

Climate change affects low trophic level marine consumers: warming decreases copepod size and abundance

Jessica Garzke · Stefanie M. H. Ismar · Ulrich Sommer

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Abstract Concern about climate change has re-ignited interest in universal ecological responses to temperature variations: (1) biogeographical shifts, (2) phenology changes, and (3) size shifts. In this study we used copepods as model organisms to study size responses to temperature because of their central role in the pelagic food web and because of the ontogenetic length constancy between molts, which facilitates the definition of size of distinct developmental stages. In order to test the expected temperature-induced shifts towards smaller body size and lower abundances under warming conditions, a mesocosm experiment using plankton from the Baltic Sea at three temperature levels (ambient, ambient +4 °C, ambient –4 °C) was performed in summer 2010. Overall copepod and copepodit abundances, copepod size at all life stages, and adult copepod size in particular, showed significant temperature effects. As expected, zooplankton peak abundance was lower in warm than in ambient treatments. Copepod size-at-immature stage significantly increased in cold treatments, while adult size significantly decreased in warm treatments.

Keywords *Acartia* sp. · Temperature–size rule · Metabolic theory of ecology

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J. Garzke (✉) · S. M. H. Ismar · U. Sommer
Department of Experimental Ecology-Food Webs, Geomar
Helmholtz Centre for Ocean Research Kiel, Duesternbrooker
Weg 20, 24105 Kiel, Germany
e-mail: jgarzke@geomar.de

Introduction

Global warming is considered to be one of the most important factors for future changes in marine ecosystems (Boyce et al. 2010; Mackas et al. 2012) with ocean surface temperatures predicted to increase by 1–6 °C within the twenty-first century (IPCC 2007).

At the basis of the marine food web, elevated temperature is associated with a decline in phytoplankton biomass (Boyce et al. 2010; Sommer and Lengfellner 2008; Sommer and Lewandowska 2011). Increasing temperatures are found to correlate with lower mesozooplankton abundances (Edwards and Richardson 2004) and have been shown experimentally to be linked with faster zooplankton die-off (Sommer et al. 2007), but experimental assessment of the direct temperature effects on zooplankton morphology, phenology, and abundance vs. indirect effects through temperature impacts on the food supply is still missing.

On a biogeographic scale, shifts in species ranges towards higher latitudes and altitudes are the most widespread ecological change ascribed to global warming (Beaugrand et al. 2002; Parmesan and Yohe 2003). Those observations are often used to forecast the effects of warming on biota and their future distribution according to climate change scenarios (Pearman et al. 2008). Besides the shifts in species range, the second widely observed response to warming is a change in phenology (Walther et al. 2002). As a third universal response to warming, rising temperature can lead to a decrease in body size (Daufresne et al. 2009; Gardner et al. 2011; Walther et al. 2002). The relationship between body size and climate is a classic macro-ecological pattern (Bergmann 1847). Bergmann's rule originally states that among endotherms, larger bodied animals tend to live in colder environments, but it has been extended to other types of

organisms by later usage. Blackburn et al. (1999) suggested applying James' rule (1970) for climate related size changes within species, while the term Bergmann's rule (1874) should be used for interspecific trends. The physiological theory of body size dependency on temperature only recently came back into focus in ecology because of the predictions of global warming (Daufresne et al. 2009; Goodman et al. 2012). Examples for declining body size with warming have been illustrated both in terrestrial (Gardner et al. 2011; Patridge et al. 1994) and aquatic ecosystems (Sweeney et al. 1986) and across different animal taxa (Goodman et al. 2012; Yom-Tov and Geffen 2011), including insects, crustaceans, fish, amphibians, birds, and mammals (Daufresne et al. 2009; Reading 2007; Sheridan and Bickford 2011). Opposite responses have been found in some study systems, increasing body size to warming in certain fish, lizards, birds, and mammals (Gardner et al. 2011; Thresher et al. 2007; Yom-Tov et al. 2010). Interestingly, Forster et al. (2012) found in their meta-analysis that aquatic species respond with a ten times stronger body mass decrease to warming ($-5\% \text{ } ^\circ\text{C}^{-1}$) than found in terrestrial species ($-0.5\% \text{ } ^\circ\text{C}^{-1}$) and discuss that O_2 changes tend to be the driver of size changes in aquatic organisms. Climate related size changes in natural communities can be attributed to the effects of three distinct components: (1) species shifts, (2) shifts in the age structure of populations, and (3) size shifts at defined age or developmental stage (Daufresne et al. 2009).

Copepods are the most important trophic link between primary producers and heterotrophic protists, and fish and other higher level consumers in the pelagic food web (Möllmann et al. 2005), and are known to exhibit all three universal responses to warming, with hypothesis three to date being the least investigated. Batten and Walne (2011) and Beaugrand et al. (2002) showed zooplankton distribution shifts with warming. Also, positive changes in abundance with temperature shifts were shown by Möllmann et al. (2008) and larger shifts in seasonality forward in holoplanktonic organisms (Edwards and Richardson 2004). Lastly, intra-specific changes in copepod body size with warming have been scarcely investigated. The laboratory studies of Escribano and McLaren (1992) combined food quality and quantity with water temperature as well as field observations to show that copepods of the same genus are smaller than relatives in cooler environments (Kobari and Ikeda 2001 in *Neocalanus plumchrus*, and Gaudy and Verriopoulos 2004 in *Acartia tonsa*).

Here we investigate temperature effects on copepod body size intra-specifically in the same environment and across copepodit and adult stages, while controlling for food availability effects.

Materials and methods

Experimental design

A 28-day experiment was conducted in early summer (June 16, 2010). A natural plankton community containing algae, bacteria, and protozoa from the Kiel Fjord was used as experimental system, using nine 1,400-L mesocosms in three climate chambers. Additionally, mesozooplankton, mainly consisting of copepods of the taxa *Acartia* sp., were added from wild net catches. Apart from copepods (adults, copepodits, and nauplii), the zooplankton inoculum contained larval stages of polychaetes, *Balanus* sp., and bryozoa in natural abundances, but these disappeared after 2 weeks. A target copepod concentration of 10 individuals L^{-1} was added on day -3 to each mesocosms in order to mimic natural densities (Behrends 1996). The plankton was gently stirred by a propeller to guarantee homogeneous mixing of the water column without incurring zooplankton mortality (Sommer et al. 2007). Temperature was controlled at in situ values of the Kiel Fjord ($13.5\text{ } ^\circ\text{C}$) in one climate chamber, and at $+4$ ($17.5\text{ } ^\circ\text{C}$) and -4 ($9.5\text{ } ^\circ\text{C}$) in the other two chambers, mimicking the extent of warming predicted for this region and season (IPCC 2007). A symmetric design of temperature manipulations (warming and cooling) was chosen in order to distinguish effects of the direction of temperature change from effects of change as such. Light supply and day length were adjusted according to the seasonal patterns expected at this latitude.

Methods

Zooplankton was sampled weekly by three vertical net hauls, starting on day 0 of the experiment, with a hand-held plankton net of $64\text{ }\mu\text{m}$ mesh size and 12 cm diameter. Each net haul sampled a volume of 5.1 L. All samples were fixed with Lugol's iodine. Each zooplankton sample was gently and homogeneously mixed, and divided with a zooplankton divider. One fourth of each sample was identified to taxon level and developmental stage, and if possible, sexes of all copepods were determined. The body size constancy between molts enabled a clear assignment of size to stage. All copepods were identified to genus level using a ZEISS Discovery V.8 microscope with magnifications between $2.5\times$ and $4.0\times$, and whenever possible, developmental stage and sex of each individual were recorded. The mean developmental index was calculated after a modified formula used by Villegas and Kanazawa (1979):

$$\text{DI} = A/\text{total number of copepods staged}$$

where $A = \sum(\text{assigned stage value} \times \text{number of copepods at stage})/\text{number of total staged copepods}$.

Stages were scored as:

C1 = 1, C2 = 2, C3 = 3, C4 = 4, C5 = 5, Adult = 6

Because of observed differences in developmental cycles in the different temperature treatments, the population age structures of the last day of the experiment were compared.

Prosome lengths of identified copepods were digitally measured via photographs and digital software (ZEISS AxioVision 4.8 and AxioCam MRc) with a precision to the nearest μm ; each magnification and parallel photographs of each magnification were individually calibrated. Means and standard deviations were calculated stage-specifically for copepods of each genus found in each mesocosm.

The diversity of the copepod community in the mesocosms was compared by calculating the Shannon-Wiener Diversity Indices (Shannon and Weaver 1963) for all sampling days and mesocosms. Means of diversity indices of the last sampling day were compared between the different temperature treatments. A fixed effect model was conducted to identify possible changes in copepod diversity.

Phytoplankton was sampled three times a week, starting on day 0 of the experiment. Samples of 250 mL were taken from 10-L bulk water samples. All samples were fixed with Lugol's iodine. Mixed phytoplankton samples were divided into 100-mL sub-samples, and phytoplankton $>5 \mu\text{m}$ were counted by the inverted microscope method (Utermöhl 1958); phytoplankton species were identified to genus level and cell size measured. Edible phytoplankton species were the diatoms *Proboscia* sp., *Nitzschia* sp., *Thalassionema* sp., and *Skeletonema* sp., the cryptophyte *Teleaulax* sp., and the ciliates *Strobilidium* sp. and *Strombidium* sp. Total phytoplankton biomass consisted mainly of the species *Dactyliosolen fragilissimus* (ESM Fig. 1).

Acartia sp. biomass was calculated according to Gismervik et al. (2002), ciliate biovolume was calculated according to Hillebrand et al. (1999), size corrected for shrinkage caused by fixation (Müller and Geller 1993), and converted to carbon content (Putt and Stoecker 1989). Phytoplankton biomass was calculated from counts and volume measurements according to Menden-Deuer and Lessard (2000).

Temperature-dependent developmental rates of *Acartia* sp. were taken from Leandro et al. (2006) to calculate the loss during the development from nauplii stages to copepodit stages (ESM Table. 1). These loss terms were subtracted from the total observed nauplii abundance to calculate the survival rate from one sampling date to the following. The survival rate was calculated for ambient and cold temperature treatments from nauplii to copepodit stage C2. The survival rate for warm temperature treatments was estimated from nauplii to C2 by linear interpolation, because copepodits reached the C5 stage within the 7-day sampling interval.

Statistical analysis

The copepod biomass, prosome length, and log transformed abundances ($n + 1$) were firstly tested for normal distribution and equal variance applying Kolmogorov–Smirnov tests followed by a Kruskal–Wallis ANOVA on ranks test for temperature effects ($\alpha = 0.05$) in SigmaPlot version 11.0 (Systat Software, San Jose, CA, USA). Subsequently, linear mixed models were formulated in Rstudio 2012, version 0.97.551, to investigate temperature effects on copepod biomass, abundance, prosome length, and diversity. The linear mixed models for abundance and prosome length were run for all occurring taxa of copepodits and adults as well as for the predominant taxon *Acartia* sp. (Cottingham et al. 2005; Krueger and Tian 2004). Temperature and taxon were set as categorical factors, time in days as repeated measures (continuous).

Abundance

Linear mixed models for copepod abundance statistics were run for nauplii, adult copepods of all taxa, and all developmental stages of the predominant taxon *Acartia* sp. Temperature and species were set as categorical factors, time as a repeated measure and mesocosm ID as a random factor.

Edible phytoplankton biomass was analyzed by cross-correlations through time within mesocosms and following ANOVA with correlation coefficients for temperature effects. Additionally, correlation analysis of total phytoplankton and ciliate biomass were measured on the final day of the experiment to examine general trends.

Size

An *Acartia* sp. size analysis was conducted in a linear mixed model over time. Temperature and developmental stage were set as explanatory categorical factors, and time as a repeated measure. Mesocosm ID was used as random factor.

Size analyses of all adult copepods of every occurring taxon were conducted as linear mixed models over time. Temperature and species were set as categorical factors, time as a repeated measure, and mesocosm ID was used as a random factor.

Temperature effects on size as of the last experimental day were analyzed using ANOVA with size means of each species and developmental stage for every mesocosm.

Diversity

The diversity analysis was conducted in a linear mixed model. The Shannon-Wiener Index (H') was calculated for each treatment and replicate (Shannon and Weaver 1963).

Table 1 Linear mixed effect model results of total copepodit abundance changes between temperatures over the course of the experiment

Test	Term	Std. Error	<i>t</i> ratio	<i>P</i>	<i>df</i>
Total copepodit abundance changes	Intercept	60.041	10.805	<0.0001*	33
	13.5 °C	4.399	0.214	0.036*	6
	17.5 °C	3.457	0.342	0.031*	6
	Time	0.794	5.574	<0.001*	33
	13.5 °C:time	1.123	−1.458	0.154	33
	17.5 °C:time	1.123	−3.662	0.001*	33
Adult copepods of all occurring taxa ($R^2 = 0.4604$)	Intercept	1.349	−2.220	0.027*	
	Time	0.007	2.620	0.009*	1
	Temperature	0.138	5.823	0.039*	2
	Species		43.583	<0.001*	5
	<i>Acartia</i> adult	0.162	14.760	<0.001*	4
	<i>Centropages</i> adult	0.164	−2.690	0.008*	4
	<i>Oithona</i> adult	0.162	−3.220	0.001*	4
	<i>Paracalanus</i> adult	0.162	−3.060	0.002*	4
	<i>Pseudocalanus</i> adult	0.162	−2.740	0.007*	4
	13.5–9.5 °C	0.136	−1.810	0.121	2
	17.5–13.5 °C	0.139	−1.610	0.158	2
	Total abundance nauplii changes between temperatures	Intercept	28.547	0.116	0.908
13.5 °C		40.371	0.538	0.610	6
17.5 °C		40.371	−0.085	0.935	6
Time		1.665	7.280	<0.001*	33
13.5 °C:time		2.355	−3.199	0.003*	33
17.5 °C:time		2.355	−4.103	<0.001*	33

* $P < 0.05$

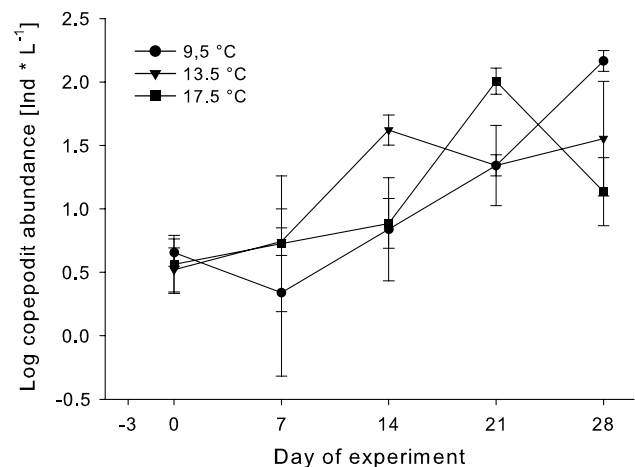
H' was used as a continuous response variable, temperature as a categorical variable, and time set as a repeated measure. The mesocosm ID was set as a random factor.

All tests were conducted at a significance threshold of $\alpha = 0.05$ and with post hoc Bonferroni-corrected Mann–Whitney tests.

Results

Copepod abundance

Total copepodit abundance of all occurring taxa was significantly affected by temperature ($P = 0.0358$, $df = 7$, $N = 270$) and time ($P = 0.0014$, $df = 69$, $N = 255$), as well as the interaction term of temperature and time ($P = 0.0353$, $df = 69$, $N = 225$, Table 1; Fig. 1). The linear mixed model results for adult copepods revealed significantly lower abundances in warm than in cold treatments ($P = 0.039$, $df = 2$, $N = 269$) and with time ($P = 0.009$, $df = 1$, $N = 254$, Table 1). The abundance of *Acartia* sp., including all copepodit stages, was lower in warm than in ambient and cold treatments (Figs. 2, 3). The highest

**Fig. 1** Log abundance of all developmental stages of all taxa over the experimental period

nauplii abundance was found in cold and the lowest in the warm treatments (Fig. 4). Also, nauplii abundance was significantly affected by temperature ($P < 0.001$, $df = 2$), time ($P < 0.001$, $df = 4$), and the interaction of temperature

Fig. 2 Mean abundance and development succession of *Acartia* sp. over time of all developmental stages in all temperature scenarios **a** 9.5 °C, **b** 13.5 °C and **c** 17.5 °C

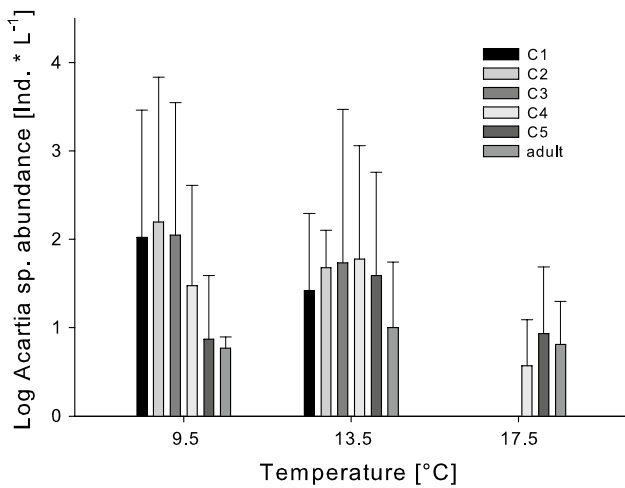
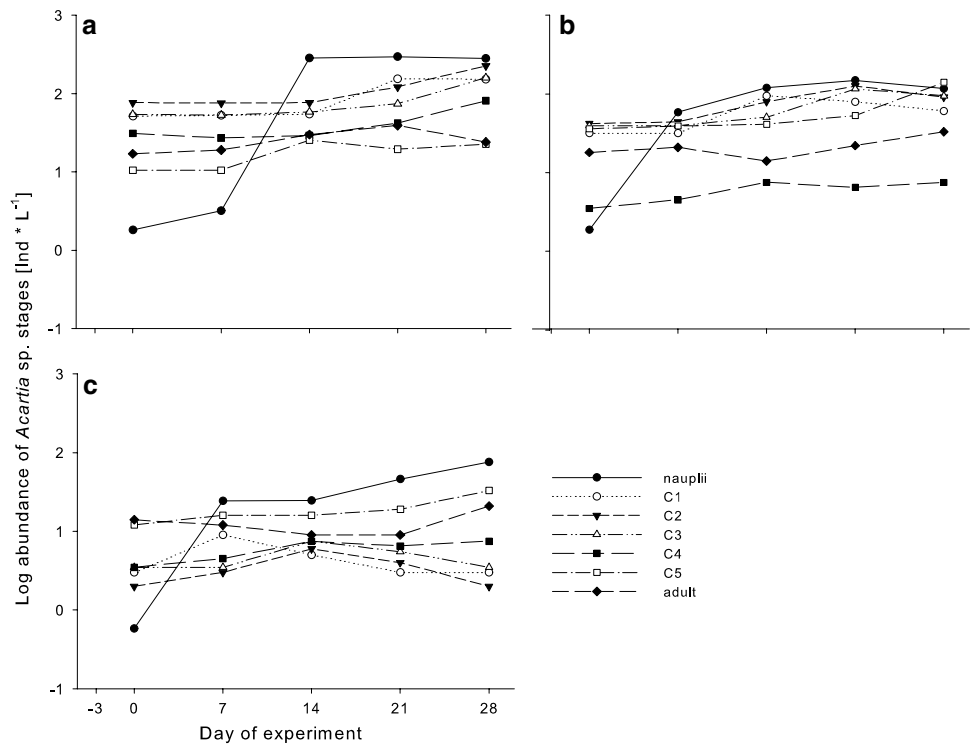


Fig. 3 Mean abundances of *Acartia* sp. developmental stages of the last experimental day in all temperature scenarios

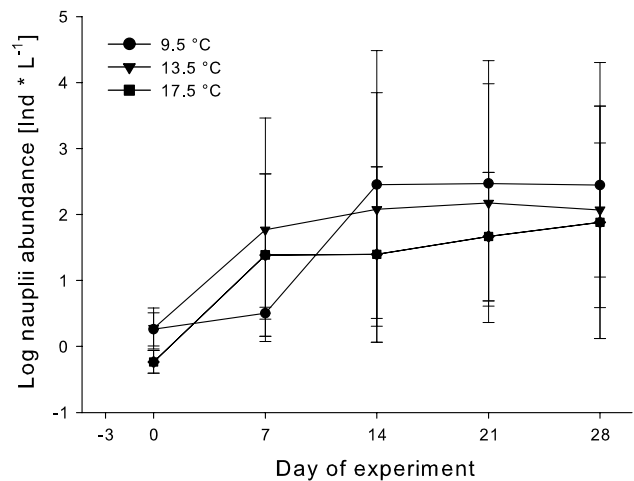


Fig. 4 Log nauplii abundances of all temperature scenarios during the experimental time

and time ($P < 0.001$, $df = 34$, Table 1). This represents the reproductive success of all copepod taxa during the experiment.

The estimated mean survival rates of the cooling scenario were 14.51 % (± 3.55 SD) and 17.13 % (± 8.73 SD) in ambient temperature from nauplii to the C2 copepodit stage. The estimated mean survival rate of the warming scenario was 12.51 % (± 6.82 SD) from nauplii to the C5 copepodit stage within 7 days (Table 2). However, the

development time within ambient and cold temperature was 7 days from nauplii developmental stage C2, but in the warm temperature treatments the copepodit stage C2 was reached after 2 days (Table 2). Therefore, the stage specific survival rate in 17.5 °C was higher from nauplii to stage C2 (75.01 %) in spite of a lower time, within 2 days, compared to the cold and ambient treatments, where 7 days were needed to develop from nauplii to stage C2. However, after 7 days, the survival rates were similar among all treatments.

Population age structure shift

The Mean Developmental Index indicated a population age shift between temperature treatments. The warming scenario (+4 °C to in situ temperature) had an MDI of 5.01, which indicated a dominance of developmental stage C5. The MDI of the in situ temperature treatments with 2.76 and the cooling scenario (4 °C below in situ temperature) with 2.47 represent a mixture of the stages C2 and C3. The observed differences of the mean developmental indices show that, at warmer temperature, copepods developed faster (stage C5) than at colder temperatures (C2–C3). This can also be seen from the relative abundances of the different developmental stages at day 28 (Fig. 3).

The cross-correlation coefficients of edible phytoplankton and ciliate biomasses, as copepod food sources of the whole experimental period, were negative for all treatments ($P = 0.4516$, $df = 2$, $N = 9$) (ESM Table 2). The ANOVA analysis of all correlation coefficients over the experimental time and all tanks indicated that food biomass (edible phytoplankton and ciliates) did not significantly vary with temperature ($P = 0.5869$, $df = 2$, $N = 162$) (ESM Table 3, Fig. 5a, b). The negative correlation coefficients indicate that temperature had no direct effect on the food biomass and that copepods of all treatments had comparable biomasses of edible phytoplankton and ciliates available over the course of the experiment (Fig. 5b). Additionally, we performed correlation analyses of food biomasses with adult *Acartia* sp. biomasses, which indicate that food biomass in ambient ($R^2 = 0.9492$) and warm ($R^2 = 0.9701$) temperature treatments were affected positively by adult *Acartia* sp. biomasses on the last experimental day (ESM Table 4). Yet, these effects did not differ between warm and ambient treatments. Edible phytoplankton and ciliate biomass of the cooling scenario was highly negatively correlated with adult *Acartia* sp. biomass ($R^2 = -0.9936$, ESM Table 4). Also, analysis of variance of the correlation coefficients between food (edible phytoplankton and ciliates) and adult *Acartia* sp. biomasses show no temperature-dependent difference (ESM Table 5). Consequently, no significant effect of food availability on adult *Acartia* sp. could be identified (ESM Table 5, Fig. 5a, b).

Size

The mean prosome length of adult copepods of all occurring taxa significantly decreased over time ($P < 0.001$, $df = 4$, $N = 1048$), and female adult copepods ($N = 477$) significantly decreased more strongly in size than males ($N = 571$) ($P < 0.0001$, $df = 2$, Table 3). All adults of the occurring taxa had significantly smaller prosome lengths at warmer temperatures ($N = 327$) ($P = 0.007$, $df = 2$) than at colder temperature ($N = 721$) over the course of the experiment (Table 3). Copepod size analysis of the final experimental day also showed that adult copepod prosome lengths of all taxa, decreased significantly with warming compared to adults at colder temperatures ($P = 0.0086$, $df = 2$, $N = 647$, Table 4).

Adult *Acartia* sp. mean prosome length was significantly smaller with warming ($P = 0.0118$, $df = 2$, $N = 308$) and over time ($P < 0.001$ $df = 4$, $N = 975$, Table 3). However, on the last experimental day the mean prosome length of *Acartia* sp. across all stages was significantly larger in the cold treatments ($P = 0.032$, $N = 199$), but did not show a further significant decrease between warming ($N = 182$) and ambient temperature ($P = 0.137$, $N = 225$, Table 4). *Acartia* sp. mean prosome length change results of the last experimental day showed a significant decrease with warming ($P < 0.0001$, $df = 2$, Table 4). The effect of smaller prosome size with warming was bigger between the warmest and coldest temperature treatment ($P < 0.001$) than between the ambient and the warming temperature treatment ($P = 0.0369$, Table 4). There was no significant temperature effect on mean prosome length over the experimental period between ambient and warming treatments. Adult *Acartia* sp. mean sizes showed stronger relative decrease with temperature than juvenile stages (Table 4; Figs. 5, 6). In contrast to the significant size increase of all copepod developmental stages with cooling, the mean prosome length of adult copepods of all taxa was significantly smaller in warm treatments compared to the ambient temperature (Tables 3, 4). However, in the adult *Acartia* sp. the size change mounted to 123 μm (16.89 %) across the temperature gradient of 8 °C (ESM Table 6) showing that,

Table 2 Estimated *Acartia* sp. survival rates (%) per week of new produced and incubated nauplii

Temperature	Day 7–14	Day 14–21 (%)	Day 21–28 (%)	Mean (SD)
9.5 °C		12 (Nauplii–C2)	17.02 (Nauplii–C2)	14.51 (± 3.55)
13.5 °C		23.3 (Nauplii–C2)	10.96 (Nauplii–C2)	17.13 (± 8.73)
17.5 °C	7.14 (Nauplii–C5)	10.21 (Nauplii–C5)	20.18 (Nauplii–C5)	12.51 (± 6.82)
Interpolation 17.5 °C for estimated development time from Nauplii to C2	73.47 (Nauplii–C2) day 7–9	74.36 (Nauplii–C2) day 14–16	77.19 (Nauplii–C2) day 21–23	75.01 (± 1.95)

Table 3 Linear mixed model results for mean prosome size changes over the experimental time

Test	Term	Std. Error	t Ratio	P	df
adult copepods of all taxa ($R^2 = 0.4137$)	Intercept	36.795	17.32	<0.001*	1
	Time	0.185	3.33	0.001*	4
	Temperature		12.849	0.007*	2
	Species		43.193	<0.001*	5
	13.5–9.5 °C	13.997	–1.91	0.106	2
	17.5–13.5 °C	14.088	–3.15	0.019*	2
	<i>Acartia</i> sp.	6.293	–8.20	<0.001*	3
	<i>Centropages</i> sp.	9.687	4.59	<0.001*	3
	<i>Paracalanus</i> sp.	14.721	–0.56	0.572	3
	<i>Pseudocalanus</i> sp.	13.371	6.14	<0.001*	3
Stage-specific copepod size of <i>Acartia</i> sp. ($R^2 = 0.902041$)	Intercept	15.974	46.720	<0.001*	1
	Time	0.069	–17.600	<0.001*	4
	Temperature		10.315	0.012*	2
	Stage		3339.001	<0.001*	6
	Adult	3.907	45.340	<0.001*	6
	C1	4.365	–40.590	<0.001*	6
	C2	4.364	25.780	<0.001*	6
	C3	4.274	–8.480	<0.001*	6
	C4	3.817	2.640	0.008*	6
	C5	3.874	28.870	<0.001*	6
	9.5–13.5 °C	11.641	–2.800	0.032*	2
	13.5–17.5 °C	11.727	–1.720	0.137	2

* $P < 0.05$

particularly, warming leads to a bigger relative size change (16.86 %) than cooling (7.79 %, ESM Table 6).

Copepod taxonomic composition

The copepod community included the genera *Acartia* sp., *Centropages* sp., *Oithona* sp., *Paracalanus* sp., and *Pseudocalanus* sp. The initial dominance of *Acartia* sp. became stronger in the ambient and cold treatments, while it was slightly reduced in the warm treatment (ESM Fig. 2).

Only time had a significant decreasing effect on Shannon-Wiener indices as a measure of diversity, while diversity of copepod communities did not depend on temperature in our set-up, reflecting a marked dominance of *Acartia* sp. across all temperatures (Table 5).

Discussion

Abundance and population age structure shifts

Observed effects on zooplankton with warming include a decline in total abundance of nauplii, copepodites, as well as fewer adult copepods with warming, and a simultaneous shift from a copepodite- to a nauplii-dominated population structure. This can be explained by (1) an accelerated

hatching process of copepods with rising temperature, (2) lower reproduction, or (3) higher mortality of copepodites at warmer temperatures. Not only are egg production and hatching of copepods affected by rising temperature, but also earlier reproduction with increasing temperature can be expected (Kordas et al. 2011). Klein Breteler and Schogt (1994) found that copepods have a higher daily mortality with increasing temperature than copepods in colder environments. This leads to the suggestion that the stage-specific survival rate might be higher while development is slower in colder temperatures and vice versa for copepods in warm temperatures during the present study. An increasing daily mortality at warmer temperatures can be partially, fully, or over-compensated by a faster development time at warmer temperatures because of a faster transition from stage to stage (Campbell et al. 2001; Hirst and Kiorboe 2002; Leandro et al. 2006). This is in agreement with the estimated survival rates in this study. The daily survival rate within the sampling period of 1 week is slightly lower in warmer than in colder temperatures. Lower copepod daily mortality and higher food availability, phytoplankton biomass (Sommer and Lewandowska 2011), leads to the suggestion that the relative survival rate of nauplii is higher at colder than at warmer temperatures. Not only does the faster turnover of generations at warmer temperatures have to be considered, but also the direct effect of warmer temperature

Table 4 ANOVA results for mean prosome length changes of last experimental day

Test	Term	Sum Sq	Mean Sq	F value	P	df
Adults ($R^2 = 0.946801$)	Temperature	30,293	30,293	8.958	0.008*	1
	Species	142,547	35,637	10.538	<0.001*	4
	Temperature:species	6,407	2,136	0.632	0.605	3
<i>Acartia</i> sp. development stages ($R^2 = 0.9945$)	Intercept	3.032	154.19	377.4886	<0.001*	16
	Temperature			100.2368	<0.001*	2
	Stage			869.4145	<0.001*	5
	Temperature:stage			13,385.4	<0.001*	9
	13.5 °C	-7.496	-2.18		0.037*	1
	17.5 °C	-24.750	-4.41		0.001*	1
	C1	-195.563	14.17		<0.001*	
	C2	-110.082	-20.03		<0.001*	
	C3	-52.588	-11.13		<0.001*	
	C4	24.585	5.54		<0.001*	
	C5					
	Adult	202.813	45.7		<0.001	
	13.5 °C:C1	16.909	1.23		0.229	
	13.5 °C:C2	-1.704	-0.25		0.803	
	13.5 °C:C3	-0.732	-0.12		0.906	
	13.5 °C:C4	-7.621	-1.72		0.096	
	13.5 °C:C5					
	13.5 °C:adult	9.901	1.66		0.106	
	17.5 °C:C1	-6.678	-0.26		0.8	
	17.5 °C:C2	34.083	3.33		0.002	
17.5 °C:C3	5.939	0.69		0.494		
17.5 °C:C4						
17.5 °C:C5						
17.5 °C:adult	-38.028	-4.79		<0.001		

* $P < 0.05$

on the individual metabolism is suggested for changes in population ecology. Brown et al. (2004) stated within the ‘Metabolic Theory of Ecology’ that faster metabolism at warmer temperatures is able to change the energy demands of the individual organism. A higher metabolic rate might lead to higher energy demands, which have to be covered by higher feeding rates on the copepods’ food source (phytoplankton and ciliates). The experimental results showed that food availability, here, edible phytoplankton and ciliate biomass, did not significantly differ between the temperature treatments, either over the course of the experiment or on the last experimental day. But the correlations of food and adult *Acartia* sp. biomasses showed that at colder temperatures food biomass declined with higher adult *Acartia* biomass. This might occur because larger bodied adult *Acartia* were more abundant than smaller bodied adult *Acartia* at warmer temperatures for similar food source amounts. This may be taken to indicate that larger *Acartia* sp. adults in the colder treatments were able to graze more efficiently on the available food. Top-down control was thus only executed of copepods in the cold treatments, while in ambient and warm treatments of copepod biomass was bottom-up regulated on

the last experimental day. Because of the opposite direction of correlation between phytoplankton and ciliate biomass on adult *Acartia* sp. biomass in the different temperature treatments, there is no significant effect shown by our results. However, within temperature treatments, our results uncover grazer and food biomass dependencies.

A predominance of mortality effect would be manifested in a lower density of calanoid copepods and nauplii, as shown by a mesocosm experiment in the warm temperate coastal north Atlantic Ocean by O’Connor et al. (2009), and also in this present experiment at the cold temperate Baltic Sea coast. Hirst and Kiorboe (2002) found that predation mortality contributes an ambient temperature-independent proportion of two thirds to three quarters to total mortality. However, predation can be excluded as a result for mortality changes between the different temperature treatments in this study.

Size

Reduction of prosome length in adult copepods could be a result of increasing metabolic demands with increasing

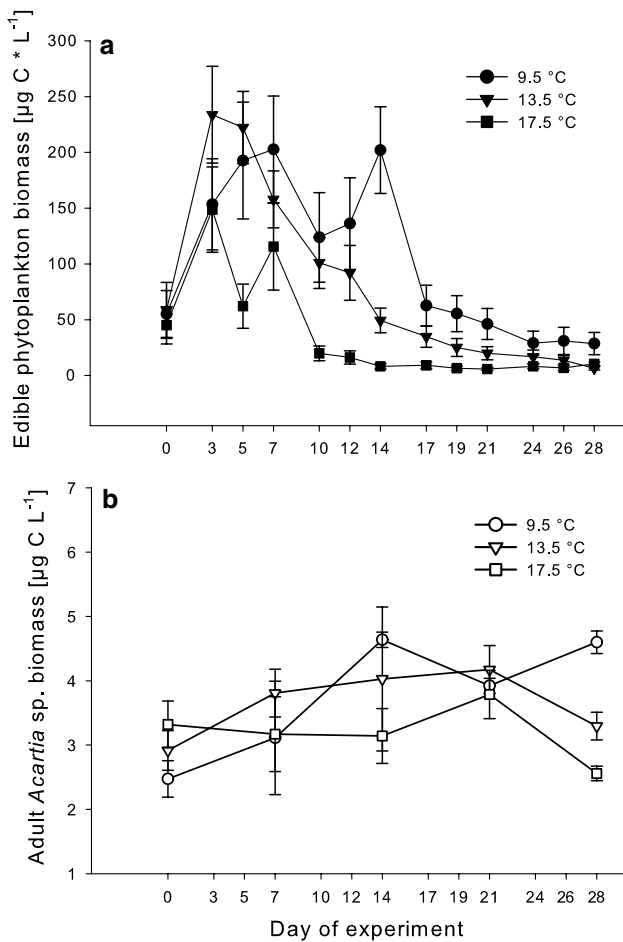


Fig. 5 Biomass (mean \pm SD) of **a** edible phytoplankton and **b** adult *Acartia* sp. over time for all temperature scenarios

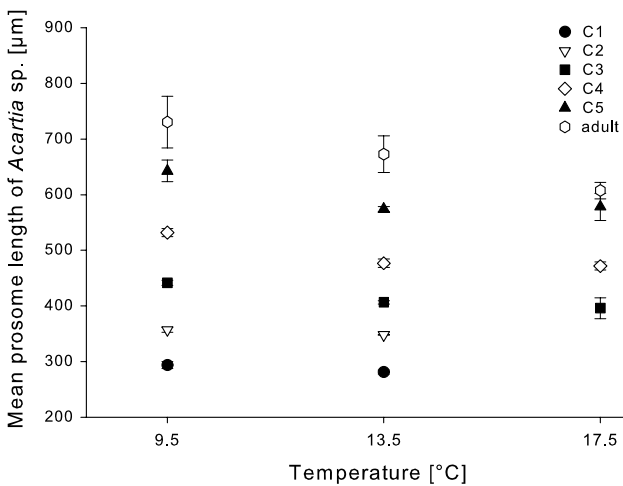


Fig. 6 Prosome length (mean \pm SD) of *Acartia* sp. on the last day of the experiment for all temperature treatments

Table 5 Linear mixed model results of diversity changes in copepods and copepodits ($R^2 = 0.212501$)

Term	Std. Error	<i>t</i> ratio	<i>P</i>	<i>df</i>
Intercept	0.789	2.60	0.013*	
Time	0.004	-2.16	0.038*	1
Temperature	0.067	1.524	0.292	2

* $P < 0.05$

temperature. Brown et al. (2004) postulated in their 'Metabolic Theory of Ecology' that smaller organisms have faster metabolisms because of basic biochemical and physiological laws. For increasing energy demands to maintain a basal (for staying alive and healthy) and active metabolism (growth and reproduction), it becomes necessary to find a higher quantity or higher quality of food (Claireaux and Lefrancois 2007). Earlier mesocosm studies of Sommer and Lengfellner (2008) showed that the biomass and mean cell size of phytoplankton decreased with increasing temperature. These observations could lead to the conclusion that energy demands of higher metabolic rates cannot be sufficiently fulfilled because of a loss of phytoplankton in biomass and cell size (Brown et al. 2004; Lewandowska and Sommer 2010). Biomass data of our experiment did show that food biomass was not directly affected by temperature, but that with increasing temperature, the correlation of copepod and edible phytoplankton biomass changed. Warming increased the grazing rate of copepods on phytoplankton due to the need for covering the increased energy demand at the warmer temperatures. Stoichiometry analysis of the bulk water components, including all phytoplankton species (edible and non-edible), ciliates, and bacteria, showed that the C:N ratio in particulate organic matter increased with increasing temperature (Taucher et al. 2012). These differences in C:N ratio might be a hint for lower protein content, or higher lipid or carbohydrate content. However, we cannot exclude that maturation at lower size is a genetically fixed adaptation to higher food demands at higher temperatures. We can also support the model of Forster et al. (2011) that early life cycle stages show a less pronounced effect in size reduction than adults. The observed *Acartia* sp. stage C1 had 10 μm smaller prosome lengths at 13.5 $^{\circ}\text{C}$ than the mean prosome length of C1 *Acartia* sp. copepodits within the cooling scenario with 9.5 $^{\circ}\text{C}$. The prosome length difference between the temperature treatments increased with increasing developmental stage. Also, in the other taxa, declining cell and body sizes could be observed. The phytoplankton, as in other studies, showed a decreasing average cell size and effective particle size (Sommer, pers. Comm.).

One additional factor affecting the food web (phytoplankton—zooplankton) is the change in biogenic carbon flow with rising temperature (Wohlers et al. 2009). Change in biogenic carbon flow results from changes in size (algae and copepods) and relative abundant activities of heterotrophic nanoflagellates, ciliates, and copepods. This observation could show changes in size of algae and copepods, as well as in heterotrophic nanoflagellates that could reduce the transfer of primary produced organic matter to higher trophic levels. Wohlers et al. (2009) observed higher community level respiration with increasing temperature. The combination of a decreasing transfer of organic matter to higher trophic levels, the need for more energy for the basal metabolism of individuals, and the decreasing size of organisms can lead to a big loss in energy for copepods. Thus, the biomass of algae as prey for copepods decreases with temperature and, in addition, the cell size of algae is also decreasing. These observations lead to the opinion that smaller algae are more favorable for heterotrophic protists than for copepods. Warmer temperature might have the potential to decrease the energy transfer through the food web which could result in a re-structuring of the food web to a system dominated by smaller-sized species (e.g. protists) (Lewandowska and Sommer 2010). Dominance of smaller sized individuals at warmer temperatures may result in the loss of trophic links for herbivorous and carnivorous consumers (Petchey et al. 1999; Winder and Sommer 2012). A loss in accessible energy for higher trophic levels like fish larvae might lead to a decrease of these higher trophic levels, e.g. loss in fish abundance or lower reproduction rates. Bochsanský et al. (2005) found that fish larvae have higher mortality with food limitation in combination with higher metabolic rates. This would mean that temperature would lead to higher metabolism in fish and their larvae, as predicted by the metabolic theory (Brown et al. 2004), and would be influenced directly by temperature, but also indirectly by limited food sources due to decreasing copepod abundance.

Interestingly, the results show that warmer temperatures significantly decrease the mean body size in the population by causing higher abundance ratios of nauplii-to-copepodites and, additionally, by causing smaller stage-specific sizes. Thus, our results could have consequences for food availability to higher trophic levels, like fish larvae. Less available food with smaller prey may lead to food limitation of favored size classes to cover the needs of copepod-dependent higher trophic levels. While it is known that differences in food quality can lead to slower development, smaller body size, and reduced egg production in copepods (Klein Breteler et al. 1990; Koski et al. 1998), in our experiment we did not assess temperature driven quality changes for phytoplankton and ciliates as food sources for copepods, such as differences in fatty acid content or carbon-to-nutrient ratios.

The observed and expected patterns of decreasing copepod body size with higher temperature are in line with widely found trends exhibited by different taxa in terrestrial and aquatic ecosystems, spanning from insects and crustaceans, to birds and mammals (Sheridan and Bickford 2011). Consequences of these temperature-induced body size shifts are likely to alter prey spectra, food availability, and feeding efficiency for higher level predators, and thus impact on nutrient transport and biomass build-up at higher trophic levels.

Future research to identify possible changes in the marine planktonic food web could involve more factors that are predicted to change. Ocean acidification might additionally influence the mesozooplankton communities in the world oceans and might enhance the effects on food web structure. To be able to predict possible changes to the marine food web due to global change, it is important to estimate future effects and their implications for ecosystem services.

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