43/October	–	–
2009	06/February	51/December	14/April	51/December
2010	05/February	32/August	11/March	37/September
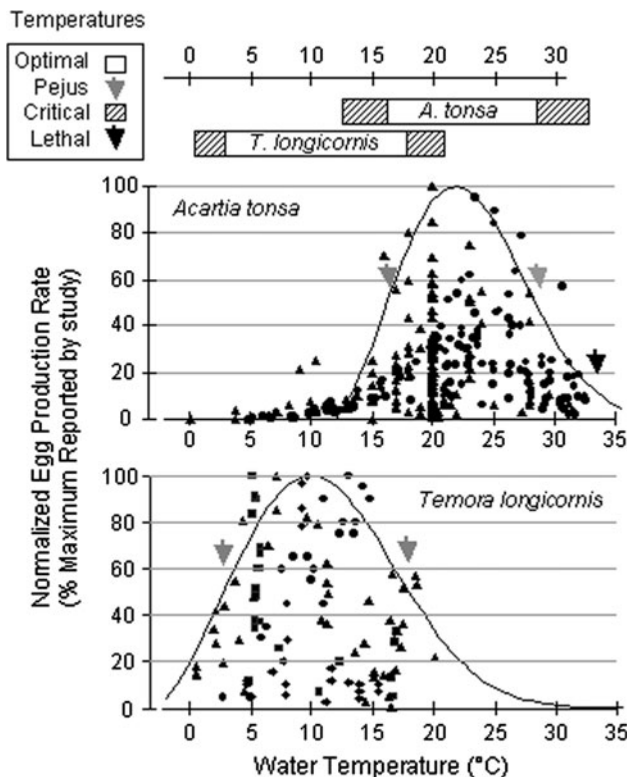
Fig. 2 Normalized egg production rate [% maximum rate (eggs female^{-1} day^{-1}) reported by study] of *Acartia tonsa* and *Temora longicornis* versus water temperature (°C) showing optimal (T_{OPT}), pejus (T_P) and critical (T_{CRIT}) temperatures. Lower and upper T_P were set equal to 50 % maximum egg production rate. For *A. tonsa*, data were pooled and normalized from >10 laboratory and field studies (see Holste 2010). For *T. longicornis*, the data from 3 studies were utilized (Fransz and Gonzalez 1990; Halsband and Hirche 2001; Holste et al. 2009)

(Fig. 3b). At 8 psu, the proportion of *SBE* (*RE*) decreased (increased) with decreasing *EPR* (Fig. 3b).

Field data–based findings

Among adult females of the studied copepods, *Acartia* spp. was most abundant at both sites and obtained higher peak abundance at *Pier* compared to *NOK* (Fig. 5a, Table 2). At *NOK* *E. affinis* was often abundant but was rare or absent at

Pier (Fig. 5b, Table 2). At *Pier*, peak abundances of *E. affinis* were between 4 and 435 m^{-3} and their temporal occurrence was more variable (end of April until August) compared to *NOK*. Finally, *T. longicornis* was never found at *NOK* but was regularly encountered at *Pier* (Fig. 5c, Table 2). Irrespective of the sampling site, peak abundances of *E. affinis* and *T. longicornis* were similar and were 10–25 % those of *Acartia* spp. (Fig. 5a–c).

Although *Acartia* spp. were abundant at both sites (Fig. 5d), the different salinity conditions between *NOK* (4.9–12.4 psu) and *Pier* (11.9–21.4 psu) coincided with differences between presence/absence and/or abundance of *T. longicornis* (Fig. 5e) and *E. affinis*, (Fig. 5f). Despite warmer temperatures and higher *Chl a* concentrations at *NOK*, *Acartia* spp. were most abundant at *Pier* (Figs. 4, 5) where *Acartia* spp. females were found at 0 °C at *Chl a* concentrations generally <5 µg L^{-1} (Fig. 6a). In contrast, at the *NOK* site, *Acartia* spp. was absent when samples were collected at <10 °C and occurred infrequently at <15 °C (Fig. 6a). Peak abundances of *E. affinis* occurred at ∼15 °C at *NOK* (Fig. 6b). Given the low occurrence of *E. affinis* at the *Pier* site, no trends were described. At *Pier*, the peak abundance of *T. longicornis* occurred in waters colder than 15 °C when *Chl a* concentrations were <5 µg L^{-1} (Fig. 6c).

The mean abundance of *Acartia* spp. females increased with increasing day length (7–17 h) and water temperature at *Pier* (Fig. 7a) but, despite equal if not warmer temperatures later in the summer, mean abundance sharply declined as soon as day lengths started to decrease. At the same temperature, the abundance of *Acartia* spp. females at *Pier* was always higher at increasing as opposed to decreasing day lengths (with the exception of one sampling point equally high at ∼16 °C) (Fig. 7a). At *NOK*, the increase in mean *Acartia* spp. abundance was delayed until much longer day lengths compared to the *Pier* site and the decrease in abundance with decreasing day length was much slower. Consequently, peak abundance occurred when day lengths were decreasing at *NOK*. At this site, *E. affinis* abundance increased with increasing day length and when waters were colder than ∼15 °C (Fig. 7b).

Fig. 3 The relationships between the types of eggs produced by *Acartia tonsa* when females were reared at different day lengths (h) (**a**) versus time (female age) at 8 psu and 18 psu (**b**) and in relation to egg production rate (eggs female^{-1} day^{-1}) (**c**). In **a** and **c**, the proportion of subitaneous eggs (*SBE*, those hatching within 48–72 h) are shown (modified after Peck et al. 2008). In **b**, three egg types are shown: (1) *SBE*, (2) potential resting eggs (*RE*) that did not hatch or disintegrate after 3 weeks and (3) '*Other*', eggs which disintegrated within 3 weeks. In **c**, regression equations are $SBE_{18psu} = 0.854EPR + 28.4$, $r^2 = 0.25$, $p = 0.055$; $SBE_{8psu} = 0.837EPR + 22.1$, $r^2 = 0.7$, $p < 0.0001$
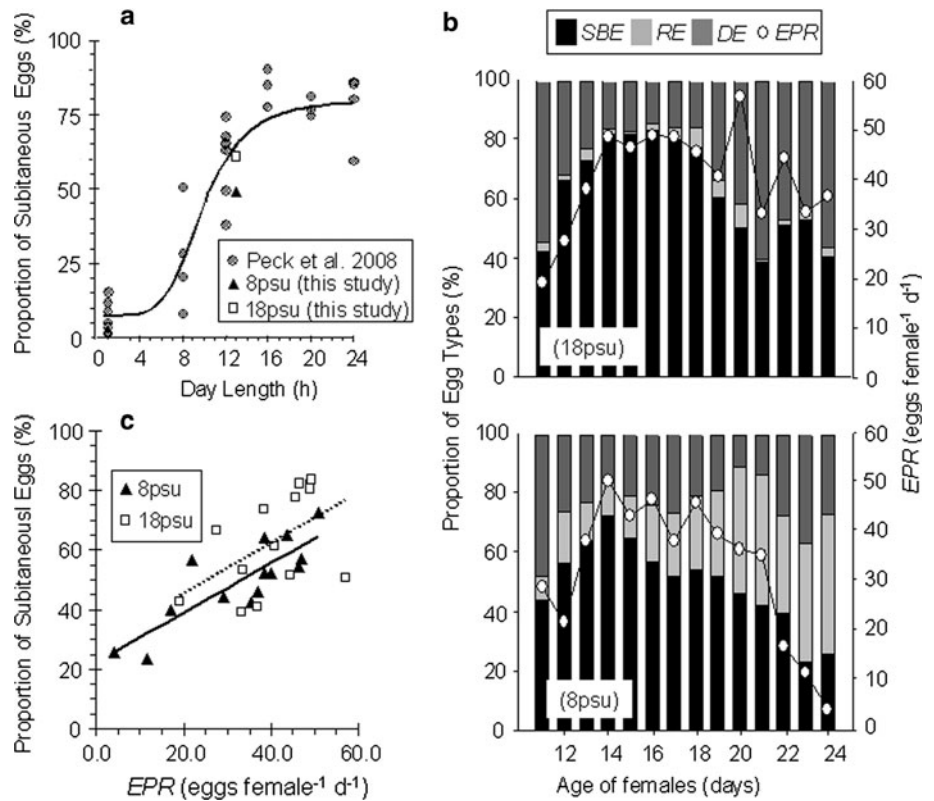

Table 2 Summary of maximal abundances of *Acartia* spp., *T. longicornis*, *E. affinis* and environmental conditions

		Maximal abundances					
		Calender week	Day length (h)	Temperature (°C)	Salinity (psu)	Chl a (μg L^{-1})	Abundance (No. m^{-3})
Acartia spp.	2007 *Pier*	25	17.25	16.8	14.8	9.3	1,524
	2007 *NOK*	34	14.5	19.1	8	15.9	16,764
	2008 *Pier*	35	14.25	16.6	16.7	6.7	1,023
	2009 *Pier*	24	17	15.4	14.6	9.4	7,620
	2009 *NOK*	23	17	16.7	8.8	10.5	3,576
	2010 *Pier*	26	17.25	17.5	13.4	19.9	21,771
	2010 *NOK*	20	16.25	10.3	9.3	3.5	980
T. longicornis (only *Pier*)	2007	23	17	14.3	14.8	10.6	871
	2009	16	14	6	16	2.4	435
	2010	12	12.5	1.5	16.3	4	1,959
E. affinis (only *NOK*)	2007	20	16	13.9	6.2	10.1	2,047
	2009	20	16	13.3	8.2	7.4	2,939
	2010	21	16.5	12.6	8.9	4.5	686

Longer day lengths and warmer temperatures were associated with dramatic decreases in the abundance of *E. affinis*. Interestingly, the abundance of *E. affinis* did not increase in the autumn when temperatures declined below 15 °C. Lastly, the mean abundance of *T. longicornis* females was highest at day lengths between 10 and 17 h and when both day length and water temperature were increasing (Fig. 7c).

Back-calculations of the time of hatch could be made for *T. longicornis* and *Acartia* spp. at *Pier* in 2007. In that year, peak abundances occurred in calendar weeks 22 (May 29th) and 25 (June 18th). Based upon in situ temperatures, development times needed for *T. longicornis* and *Acartia* spp. to reach the adult stage were estimated to be 25 and 53 days, respectively. Hatch dates would be approximately May 5th and April 27th, respectively. For *E. affinis* and
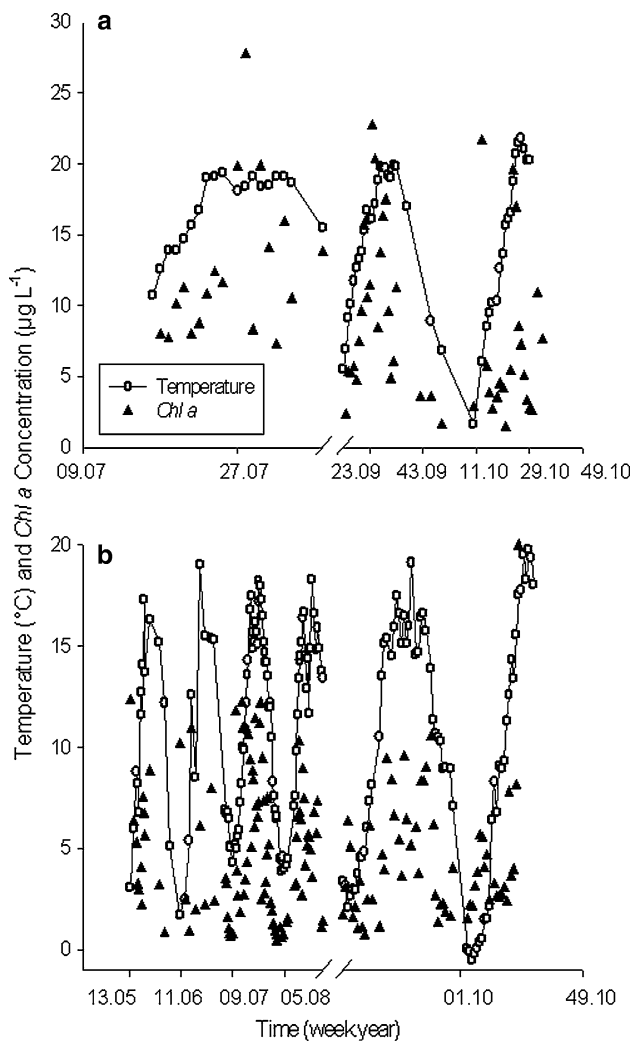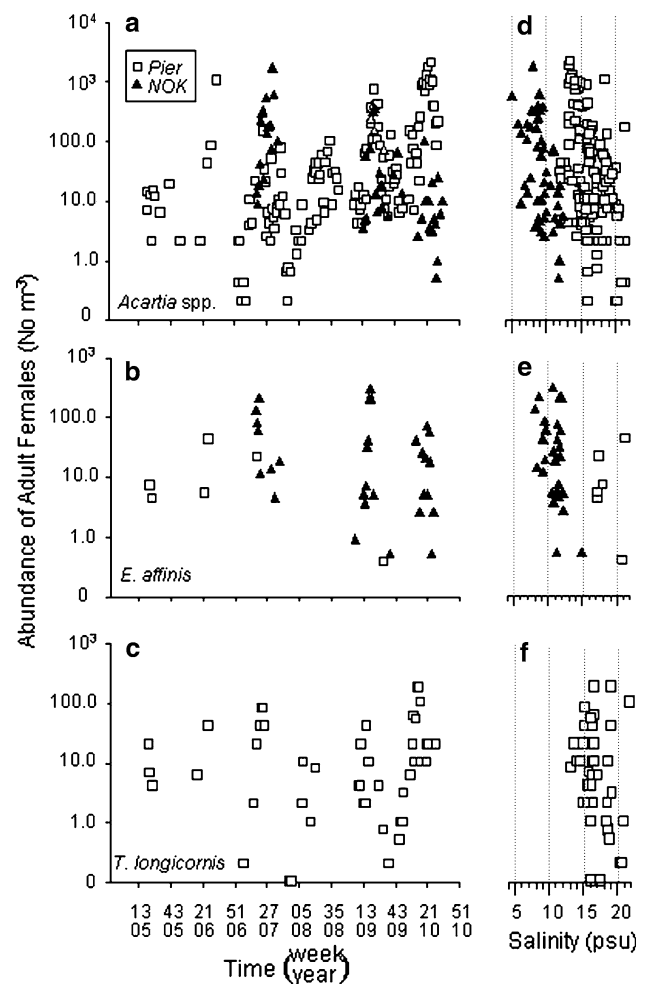
Fig. 4 *Chl a* concentration (μg L^{-1}) and water temperature (°C) measured at 7-m depth at *NOK* (**a**) and *Pier* (**b**) sampling sites versus time (shown as year and week, yyww) from March 2005 until September 2010. Note, sampling was not continuously performed at either location

Fig. 5 The abundance (individuals m^{-3}) of female copepods of *Acartia* spp. (**a**, **d**), *Eurytemora affinis* (**b**, **e**) and *Temora longicornis* (**c**, **f**) at the two sampling sites (*NOK* and *Pier*) versus time (shown as week and year) as well as water salinity at capture. Note, sampling was not continuously performed at either location

Acartia spp. at *NOK* in 2009, peak abundances occurred in calendar weeks 15 (May 25th) and 23 (June 2nd), and calculations suggested that development times of 20 and 52 days would have been required for eggs to reach the adult stage. At *NOK*, therefore, hatching of *E. affinis* and *Acartia* spp. was predicted to have occurred on May 5th and April 11th, respectively. These dates at the two sites suggested that eggs hatched at temperatures of approximately 9.2, 9.9 and 12.7 °C for *Acartia* spp., *T. longicornis* and *E. affinis*, respectively.

Discussion

Understanding species-specific differences in physiological optima and tolerances can provide insight into how

climate-driven changes in bottom–up factors can lead to changes in species abundance, distribution and composition (Pörtner and Peck 2010; Somero 2010). Once robust estimates of these physiological limits have obtained, changes in populations can then be assessed with respect to other (trophodynamic) processes such as the role of key predators. The present study reviews how important environmental factors affect the reproductive success and abundance of calanoid copepods inhabiting shallow, brackish waters of the south-west Baltic Sea. After a brief overview of the *Acartia* species complex in the Baltic Sea, we review how various controlling, masking and directive factors affect copepod reproductive rate and survival and reproductive strategy (production of different egg types). In each case, a brief summary of previous field and laboratory findings is provided as a backdrop for patterns observed in our field data. Moreover, within each

Fig. 6 The abundance (individuals m^{-3}) of female copepods of *Acartia* spp. (**a**), *Eurytemora affinis* (**b**) and *Temora longicornis* (**c**) versus water temperature (°C) and *Chl a* concentration (μg L^{-1}) at the two sampling sites. Note, the data from 5 years of sampling are pooled
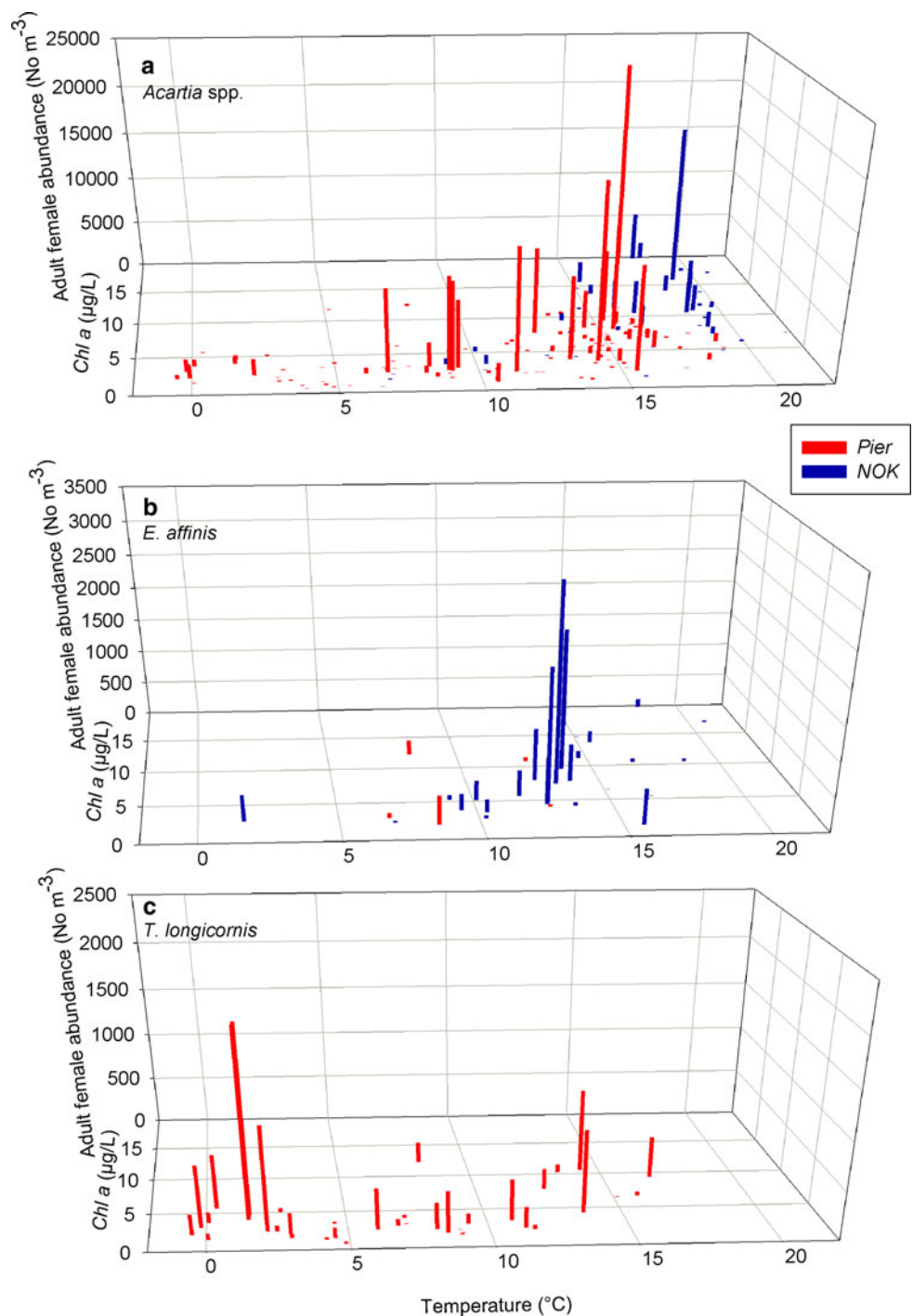

sub-section, we first discuss *Acartia* spp., then *T. longicornis* and finally *E. affinis*. If not otherwise stated, all literature data discussed were collected on populations inhabiting the Baltic Sea.

Acartia spp. in the Baltic Sea

In the present study, copepods in the *Acartia* genus were not identified to species, and some general remarks are needed with respect to distribution and physiology of different species. Three congeners (*Acartia bifilosa*, *A. longiremis* and *A. tonsa*) have been reported by Christiansen (1988) and Postel (2005) from seasonal collections made in our study region [the Schlei estuary (north-west of Kiel Bight) and north-east of Kiel Bight up to the Gotland Sea, respectively]. Thus, we assume the *Acartia* spp. category in our study consists of these three species. Previous field collections reported that *A. bifilosa* and *A. longiremis* occur

Fig. 7 The abundance (individuals m^{-3}) of female copepods of *Acartia* spp. (**a**), *Eurytemora affinis* (**b**) and *Temora longicornis* (**c**) versus water temperature (°C) and day length (h) at the two sampling sites. Note, the data from 5 years of sampling are pooled
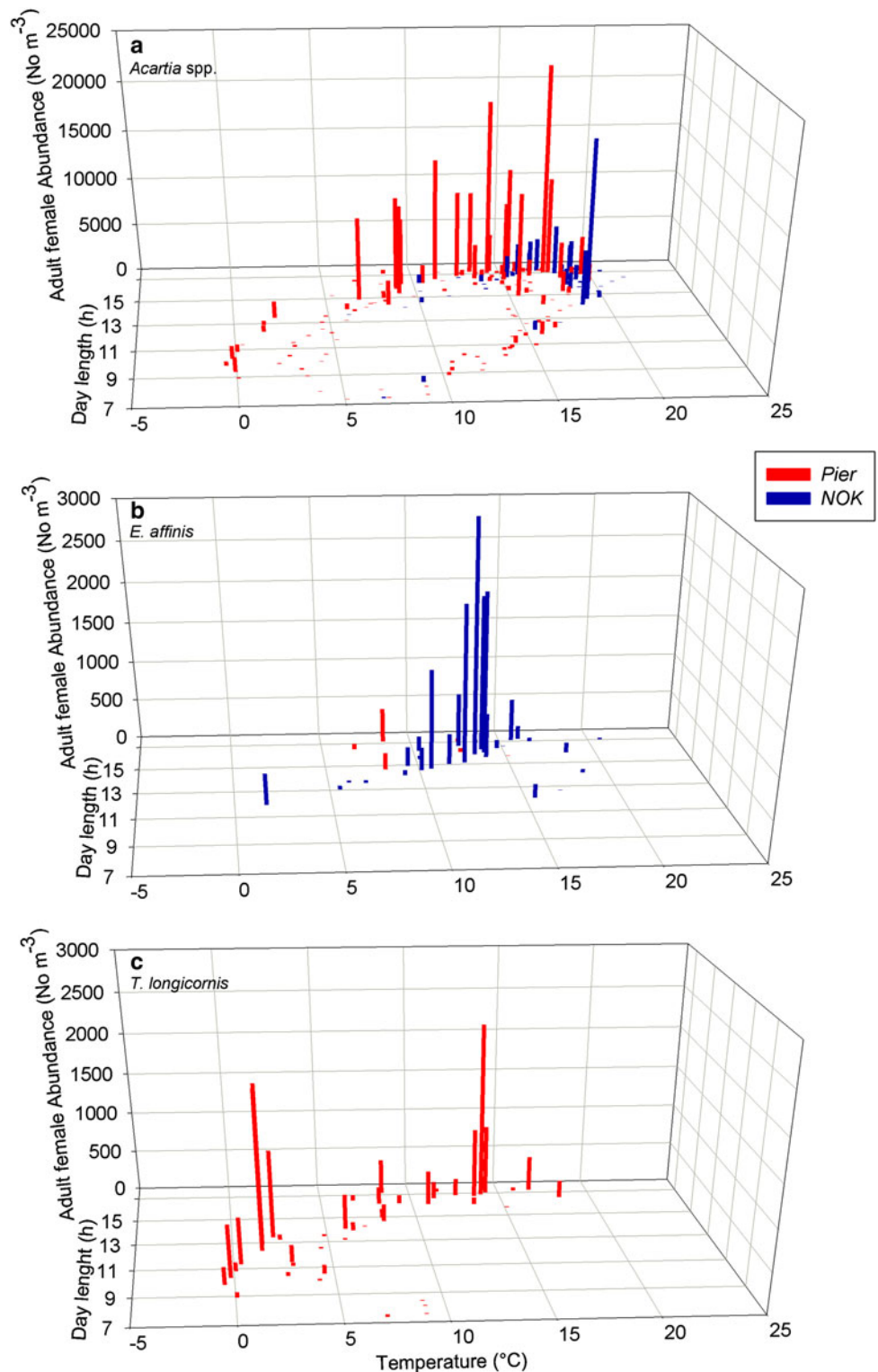
throughout the year while *A. tonsa* was absent in the cooler months [e.g. December through May, (Christiansen 1988)]. *Acartia longiremis* females undergo dormancy during winter (Davis 1976; Norrbin 1996) while *A. bifilosa* is adapted to colder temperatures (Schnack 1975) and over-summers as resting eggs (*RE*) in the North Sea (Chinnery and Williams 2003). *Acartia tonsa* is originally a tropical species and has been reported in the Baltic since the 1930s (Brylinski 1981 and references therein). Genetic analyses by Drillet et al. (2008) suggested that the Baltic population of *A. tonsa* probably originated from a population in Narragansett Bay, Rhode Island (USA) or adjacent waters.

This species is adapted to warmer temperatures and produces *RE* as an overwintering strategy (Zillioux and Gonzalez 1972; Sullivan and McManus 1986; Drillet et al. 2011). The previous work by Postel (2005) suggested that the three species tend to vary in dominance depending upon the year. However, we assume that *A. tonsa* represented the largest part of the *Acartia* spp. stock at least during some periods of each year because its *EPR* (20–41 eggs female^{-1} day^{-1}) can be 2 to >5 times higher than that of *A. bifilosa* (up to 22 eggs female^{-1} day^{-1}) and *A. longiremis* (5 eggs female^{-1} day^{-1}) in the Baltic Sea (Dutz et al. 2004a; Peck and Holste 2006).

Reproductive rate and survival

Controlling and directive factors: thermal windows, prey concentrations and day length

The majority of net energy available for growth of adult copepods, after allocating energy for metabolic costs, is allocated to the production of eggs (reproductive tissue). Therefore, thermal windows supporting growth can be gauged by examining *EPR* at different temperatures. There are only a few studies that have measured *EPR* over a wide enough range of temperatures to properly estimate thermal windows. Optimum temperature (T_{opt}) for *A. tonsa* in the Baltic and North Sea was 23 °C (Fig. 2). Studies examining wider ranges in temperatures and working with southwest Baltic populations reported 100 % mortality at 34 °C for *A. tonsa* (Holste and Peck 2006). In contrast, *A. bifilosa* is adapted to colder temperatures with Koski and Kuosa (1999) reporting highest *EPR* between 13 and 18 °C and high mortality at 24 °C. *Temora longicornis* has a similar thermal window as *A. bifilosa* with highest *EPR* occurring at 17 °C and 100 % mortality at 24 °C (Holste et al. 2009). Although using *EPR* is a good approximation of the energy available for growth and the shape of thermal windows, adult body size decreases at warmer temperatures, which reduces absolute *EPR* (eggs per female) (see Landry 1978). The relationship can be complex since the size of eggs also decreases at warmer temperatures (Hansen et al. 2010). Future studies exploring thermal windows should employ mass- and/or carbon-specific *EPR* for the most robust estimate of the relative physiological benefit accrued at optimal compared to sub-optimal temperatures.

As opposed to *Acartia* spp. and *T. longicornis* that are broadcast spawners, *E. affinis* produces fewer eggs that are brooded in separate clutches in an egg pouch. It is more difficult to estimate the thermal window supporting *EPR* in *E. affinis* compared to *A. tonsa* and *T. longicornis*. Ban (1994, study site: Lake Ohnuma, Japan) and Hirche (1992) estimated *E. affinis EPR* from measurements of clutch size (number of eggs) and inter-clutch duration. Laboratory-derived estimates of *EPR* were 19.0, 34.2 and 34.1 eggs female^{-1} day^{-1}, at 10, 15 and 20 °C, respectively (Ban 1994). Field-derived estimates of *EPR* reported by Hirche (1992) were lower (5.5–7.8 eggs female^{-1} day^{-1} from 5 to 20 °C). After combining temperature-dependent functions of clutch size, egg development rate and female size, those field data (collected in the same system investigated in this study) suggested that *E. affinis* had its peak *EPR* at ~12 °C. Controlled laboratory experiments conducted on *E. affinis* suggest a broader thermal window. For example, successful egg hatching in *E. affinis* is quite broad (0–25 °C) [see Andersen and Nielsen (1997, study site: North Sea) and references therein]. This agrees with findings by Devreker et al. (2009) who found relatively high hatching success of *E. affinis* eggs in the Seine estuary at 10 and 15 °C, but embryonic development time, inter-clutch time and cumulative clutch size were markedly decreased at 10 °C. They showed that *EPR* was significantly higher at 15 °C with 13 eggs female^{-1} day^{-1} compared to 10 °C (4 eggs female^{-1} day^{-1}). An individual-based model parameterized for *E. affinis* in the Seine estimated maximal *EPR* between 17 and 19 °C (Dur et al. 2009).

Temperatures optimal for *EPR* in *T. longicornis* and *E. affinis* in the laboratory occurred at our field sites but these species were nearly absent at temperatures warmer than 15 °C (Fig. 6). At those warmer temperatures, *Acartia* spp. dominated samples. In general, *Acartia* spp. were clearly (4 to 10 times) more abundant than *E. affinis* and *T. longicornis* at both field sites throughout the year, which was contrary to our expectations that *T. longicornis* and, especially *E. affinis,* would dominate the copepod assemblage at least during specific times of the year. The fact that the highest peaks in abundance of *Acartia* spp. females occurred between mid-May and mid-October were most likely due to increased productivity of *A. tonsa*, but data with increased taxonomic resolution are needed to confirm this.

As previously mentioned, seasonality in copepod productivity (within temperate systems) will also be affected by changes in the size of females within cohorts produced during relatively warm and cold periods of the year, an aspect that was not measured in our time series samples. Ambler (1985) found the prosome length of *A. tonsa* off the coast of Texas to decrease from 0.79 to 0.61 mm between 21 and 29 °C, respectively. Hansen et al. (2010) reported also that *A. tonsa* eggs decreased in size with increasing temperatures. Nevertheless, the eggs were 6 % bigger at 6 °C compared to 24 °C while the size of females at 9 °C was 18 % bigger compared to females at 24 °C. Hirche (1992) reported nearly 2-fold differences in *E. affinis* adult prosome length between the winter (0.93 mm, 5 °C) and summer (0.55 mm, 20 °C) for *E. affinis*. Ban (1994)

reported that adult body size of *E. affinis* was more influenced by food shortage than by temperature; female prosome length decreased by 10 % between 10 and 20 °C, but decreased by 25 % between ad libitum and low phytoplankton concentrations. Prey concentrations <9.5 μg *Chl a* L^{-1} caused more dramatic decreases in adult body size in that field study. That finding highlights the importance of feeding conditions as a controlling factor of copepod productivity.

While various studies have focused on temperature as the main factor controlling copepod production, match–mismatch dynamics with phytoplankton often control the productivity of species such as *A. tonsa* in the field (Durbin et al. 1983, study site: Narragansett Bay). Koski and Kuosa (1999) reported that *A. bifilosa* had maximum *EPR* at food concentrations >14–20 μg *Chl a* L^{-1}. However, *A. bifilosa* seemed well adapted to changes in *Chl a* concentrations and displayed relatively high *EPR* even at 5 μg *Chl a* L^{-1}, a critically low threshold food concentration for *EPR* in *A. tonsa* (Ambler 1986). In Narragansett Bay, Durbin et al. (1983) reported that *EPR* by *A. tonsa* decreased to negligible levels when *Chl a* was 1–2 μg L^{-1}. Peterson and Bellantoni (1987) reported that *T. longicornis* off central Chile required higher concentrations of *Chl a* than *A. tonsa* to obtain maximal *EPR*. Castellani and Altunbaş (2006) measured highest *EPR* of *T. longicornis* in the Irish Sea when *Chl a* increased above 1 up to 3.5 μg *Chl a* L^{-1}.

Our field measurements indicated that *Chl a* concentrations were rarely <2 μg L^{-1} at *NOK* (only on two sampling dates) but were often lower than this at the *Pier* site (22 % of all sampled dates). *Acartia* spp. was abundant at *Pier* even when *Chl a* concentrations were relatively low. Similarly, the majority of *T. longicornis* was found at *Chl a* concentrations <5 μg L^{-1}. Finally, despite reports that *E. affinis* is able to effectively select food in turbid conditions (Gasparini and Castel 1997, study site: Gironde estuary; Tackx et al. 2003, study site: North Sea) most samples containing *E. affinis* in our study were collected when *Chl a* was >5 μg L^{-1}. Although such threshold concentrations of *Chl a* are interesting to compare between species and years, it is important to note that *Chl a* is only a proxy of the available prey resources available to copepods. Not only food quantity but also quality (size, biochemical composition) are critical features affecting growth and reproductive success of calanoid copepods (e.g. Houde and Roman 1987, study site: Chesapeake Bay; Dutz et al. 2008, copepods from the North Sea; Diekmann et al. 2009). To better understand the role of phytoplankton as a controlling factor of copepod production, studies of food quality at our study site are needed.

Many environmental factors co-vary and, in this respect, it is difficult (and often impossible) to disentangle the direct influence of day length from effects of temperature

and prey in field data. Patterns in our field data on adult female abundance suggested that *Acartia* spp. abundance was more linked to increasing day length despite experiencing warmer water temperatures when day lengths started to decline after the summer solstice. Note, predation likely plays an important role in controlling zooplankton populations at this time of the year and is discussed in a later section. For *T. longicornis*, other authors have reported maximum abundances from autumn until spring (Rae and Fraser 1941; Fransz 1975, study site: North Sea), which contrasts with patterns in our field data. At the *Pier* site, *T. longicornis* only occurred under medium and high day lengths and when day lengths were increasing (despite very few exceptions with low abundances). Furthermore, the abundance of adult *E. affinis* did not increase again with decreasing day lengths in the autumn at similar temperatures as in spring. This agrees with previous field studies reporting dominance of *E. affinis* during March–June (Devreker et al. 2007; Mouny and Dauvin 2002, study sites: Seine estuary). The beginning of decreasing day length might therefore be a cue in *E. affinis'* life history.

Masking factors: salinity

Copepods are osmoconformers and display species-specific differences in their abilities to cope with high and low salinity, and fluctuations in salinity can affect different copepods, even members of the same genus, in different ways (Calliari et al. 2008). Hence, changes in salinity may also be more important than changes in temperature in structuring the copepod community composition and productivity of estuarine regions (Attrill 2002).

At extreme levels, hyper- or hypo-osmostic conditions cause death, but the ability to cope with osmotic stress can be influenced by other factors. Lance (1963) was the first to demonstrate that temperature affected low salinity tolerance of *A. tonsa*. The species (UK coastal population) was most tolerant to low salinities at 16–20 °C (3.6 psu) compared to 10 or 24 °C (5.4 psu) or 4.5 °C (9 psu). The ability of *A. tonsa* to utilize free amino acids in hypo-osmoregulation (Farmer and Reeve 1978, copepods off Florida) appears to be limited at cold (winter) temperatures. Without sufficient time to acclimate to low temperatures (e.g. during periods of rapid cooling), mass mortality could occur in areas of low ambient salinity (0–6 psu). In *E. affinis*, Devreker et al. (2009) reported a very high post-embryonic mortality (85 %) at 25 psu when combined with a low temperature (10 °C).

Within tolerable limits of salinity, sub-lethal effects of the increased metabolic load associated with osmotic regulation at sub-optimal salinities result in lower *EPR*. For example, when measured at 6, 10, 14, 20 and 30 psu, the *EPR* by *A. tonsa* was highest at 14 psu (Peck and Holste

2006). This agrees with the findings of Cervetto et al. (1999) who reported that *A. tonsa* from a Mediterranean estuary can tolerate a wide range of salinities (1–72 psu) for short time periods (<10 h) but that longer-term (72 h) optimal salinities were between 15 and 22 psu. Castro-Longoria and Williams (1999, study site: Southampton Water, UK) found *A. bifilosa* hatching success (%) to be highest at 25 psu with lower values occurring at both higher and lower salinities. For *T. longicornis*, Holste et al. (2009) reported much reduced *EPR* at 8 psu compared to higher salinities. In the Baltic Sea, *T. longicornis* has been collected at 7 psu (Peters 2006) but the species is known to occur at higher (marine) salinities around 33 psu (e.g. in the North Sea: Krause et al. 1995). In a study by Viitasalo et al. (1994), *E. affinis* avoided salinities above 6.5 psu, and respiration rates of adult *E. hirundoides* (likely *E. affinis*) suggested metabolic stress at 9 psu, particularly at the warmest of three temperatures tested (6, 11 and 16 °C) (Gyllenberg and Lundqvist 1979). Cailleaud et al. (2007) found salinities between 5 and 15 psu to be optimal for maximum expression in enzymatic activities of *E. affinis* from the Seine estuary, and Devreker et al. (2009) reported a high salinity of 25 psu to have a negative effect on embryonic development time, inter-clutch time and cumulative clutch size.

The results of laboratory studies suggest that important, stage-specific differences in salinity tolerance can exist within copepod species. For example, the salinity experienced by nauplii of *T. longicornis* may be particularly relevant for survival and population persistence in the Baltic Sea (Holste et al. 2009). Again, an interaction with temperature was apparent with naupliar mortality at lower salinities increasing at warmer temperatures (Holste et al. 2009). A similar temperature x salinity interaction was reported in a laboratory study by Devreker et al. (2004) working on *E. affinis* naupliar survival at 0–35 psu. In that study, survival was highest at 15 psu but was only reduced at the extreme values of salinity (0 and 35 psu).

Our field data thus agree with reported tolerances of these six species to salinity. *Acartia* spp. are known to be euryhaline and were abundant across the entire range of salinities at both sites (4.9–12.4 psu at *NOK* and 11.9–21.4 psu at *Pier*). Of the six species examined here, *T. longicornis* is the least tolerant of low salinity and was absent from the *NOK* site. At the *Pier* site, *T. lonigcornis* was only found at salinities >13 psu, which appears to be the threshold value for population persistence. Maximal abundances of *T. longicornis* occurred at higher salinities (~16 and 19 psu). The abundance of *E. affinis* was highest between 5 and ~10 psu, rapidly declined at higher salinities and was absent above 19 psu. At the *Pier* site (11.9–21.4 psu), the extremely low and highly variable abundance of *E. affinis* likely indicates that adults

were merely, occasionally transported to the site via advection.

Reproductive strategy

Production of different egg types

Most of the species examined here produce different egg types including resting eggs as a strategy to survive unfavourable conditions. Understanding the intrinsic and extrinsic (environmental) triggers for the production of different egg types is critical for understanding patterns in phenology and factors influencing population persistence. In the copepod literature, there is a potentially confusing array of terms given to different egg types, but most authors have classified eggs based upon the time required for hatching. 'Subitaneous eggs' (*SBE*) hatch rapidly within hours to days (Grice and Marcus 1981), while 'delayed hatching eggs' (*DHE*) require days to weeks to hatch (Chen and Marcus 1997). Finally, in our definition, resting eggs (*RE*) include quiescent and diapausing eggs that are dormant over a longer period of time. As diapausing eggs require an obligatory refractory phase before hatch, quiescent eggs hatch when conditions become favourable, Grice and Marcus (1981) define the latter as quiescent subitaneous. A myriad of factors (intrinsic and extrinsic) have been related to the production of different eggs types and, in the following, we discuss the main, directive factors.

Key directive factors

Most of the controlled laboratory studies examining the triggers for the production of different egg types (*SBE*, *DHE* and *RE*) have been conducted on *A. tonsa* (Holste and Peck 2006; Hansen et al. 2010; Drillet et al. 2011). In terms of eggs that rapidly hatch (*SBE*), Peck et al. (2008) reported a non-linear decrease in rapid (48-h) hatching success of *A. tonsa* eggs with decreasing day length (photoperiod) experienced by adults (see also Fig. 3a). In a different study (Diekmann et al., unpublished data) eggs produced at relatively long day lengths (16 h) and temperature of incubation (and acclimation of adults) had no influence on the proportions of *DHE*, *RE* or *DE* categories. Second, egg types (categories) produced at the warmest temperature (25 °C) did not differ among short (6 h), medium (11 h) or long (16 h) day lengths. When females were acclimated to colder temperatures (9–12 °C), Holste and Peck (2006) and Hansen et al. (2010) suggested that the production of *RE* was markedly higher. Finally, Drillet et al. (2011) reported that poor feeding conditions induced the production of *DHE* that synchronously hatched after incubation for several months at conditions that mimicked winter (dark,

1.5 °C). Taken together, these results suggest that *A. tonsa* is expected to produce resting eggs during unfavourable feeding conditions during short day lengths and at relatively cold (<12 °C) temperatures. Furthermore, Holmstrup et al. (2006) reported subitaneous eggs from *A. tonsa* at the Limfjord to enter quiescence when incubated in anoxia and cold temperatures.

Given the brackish environment inhabited by some *Acartia* populations (such as the south-west Baltic), it is important to consider the potential masking effects of salinity on the life-history strategy of producing different egg types. In our experiment concerning egg hatching and development, significantly more *RE* were produced at 8 psu compared to 18 psu. Furthermore, at 8 psu, the proportions of *SBE* (*RE*) decreased (increased) with decreasing *EPR* (Fig. 7c). As previously discussed, other studies have reported increased *RE* production when *EPR* decreased due to unfavourable feeding conditions, when copepods experienced unsuitably low temperatures or when adults experienced short day lengths (Holste and Peck 2006; Peck et al. 2008; Hansen et al. 2010; Drillet et al. 2011). Since temperature and day length were both constant in our experiment, salinity is the most likely factor causing *A. tonsa* to increase the proportion of resting eggs (*RE*) produced.

Female *A. bifilosa* can be found in samples collected during winter in the Baltic Sea and continue to produce eggs at that time, albeit at relatively low rates (Schmidt et al. 1998). *A. bifilosa* do not appear to produce *RE*, at least not as an overwintering strategy. The third congener, *A. longiremis*, is an Arctic relict species that exhibits adult diapause in Norwegian fjords (Norrbin 1994). That strategy may be an adaptation to the deep water habitats that are unsuitable for *RE* (Norrbin 1994). Winter temperatures in the shallow waters of the Baltic Sea are likely warm enough to support active reproduction, and Peters et al. (2007) found high abundances of *A. longiremis* nauplii during winter in the south-west Baltic (Bornholm Basin). The life-history strategy of *A. longiremis* in the Baltic Sea is not well studied and it is unknown, for example, how this species survives the summer period.

In contrast, *T. longicornis* appears to utilize a completely different strategy with regard to the production of resting eggs. In the Irish Sea, *T. longicornis* produced mostly *RE* when *EPR* was highest during the spring and early summer shortly after periods of peak *Chl a* concentrations (5 to >20 μg L^{-1}) (Castellani and Lucas 2003). Those authors suggested that the timing of *RE* production during peak *Chl a* would be advantageous to the population in terms of avoiding predation pressure. In the north-west Atlantic, Maps et al. (2005) documented marked declines in hatching success of eggs produced and incubated at temperatures warmer than 14 °C. In those experiments,

EPR increased with increases in temperature from 2 to 18 °C indicating that, at least for *T. longicornis*, the production of potential resting eggs occurs when *EPR* is relatively high.

Work on *E. affinis* at different sites suggests the production of eggs that did not rapidly hatch were related to short day lengths, cold temperatures and high copepod population densities (Ban 1992; Flinkman et al. 1994; Katajisto 1996; Andersen and Nielsen 1997; Katajisto et al. 1998; Roman et al. 2001). For example, Ban (1992) collected nauplii of *E. affinis* in lake Ohnuma, Japan, during late autumn (November) and reared them in the laboratory under spring conditions (15 °C, 12 h). Females raised from these nauplii produced exclusively subitaneous eggs, whereas those raised from nauplii, collected in spring (May) and incubated under late autumn conditions (10 °C, 10 h), produced exclusively diapause eggs (here eggs that did not rapidly hatch). Hence, *E. affinis* appears to have a strategy similar to *A. tonsa* with regard to cues for the production of potential resting eggs.

Although we only examined in situ female abundance in our field study, the literature (previously reviewed) suggests that populations of some of these species should persist, during portions of the year, as resting eggs at our field sites (Madhupratap et al. 1996). *DHE* would be a good life-history strategy to allow populations to persist through seasons of unfavourable conditions as well as to spread to different areas (Drillet et al. 2011). Drillet et al. 2011 reported that 50 % of *A. tonsa* females produced subitaneous and *DHE* eggs and that the latter displayed a synchronous, 80 % hatch after a 5-month cold storage period but lower *HS* after longer-term storage. In an earlier study, Drillet et al. (2006) found no change in the viability and biochemical composition of eggs stored for ≤1 year at 2–3 °C. Concerning salinity, at least the eggs produced by *A. tonsa* appear unaffected by changes in salinity during their resting period as reported by Hansen et al. (2012). Using short-term (24 h) incubations at different salinities, they reported that changes in salinity affected egg volume but that the embryo was able to maintain its volume and osmolality as it is protected by an impermeable plasma membrane. Utilizing longer-term incubations, Holmstrup et al. (2006) observed that *A. tonsa* eggs were viable for up to 20 weeks at salinities between 10 and 50 psu, but very low salinities were only tolerated for a short time. Katajisto (2006, study site: Northern Baltic Sea) found that the development of *A. bifilosa* eggs was not affected by darkness and low temperature but that eggs became quiescent under anoxic conditions. The eggs remained viable for 1 year in anoxic water and for 2 years in the sediment (Katajisto 2006). After a sufficient amount of time (refractory phase), the triggers for hatching of resting eggs of calanoid copepods are similar to those for cladocerans

and rotifers (May 1987; Vandekerkhove et al. 2005) and include specific temperatures and day lengths (Katajisto et al. 1998; Dutz et al. 2004b). Our back-calculated hatching dates of adults at peak abundance suggested that eggs (RE or DHE) hatched at ∼9, 10 and 13 °C for *Acartia* spp., *T. longicornis* and *E. affinis*, respectively. Thermal thresholds required for egg hatching in these copepods are not known but temperatures between 9 and 12 °C agree with those reported in the literature for *Acartia* spp. [10 °C by Christiansen (1988)] and *T. longicornis* [∼5–10 °C by Castellani and Lucas (2003)]. However, thermal triggers for *RE* hatching in *E. affinis* (if they exist) are expected to be colder than 13 °C. Hirche (1992) reported minimum fecundity values at 12 °C and decreases in field abundance of adults at temperatures warmer than 12 °C. It is likely that the peak in *E. affinis* occurred earlier in the year when sampling was not conducted. Nevertheless, Katajisto (2006) reported that *E. affinis* produced two types of eggs—subitaneous and diapause eggs, with the latter to hatch after a period of chilling at a warm temperature (13 °C). Obviously, our back-calculations represent a test of how likely it is that resting eggs occur at our sampling sites. We cannot say if the adults we sampled were hatched from eggs at the same sites or from other locations. A complex hydrography exists in the Baltic Sea, and plankton can be advected to coastal areas (Hinrichsen et al. 2001).

The role of predators

Although the present study has focused on the role of abiotic and biotic (bottom–up) factors affecting copepod productivity in shallow coastal water, copepods are the primary diet item of most secondary consumers in marine and estuarine environments and top–down control of their populations is possible, particularly in the Baltic Sea (Möllmann et al. 2008). The present field locations and other coastal areas represent important sites for spring and autumn spawning herring (*Clupea harengus*) and it can be assumed that herring larvae and juveniles likely have a severe predation effect on the copepod populations in these areas (Aro 1989). Sprat (*Sprattus sprattus*) is the dominant clupeid in Baltic waters that can exert top–down control of its copepod prey (Rudstam 1988; Möllmann et al. 2008). Trophic cascades documented in offshore areas of the Baltic Sea highlight the tight inter-dependence of copepods and clupeid fishes (e.g. Möllmann et al. 2008; Casini et al. 2011). In offshore areas such as the Gotland Basin, *T. longicornis* was more important than *Acartia* spp. in the diets of sprat (Möllmann and Köster 2002). In the Bornholm Basin and Central Baltic Sea, *Acartia* spp. and *T. longicornis* formed the highest proportions of gut contents in larval sprat (Dickmann et al. 2007). Large schools of sprat have been found in starving condition during late

summer (August) at locations close to those to our field sampling sites (Baumann et al. 2007), highlighting the importance of fishes as regulators of the copepod community at that time of year. Furthermore, ctenophores and other gelatinous zooplankton can be important predators of copepod populations during summer months (Javidpour et al. 2009). Thus, changes in adult copepods documented in our time series, particularly during late spring and summer, are attributable to a combination of both bottom–up and top–down processes.

Conclusions

The present study described how various environmental factors affect key calanoid copepods in shallow, brackish and temperate waters using a metabolic framework originally proposed by Fry (1971). Environmental factors such as temperature, salinity, day length and prey availability act synergistically (with predation) to influence vital rates. We provide examples of key interactions by reviewing how temperature, salinity, day length and/or prey abundance affect survival, reproductive success (EPR) and reproductive strategy (types of eggs produced) in the dominant calanoid copepods inhabiting the south-west Baltic Sea. This framework distinguishing controlling, masking and directive factors was discussed in the light of laboratory research on reproductive strategy and success, and field time series data on seasonal abundance of adult females of *Acartia* spp., *T. longicornis* and *E. affinis*. Our literature review highlights thermal windows that control productivity, the potential affect of day length as a 'directive factor' for reproductive strategy and the importance of salinity as a key 'masking' factor interacting with temperature to alter reproduction in adult calanoid copepods. Many species live at the edge of their salinity tolerance in the Baltic Sea and this is highlighted by differences in the abundance of *T. longicornis* and *E. affinis* between two, relatively nearby field locations. Our review also highlights the need to examine earlier life stages due to potential ontogenetic differences in the sensitivity to environmental factors. Furthermore, more research is needed on the physiology, vital rates and life-history strategy of *A. longiremis*, a copepod highly abundant in the Baltic, but poorly understood.

To understand how interactions among different metabolic stressors (e.g. temperature, salinity and prey level) constrain the life-history strategy of copepods, estimates of metabolic scope are needed under different combinations of key factors (TxS, etc.). Such estimates could be made by combining measurements of respiration (energy loss) with grazing (energy gain) to calculate 'scope-for-growth', a common measurement technique utilized for decades in

ecotoxicological research on invertebrates (Widdows et al. 1981; Maltby et al. 1990), which is now re-emerging in climate research (e.g., Stumpp et al. 2011). The Baltic Sea is predicted to freshen and warm by 3–3.5 °C in the next 80 years (Meier 2006), and continuing to collect basic physiological data on the synergistic effects of different environmental factors (including pollutant loads in near-shore areas) will be needed if we hope to understand how climate-driven changes might impact copepods and subsequent match–mismatch dynamics between copepods, their prey and their predators.

References

Adrian R, Hansson S, Sandin B, De Stasio B, Larsson U (1999) Effects of food availability and predation on a marine zooplankton community—a study on copepods in the Baltic Sea. Int Rev Hydrobiol 84:609–626

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

Ambler JW (1986) Effect of food quantity and quality on egg production of *Acartia tonsa* Dana from East Lagoon, Galveston, Texas. Estuar Coast Shelf Sci 23:183–196

Andersen CM, Nielsen TG (1997) Hatching rate of the egg-carrying estuarine copepod *Eurytemora affinis*. Mar Ecol Prog Ser 160:283–289

Aro E (1989) A review of fish migration patterns in the Baltic. Rapp P- v Réun Cons Int Explor Mer 190:72–96

Attrill MJ (2002) A testable linear model for diversity trends in estuaries. J Animal Ecol 71:262–269

Ban S (1992) Effects of photoperiod, temperature, and population density on induction of diapause egg production in *Eurytemora affinis* (Copepoda: Calanoida) in Lake Ohnuma, Hokkaido, Japan. J Crustacean Biol 12:361–367

Ban S (1994) Effect of temperature and food concentration on post-embryonic development, egg production and adult body size of calanoid copepod *Eurytemora affinis*. J Plankton Res 16:721–735

Baumann H, Peck MA, Götze E, Temming A (2007) Starving early juvenile sprat *Sprattus sprattus* (L.) in western Baltic coastal waters: evidence from combined field and laboratory observations in August and September 2003. J Fish Biol 70:853–866

Brylinski JM (1981) Report on the presence of *Acartia tonsa* Dana (Copepoda) in the harbour of Dunkirk (France) and its geographical distribution in Europe. J Plankton Res 3:255–260

Cailleaud K, Maillet G, Budzinski H, Souissi S, Forget-Leray J (2007) Effects of salinity and temperature on the expression of enzymatic biomarkers in *Eurytemora affinis* (Calanoida, Copepoda). Comp Biochem Physiol A 147:841–849

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

Casini M, Kornilovs G, Cardinale M, Möllmann C, Grygiel W, Jonsson P, Raid T, Flinkman J, Feldman V (2011) Spatial and temporal density dependence regulates the condition of central Baltic Sea clupeids: compelling evidence using an extensive international acoustic survey. Popul Ecol 53:511–523

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

Castro-Longoria E, Williams JA (1999) The production of subitaneous and diapause eggs: a reproductive strategy for *Acartia bifilosa* (Copepoda: Calanoida) in Southampton Water, UK. J Plankton Res 21:65–84

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

Chen F, Marcus NH (1997) Subitaneous, diapause, and delayed-hatching eggs of planktonic copepods from the northern Gulf of Mexico: morphology and hatching success. Mar Biol 127:587–597

Chinnery FE, Williams JA (2003) Photoperiod and temperature regulation of diapause egg production in *Acartia bifilosa* from Southampton Water. Mar Ecol Prog Ser 263:149–157

Christiansen B (1988) Vergleichende Untersuchungen zur Populationsdynamik von *Eurytemora affinis* POPPE und *Acartia tonsa* DANA, Copepoda, in der Schlei. PhD thesis, University Hamburg, Hamburg

Conover RJ (1988) Comparative life histories in the genera *Calanus* and *Neocalanus* in high latitudes of the northern hemisphere. Hydrobiologia 167(168):127–142

Davis CC (1976) Overwintering strategies of common planktic copepods in some North Norway fjords and sounds. Astarte 9:37–42

Devreker D, Souissi S, Seuront L (2004) Development and mortality of the first naupliar stages of *Eurytemora affinis* (Copepoda, Calanoida) under different conditions of salinity and temperature. J Exp Mar Biol Ecol 303:31–46

Devreker D, Souissi S, Forget-Leray J, Leboulenger F (2007) Effects of salinity and temperature on the post-embryonic development of *Eurytemora affinis* (Copepoda; Calanoida) from the Seine estuary: a laboratory study. J Plankton Res 29(Supplement I):i117–i133

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

Dickmann M, Möllmann C, Voss R (2007) Feeding ecology of Central Baltic sprat (*Sprattus sprattus* L.) larvae in relation to zooplankton dynamics—implications for survival. Mar Ecol Prog Ser 324:277–289

Diekmann ABS, Peck MA, Holste L, John MA, Campbell RW (2009) Variation in diatom biochemical composition during a simulated bloom and its effect on copepod production. J Plankton Res 31:1391–1405

Drillet G, Iversen MH, Sørensen TF, Ramløc H, Lund T, Hansen BW (2006) Effect of cold storage upon egs of a calanoid copepod, *Acartia tonsa* (Dana) and their offspring. Aquaculture 254:714–729

Drillet G, Goetze E, Jepsen PM, Højgaard JK, Hansen BW (2008) Strain-specific vital rates in four *Acartia tonsa* cultures, I: strain origin, genetic differentiation and egg survivorship. Aquaculture 280:109–116

Drillet G, Hansen BW, Kiørboe T (2011) Resting egg production induced by food limitation in the calanoid copepod *Acartia tonsa*. Limnol Oceanogr 56(6):2064–2070

Dur G, Souissi S, Devreker D, Ginot V, Schmidt FG, Hwang J-S (2009) An individual-based model to study the reproduction of egg bearing copepods: application to *Eurytemora affinis* (Copepoda Calanoida) from the Seine estuary, France. Ecol Modell 220:1073–1089

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

Dutz J, Mohrholz V, Peters J, Renz J, Alheit J (2004a) Identification of critical stages in the population dynamics of key copepod species in the Bornholm Basin (Baltic Sea): potential linkages to physical forcing and climate variability. Int Counc Explor Sea Cph CM L12:1–11

Dutz J, Mohrholz V, Peters J, Renz J, Alheit J (2004b) A strong impact of winter temperature on spring recruitment of a key copepod species in the Bornholm Basin: potential linkages to climate variability. GLOBEC Int Newsl 10(1):13–14

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

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, Vuorinen I, Christiansen M (1994) Calanoid copepod eggs survive passage through fish digestive tracts. ICES J Mar Sci 51:127–129

Fransz HG (1975) The spring development of calanoid copepod populations in Dutch coastal waters as related to primary production. In: 10th European symposium on marine biology, Ostend, Belgium, 17–23 Sept. 2:247–269

Fransz HG, Gonzalez SR (1990) Daily egg production of *Temora longicornis* (Copepoda, Calanoida) during winter and early spring in the Marsdiep (southern North Sea). Hydrobiol Bull 25:61–64

Fry FEJ (1971) The effect of environmental factors on the physiology of fish. In: Hoar WS, Randall DJ, Brett JR (eds) Fish physiology, vol 6. Academic Press, New York

Gasparini S, Castel J (1997) Autotrophic and heterotrophic nano-plankton in the diet of the estuarine copepods *Eurytemora affinis* and *Acartia bifilosa*. J Plankton Res 19:877–890

Grice GD, Marcus NH (1981) Dormant eggs of marine copepods. Oceanogr Mar Biol Annu Rev 19:125–140

Gyllenberg G (1980) Feeding of the copepod *Eurytemora hirundoides* (Crustacea) on different algal cultures. Ann Zool Fennici 17:181–184

Gyllenberg G, Lundqvist G (1979) The effects of temperature and salinity on the oxygen consumption of *Eurytemora hirundoides* (Crustacea, Copepoda). Ann Zool Fennici 16:205–208

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

Hansen BW, Drillet G, Kozmér A, v. Madsen K, Pedersen MF, Sørensen TF (2010) Temperature effects on copepod egg hatching: does acclimatization matter? J Plankton Res 32:305–315

Hansen BW, Drillet G, Pedersen MF, Sjøgreen KP, Vismann B (2012) Do Acartia tonsa (Dana) eggs regulate their volume and osmolality as salinity changes? J Comp Physiol B. doi: 10.1007/s00360-012-0646-y

Hernroth L, Ackefors H (1979) The zooplankton of the Baltic Proper. Report, Fishery Board of Sweden, Institute Marine Research 2:1–60

Hinrichsen H–H, St. John M, Aro E, Grønkjær P, Voss R (2001) Testing the larval drift hypothesis in the Baltic Sea retention versus dispersion caused by wind-driven circulation. ICES J Mar Sci 58:973–984

Hirche HJ (1992) Egg production of *Eurytemora affinis*—effect of k-strategy. Estuar Coast Shelf Sci 35:395–407

Holmstrup M, Overgaard J, Sørensen TF, Drillet G, Hansen BW, Ramløv H, Engell-Sørensen K (2006) Influence of storage conditions on viability of quiescent copepod eggs (*Acartia tonsa* Dana): effects of temperature, salinity and anoxia. Aquac Res 37:625–631

Holste L (2010) The impact of key environmental factors on the vital rates of two Baltic Sea copepods. PhD thesis, University Hamburg, Hamburg

Holste L, Peck MA (2006) The effects of temperature and salinity on egg production and hatching success of Baltic *Acartia tonsa* (Copepoda: Calanoida): a laboratory investigation. Mar Biol 148:1061–1070

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

Houde SEL, Roman MR (1987) Effects of food quality on the functional ingestion response of the copepod *Acartia tonsa*. Mar Ecol Prog Ser 40:69–77

Huey RB, Kingsolver JG (1993) Evolution of resistance to high temperature in ectotherms. Am Nat 142(Suppl: Evolutionary Responses to Environmental Stress):21–46

Javidpour J, Molinero JC, Lehmann A, Hansen T, Sommer U (2009) Annual assessment of the predation of *Mnemiopsis leidyi* in a new invaded environment, the Kiel Fjord (Western Baltic Sea): a matter of concern? J Plankton Res 31:729–738

Jeffrey SW, Humphrey GF (1975) New spectrometric equations for determining chlorophylls a, b, c1 and c2 in higher plants, algae and natura phytoplankton. Biochemie und Physiologie der Pflanzen 167:191–194

Katajisto T (1996) Copepod eggs survive a decade in the sediments of the Baltic Sea. Hydrobiologia 320:153–159

Katajisto T (2006) Benthic resting eggs in the life cycles of calanoid copepods in the northern Baltic Sea. W. & A. de Nottbeck Foundation Sci Rep 29:1–46

Katajisto T, Viitasalo M, Koski M (1998) Seasonal occurrence and hatching of calanoid eggs in sediments of the northern Baltic Sea. Mar Ecol Prog Ser 163:133–143

Klein Breteler WCM, Gonzalez SR (1982) Influence of cultivation and food concentration on body length of calanoid copepods. Mar Biol 71:157–161

Koski M, Kuosa H (1999) The effect of temperature, food concentration and female size on the egg production of the planktonic copepod *Acartia bifilosa*. J Plankton Res 21:1779–1789

Krause M, Dippner JW, Beil J (1995) A review of hydrographic controls on the distribution of zooplankton biomass and species in the North Sea with particular reference to a survey conducted in January–March 1987. Prog Oceanogr 35:81–152

Lance J (1963) The salinity tolerance of some estuarine planktonic copepods. Limnol Oceanogr 8:440–449

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

Madhupratap M, Nehring S, Lenz J (1996) Resting eggs of zooplankton (Copepoda and Cladocera) from the Kiel Bay and adjacent waters (southwestern Baltic). Mar Biol 125:77–87

Maltby L, Naylor C, Calow P (1990) Effect of stress on a freshwater benthic detritivore: scope for growth in *Gammarus pulex*. Ecotoxicol Environ Saf 19:285–291

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

Mauchline J (1998) The biology of calanoid copepods. Elsevier Academic, Oxford

May L (1987) Effect of incubation temperature on the hatching of rotifer resting eggs collected from sediments. Hydrobiologia 147:335–338

Meier HEM (2006) Baltic Sea climate in the late twenty first century: a dynamical downscaling approach using two global models and two emission scenarios. Clim Dyn 27:39–68

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

Möllmann C, Müller-Karulis B, Kornilovs G, John MA (2008) Effects of climate and overfishing on zooplankton dynamics and ecosystem structure: regime shifts, trophic cascade, and feedback loops in a simple ecosystem. ICES J Mar Sci 65:302–310

Mouny P, Dauvin JC (2002) Environmental control of mesozoo-plankton community structure in the Seine estuary (English Channel). Oceanol Acta 25:13–22

Norrbin MF (1994) Seasonal patterns in gonad maturation, sex ratio and size in some small, high-latitude copepods: implications for overwintering tactics. J Plankton Res 16:115–131

Norrbin MF (1996) Timing of diapause in relation to the onset of winter in the high-latitude copepods *Pseudocalanus acuspes* and *Acartia longiremis*. Mar Ecol Prog Ser 142:99–109

Peck MA, Holste L (2006) Effects of salinity, photoperiod and adult stocking density on egg production and hatching success of *Acartia tonsa* (Calanoida:Copepoda): optimizing intensive cultures. Aquaculture 255:341–350

Peck MA, Ewest B, Holste L, Kanstinger P, Martin M (2008) Impacts of light regime on egg harvests and 48-h egg hatching success of *Acartia tonsa* (Copepoda: Calanoida) within intensive culture. Aquaculture 275:102–107

Peters J (2006) Lipids in key copepod species of the Baltic Sea and North Sea—implications for life cycles, trophodynamics and food quality. PhD thesis, University Bremen, Bremen

Peters J, Dutz J, Hagen W (2007) Differences in life-cycle strategies and trophic niches of the copepods *Temora longicornis* and *Acartia longiremis* in the Central Baltic Sea—a success story. GLOBEC Int Newsl 13:59–61

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

Pörtner HO, Farrell AP (2008) Physiology and climate change. Science 322:690–692

Pörtner HO, Knust R (2007) Climate change affects marine fishes through the oxygen limitation of thermal tolerance. Science 315:95–97

Pörtner HO, Peck MA (2010) Climate change impacts on fish and fisheries: towards a cause and effect understanding. J Fish Biol 77:1745–1779

Postel L (2005) Zooplankton. In: Meeresumwelt 1999–2002. Bund-Länder-Messprogramm für die Meeresumwelt von Nord- und Ostsee, Hamburg

Rae KM, Fraser JH (1941) Continuous plankton records: the copepods of the southern North Sea 1932–37. Hull Bull Mar Ecol 1:171–238

Rijnsdorp A, Peck MA, Engelhard GH, Möllmann C, Pinnegar JK (2009) Resolving the effect of climate change on fish populations. ICES J Mar Sci 66:1570–1583

Roman MR, Holliday DV, Sanford LP (2001) Temporal and spatial patterns of zooplankton in the Chesapeake Bay turbidity maximum. Mar Ecol Prog Ser 213:215–227

Rudstam LG (1988) Exploring the dynamics of herring consumption in the Baltic: applications of an energetic model of fish growth. Kieler Meeresforschung Sonderheft 6:312–322

Schmidt K, Kähler P, v. Bodungen B (1998) Copepod egg production rate in the Pomeranian Bay (South Baltic Sea) as a function of phytoplankton abundance and taxonomic composition. Mar Ecol Prog Ser 174:183–195

Schnack S (1975) On the feeding biology of copepods (Crustacea) in Kiel Bay (in German). PhD thesis, Christian-Albrechts University, Kiel

Schulz J, Möllmann C, Hirche HJ (2007) Vertical zonation of the zooplankton community in the Central Baltic Sea in relation to hydrographic stratification as revealed by multivariate discriminant function- and canonical analysis. J Mar Syst 67:47–58

Somero GN (2010) The physiology of climate change: how potentials for acclimatization and genetic adaptation will determine 'winners' and 'losers'. J Exp Biol 213:912–920

Stumpp M, Melzner F, Dupont ST (2011) CO_2 induced seawater acidification impacts sea urchin larval development I: elevated metabolic rates decrease scope for growth and induce developmental delay. Comp Biochem Physiol Part A Mol Integr Physiol 160:331–340

Sullivan BK, McManus LT (1986) Factors controlling seasonal succession of the copepods *Acartia hudsonica* and *A. tonsa* in Narragansett Bay, Rhode Island: temperature and resting egg production. Mar Ecol Prog Ser 28:121–128

Tackx MLM, Herman PJM, Gasparini S, Irigoien X, Billiones R, Daro MH (2003) Selective feeding of *Eurytemora affinis* (Copepoda, Calanoida) in temperate estuaries: model and field observations. Estuar Coast Shelf Sci 56:305–311

Vandekerkhove J, Declerck S, Brendonck L, Conde-Porcuna JM, Jeppesen E, De Meester L (2005) Hatching of cladoceran resting eggs: temperature and photoperiod. Freshw Biol 50:96–104

Viitasalo M, Katajisto T, Vuorinen I (1994) Seasonal dynamics of *Acartia bifilosa* and *Eurytemora affinis* (Copepoda: Calanoida) in relation to abiotic factors in the northern Baltic Sea. Hydrobiologia 292(293):415–422

Widdows J, Phelps DK, Galloway W (1981) Measurements of physiological condition of mussels transplanted along a pollution gradient in Narragansett Bay. Mar Environ Res 4:181–194

Zillioux EJ, Gonzalez JG (1972) Egg dormancy in a neritic calanoid copepod and its implications to overwintering in boreal waters. In: Battaglia B (ed) Fifth European marine biology symposium. Piccin editore, Padova