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RESEARCH ARTICLE

The neritic marine copepod *Centropages typicus* does not suffer physiological costs from diel temperature fluctuations associated with its vertical migration

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Abstract

Diel vertical migration exposes zooplankton to fluctuating environmental conditions. In our study, we investigated the physiological costs of diel temperature fluctuations of vertical migration in the neritic marine copepod *Centropages typicus*, and checked whether the direct effects of fluctuating temperature on copepod performance may differ from those of average temperature conditions (Jensen's inequality). We determined the rates of egestion, egg production, and respiration of copepods exposed to four temperature regimes including one treatment that simulated diel vertical migration (DVM, 10 h at 14 °C and 14 h at 19 °C) and three treatments with constant temperature (14, 17 and 19 °C). We found that the physiological performance of *C. typicus* was not significantly different between fluctuating (DVM) and average (17 °C) temperature conditions, thus indicating that differences between varying and average temperature effects might not emerge in migrant zooplankton exposed to thermal variations of moderate magnitude (5 ºC). The copepods exposed to fluctuating temperature mimicking vertical migration (DVM) showed better performance (e.g. higher egg production) than those exposed to constant depth conditions (14 °C); however, no significant differences were detected when compared to constant surface conditions (19 °C). Our study indicates that neritic marine copepods experiencing daily moderate temperature fluctuations through vertical migration may not suffer physiological costs due to temperature associated with this behaviour. In this sense, these animals might have physiological mechanisms to compensate diel temperature fluctuations, which would represent a particularly relevant preadaptation to cope with the increased thermal variability predicted in future climates.

Keywords DVM · Environmental fluctuations · Jensen's inequality · Trade-offs · Zooplankton

Introduction

Zooplankton represent a vital trophic link between primary producers and fish in aquatic ecosystems (Turner 2004; Sommer and Sommer 2006). Many species of zooplankton conduct diel vertical migrations, frequently staying in upper waters at night and moving to deeper, darker layers during the daytime (Haney 1988). This migratory behaviour results in adaptive benefits such as a lower mortality risk from visual predation, or the protection against damaging UV radiation during daylight hours (Bollens and Frost 1989, 1991; Williamson et al. 2011). However, migrant zooplankton typically face different conditions of temperature and food availability through the water column that might affect their fitness (Geller 1986; Loose and Dawidowicz 1994; Pearre 2003). McLaren (1963) and Enright (1977) initially suggested that feeding in upper, warmer layers at night and resting in deeper, colder waters during the daytime could provide an energy bonus to invest in growth and reproduction. Experimental studies, however, demonstrated that fluctuating environmental conditions experienced by diel migrators (mostly *Daphnia*) usually imply detrimental metabolic costs compared to non-migrating conditions in upper layers (Swift 1976; Orcutt and Porter 1983; Stich and Lampert 1984; Lampert et al. 1988; Loose and Dawidowicz 1994). In this respect, migrant zooplankton might be better adapted to cope with fluctuating conditions of vertical migration than non-migrants, thus optimizing the trade-offs derived from their migratory behaviour (Stich and Lampert 1984).

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Changes in temperature during vertical migration could have even a more significant impact than varying food conditions on the life history traits of zooplankton (Loose and Dawidowicz 1994; Winder et al. 2003). Generally, zooplankton exposed to diel temperature fluctuations show a physiological performance that is intermediate between the performances at the lower and upper thermal limits (Vuorinen 1987; Reichwaldt et al. 2005). The effects of fluctuating temperature on animals, however, might not be necessarily inferred from the study of average temperature effects according to the mathematical property of nonlinear averaging known as Jensen's inequality (Ruel and Ayres 1999). The differences between fluctuating and average temperature effects predicted by Jensen's inequality have indeed been confirmed for a wide variety of physiological processes in animals, particularly in insects (Colinet et al. 2015), but still remain poorly documented in aquatic organisms facing wide temperature fluctuations on a daily basis, such as migrant zooplankton. In this regard, Orcutt and Porter (1983) found that the life history parameters of *Daphnia parvula* could be positively affected by fluctuating temperature of vertical migration in comparison to constant mean temperature conditions. Lock and McLaren (1970), however, reported that the female lengths of the copepod *Pseudocalanus minutus* did not show any significant difference between varying and average temperature regimes. The recent increasing awareness of Jensen's inequality among biologists has certainly improved our capability to determine the physiological performance of organisms under natural conditions of short-term temperature fluctuations (Denny 2017; Morash et al. 2018). Despite the growing number of studies, most of the recent literature about the effects of fluctuating temperature on zooplankton has focused on freshwater cladocerans (Mikulski et al. 2017; Isanta Navarro et al. 2019; Hahn and von Elert 2020), whereas such effects remain largely unexplored in other important zooplankton groups like copepods (Zhou and Sun 2017).

Copepods are among the most abundant mesozooplankton worldwide, particularly in pelagic systems (Longhurst 1985; Boxshall and Defaye 2008). Many copepod species face temperature fluctuations through vertical migration in both freshwater and marine environments (Roe 1984; Geller 1986; Atkinson et al. 1992). It is well known that temperature can affect copepod fitness regarding their rates of growth and development (Vidal 1980; Huntley and Lopez 1992), feeding (Kiørboe et al. 1982; Durbin and Durbin 1992), egg production (Hirche et al. 1997; Koski and Kuosa 1999), and oxygen consumption (Hirche 1987; Ikeda et al. 2001). Considering the current lack of records, the study of the effects of temperature fluctuations on copepod performance is essential knowledge to improve our capability to estimate energy fluxes within aquatic food webs, as well as provide insights about the susceptibility of copepods to future climate change scenarios (Vasseur et al. 2014).

In our study, we aimed to determine the physiological costs of diel temperature fluctuations involved in vertical migration in the neritic marine copepod *Centropages typicus*, and examine the different effects that might emerge between varying and average temperature conditions (Jensen's inequality). We exposed this copepod species to four temperature regimes simulating different migratory patterns and analysed functional traits related to feeding, reproduction, and basal metabolism. *C. typicus* represents one of the dominant copepod species in coastal waters of the Mediterranean Sea, the North Sea, and different areas of the East and North Atlantic Ocean, reaching abundances of several hundreds of individuals per cubic meter (Ianora and Buttino 1990; Calbet et al. 2001; Halsband-Lenk et al. 2002; Bonnet et al. 2007). In the NW Mediterranean *C. typicus* populations show strong seasonal fluctuations in abundance with peaks in spring-early summer, and around 7 generations per year (Ianora and Buttino 1990; Saiz et al. 2014). The range of temperatures used in our experiments corresponded to those experienced by *C. typicus* populations in the NW Mediterranean throughout the extent of their vertical migration from surface waters (night hours) down to 50–90 m deep during the daytime (Alcaraz 1985; Saiz and Alcaraz 1990; Saiz et al. 1992, 1999). Additionally, we checked whether the physiological performance of copepods under fluctuating temperature conditions could be predicted accurately from their performance in the upper and lower thermal limits.

Materials and methods

Prey and copepod cultures

The dinoflagellate *Oxyrrhis marina* was used as copepod food in copepod cultures and experiments. *O. marina* was grown in 0.1-µm filtered seawater fed with the algae *Rhodomonas salina*. The stock culture of *R. salina* was grown in *f*/2 medium (Guillard 1983). The *O. marina* cultures were not supplied with food for 48 h before experiments to ensure the absence of *R. salina* cells during incubations. All the *O. marina* and *R. salina* cultures were kept in a temperature-controlled room at 19 ± 0.5 °C and a 10 h:14 h light:dark cycle.

Eggs from the calanoid copepod *C. typicus* were obtained from a copepod stock culture kept at the Institut de Ciències del Mar (ICM, CSIC). This copepod line was collected in waters off Barcelona and isolated in May 2017. Around 25,000 eggs were siphoned out from the tank bottom of the copepod stock culture and placed in a new tank with 15 L of 0.1-µm filtered seawater. The new copepod cohort was fed with *O. marina* and kept at the same temperature and photoperiod conditions as specified for the prey cultures. During the development process of the cohort, the volume of the copepod culture was increased from 15 L (nauplii) to 20–28 L (copepodites) and 32 L (adults). At the moment of the experiments, there were about 10,000–12,000 adults (1:1 sex ratio) in the tank.

Copepod acclimation to temperature regimes before experiments

Four open 72-L baths containing 33 L of filtered seawater were set at different temperature regimes using Teco water temperature conditioners (models TK2000 and TK500). The four temperature regimes were selected according to the typical temperatures that copepods (*C. typicus*) may experience in the Western Mediterranean in spring (Alcaraz 1985; Saiz et al. 1999). The temperature regimes included one treatment with fluctuating temperature that simulated diel vertical migration (DVM, 10 h at 14 °C during the daytime, and 14 h at 19 °C at night), and three treatments with constant temperatures: 14 °C (equivalent to 24 h at depth), 19 °C (equivalent to 24 h at the surface), and 17 °C (average DVM conditions considering the actual time spent at each temperature).

Four 4-L Nalgene bottles with filtered seawater were placed in each bath. In the case of fluctuating temperature treatment (DVM), the temperature of the Teco temperature-conditioner was manually switched to 14 and 19 °C at 8:30 and 18:30, respectively. Previous checks showed that the 5 °C temperature shifts in the temperature of the Nalgene bottle contents were fully reflected within a 2-h timeframe, with most of the variation (4 ºC) occurring within the first hour. Adult copepods were collected from the main copepod tank with a 335-µm mesh sieve, and 160 individuals (1:1 sex ratio) were added to each Nalgene bottle. The copepods were acclimated to the different temperature regimes and fed ad libitum with *O. marina* [> 5 ppm, van Someren Gréve et al. (2017)] for 5–7 days before the experiments (Hirche et al. 1997). The prey concentrations in the Nalgene bottles were controlled daily by removing 2 L from each bottle and adding new water and *O. marina* to reach concentrations of 11–11.5 ppm. The *O. marina* concentrations from stock cultures and Nalgene bottles were determined with a Multisizer III Coulter counter. During the acclimation period, copepods were under a 10 h: 14 h light: dark cycle.

Experimental setup and sample processing

Two consecutive experiments were conducted on 7 and 9 July 2019 at Institut de Ciències del Mar (ICM, CSIC) using copepods that were temperature-acclimated for 5 and 7 days, respectively. The experiments consisted of 24-h incubations to determine the carbon and nitrogen contents as well as the rates of feeding, egg production, and respiration of *C. typicus* at the four temperature regimes specified before (i.e. DVM, 14 °C, 17 °C, 19 °C). Before the incubations, the copepods were collected from the Nalgene bottles with a 335-µm mesh sieve and placed in 250-mL bottles with temperature-conditioned filtered seawater for ca. 2 h until been transferred to the experimental bottles.

The feeding activity of copepods was assessed according to their egestion (defecation) rates (Nejstgaard et al. 2001; Besiktepe and Dam 2002). The rates of egestion and egg production were analysed in the same incubation bottles (620 mL), whereas the respiration rates were determined in separate bottles (67 mL). For egestion and egg production rates, a suspension of *O. marina* (ESD: 18.7 ± 0.8 µm) at 8.5 ppm (ca. 2200–2800 cells mL^{-1}) was prepared using the Coulter Counter. Sixteen 620-mL Pyrex bottles (four bottles per temperature treatment) were filled with the prey suspension, and eight females of *C. typicus* were added to each bottle using a wide-mouth glass pipette. The bottles were then incubated for 24 h in the corresponding temperature treatments. At the end of the incubations, the bottle contents were sieved through a 200-µm mesh to collect copepods, and then through a 20-µm mesh to collect eggs and faecal pellets. Copepod survival was checked under a stereomicroscope, and the number of dead animals was noted (only one dead copepod in two out of thirty-two bottles considering both experiments). Copepods, eggs and faecal pellets were then fixed in either 4% formalin solution (copepods) or 2% acidic Lugol's solution (eggs and faecal pellets) for counting and size determination. The faecal pellets and eggs were counted using a stereomicroscope. Photos of ca. 15–20 copepod females and ca. 180–200 faecal pellets were taken for each temperature treatment using an inverted microscope. The prosome length of copepods, and the length and width of faecal pellets were measured with the software ImageJ (Schneider et al. 2012). An ellipsoidal shape was assumed to calculate average pellet volumes.

The respiration rates of copepods were estimated based on the decrease of water oxygen saturation in the incubation bottles. Oxygen concentration in the water was measured with a PreSens 4-channel oxygen meter fitted with PSt3 probes. Temperature-conditioned filtered seawater at 89–98% oxygen saturation was used to fill thirty-two 67-mL incubation bottles (eight bottles per treatment). Half of the bottles (four per treatment) served as control bottles (only water), and the other half as experimental bottles (water with copepods). Twelve females of *C. typicus* were pipetted into each experimental bottle and all the bottles were incubated for 24 h. The copepod densities in the bottles should not affect the respiration rates of copepods (Nival et al. 1972; Svetlichny et al. 2012). After the incubations, the oxygen saturation in the water was measured for each bottle. The final oxygen saturations in the experimental bottles (i.e.

bottles with copepods) were on average 84% and never fell below 77%. The copepods from the bottles were then sieved with a 200-µm mesh and their survival was checked under a stereomicroscope (one dead copepod in three out of thirty-two bottles in the two experiments). Subsequently, the copepods were fixed in formalin (4%) for counting, photographing and size measurements.

Finally, the carbon and nitrogen contents of copepods were determined using twenty-one pre-combusted GF/C filters in each experiment: one filter served as the filter blank (only filter), four filters as the water blanks (filter with water, one replicate per temperature treatment), and sixteen filters as the filters with copepods (ten females per filter, four replicates per temperature treatment). The filters were kept in Eppendorf vials, let dry at 60 °C for 48 h, and the carbon and nitrogen contents were determined with a FlashEA1112 Elemental Analyser.

Data analysis and statistics

The Q_{10} coefficients for the rates of egestion, egg production, and respiration of *C. typicus* were estimated based on the rates measured in the three temperature-fixed treatments (i.e., 14, 17, and 19 °C). The Q_{10} coefficients were calculated through the equation $Q_{10} = e^{\left(\frac{10E_a}{\mathrm{RT}^2}\right)}$ (Raven and Geider 1988), where E_a is the activation energy (J mol^{-1}), R is the constant gas (8.3145 J K^{-1} mol^{-1}), and T is the mean temperature (K) of the temperature range used to determine the Q_{10} coefficient. The activation energies of the different processes were obtained following the steps specified in Alcaraz et al. (2013). The rates of egg production and respiration of copepods were converted into carbon units using the conversion factor 29 ng C egg^{-1} by Saiz (unpubl.) and a respiratory quotient of 0.97 (Omori and Ikeda 1984) to determine ratios of egg production to respiration.

Statistical tests were performed using the software IBM SPSS Statistics 26. Randomized block design (RBD) ANOVA tests (carbon contents, nitrogen contents, molar C:N ratios, and egg production to respiration ratios of copepods), and a RBD MANOVA test (rates of egestion, egg production, and respiration) with experiment as block factor were applied to detect significant differences among temperature treatments. When temperature had a significant effect, Dunnett's tests were run to check for significant differences between DVM (i.e. treatment with diel temperature fluctuations) and the other treatments with fixed temperature. All the datasets met the assumptions of normality and homogeneity of variance according to Shapiro–Wilk and Levene's tests, respectively.

Finally, the rates of egestion, egg production, and respiration of copepods in the treatments with fixed temperature of 14 and 19 °C were used to predict the expected copepod physiological performance in the DVM treatment (i.e. diel fluctuations between 14 and 19 °C). For that purpose, the rates at 14 °C and those at 19 °C were weighted, respectively, by the time lengths of the day and night periods (10 and 14 h, respectively). Z tests were then run to check for significant differences between the predicted and the observed rates of egestion, egg production, and respiration of copepods in DVM conditions. The Z tests were run independently for each experiment based on the observed four replicates and using propagation of error to calculate the variances of the predicted means.

Results

Table 1 shows the prosome lengths, the carbon and nitrogen contents, and the molar C:N ratios of *C. typicus* in the different temperature treatments. As expected, the prosome lengths were very similar in all the treatments (overall mean: 1019 ± 3.5 µm), as the copepods originated from the same cohort and developed until adults under the same conditions. The average carbon contents seemed to decrease with temperature from 7.2 ± 0.23 µg C cop^{-1} at 14 °C to 6.4 ± 0.36 µg C cop^{-1} at 19 °C, although no significant differences were detected among temperature treatments (RBD ANOVA, $F(3, 27) = 1.326$, $p > 0.05$). The average nitrogen contents showed significant differences among treatments (RBD ANOVA, $F(3, 27) = 3.535$, $p < 0.05$) with higher values at 14 °C (ca. 2.0 µg N cop^{-1}) than in the other treatments (ca. 1.7 µg N cop^{-1}). The nitrogen contents were significantly different between DVM (i.e. fluctuating temperature

Table 1 Prosome lengths, carbon (C) and nitrogen (N) contents, and molar C:N ratios of *Centropages typicus* in different temperature treatments

Temperature (°C)	Prosome length (µm)	C (µg)	N (µg)	C:N ratio
DVM	1024 ± 5.1 (51)	6.6 ± 0.35 (8)	1.7 ± 0.09 (8)	4.6 ± 0.07 (8)
14	1019 ± 6.3 (28)	7.2 ± 0.23 (8)	2.0 ± 0.06* (8)	4.2 ± 0.05* (8)
17	1018 ± 4.7 (38)	6.7 ± 0.31 (8)	1.7 ± 0.08 (8)	4.5 ± 0.04 (8)
19	1014 ± 7.7 (38)	6.4 ± 0.36 (8)	1.7 ± 0.09 (8)	4.5 ± 0.06 (8)

DVM: simulation of diel vertical migration (10 h at 14 °C and 14 h at 19 °C). Data from the two experiments were pooled. Means ± SE are provided. Samples sizes are shown in parentheses. Significant differences with DVM are indicated with an asterisk (Dunnett's test, $p < 0.05$ for N, $p < 0.001$ for C:N ratio) of vertical migration) and 14 °C (Dunnett's test, $p < 0.05$), but not between DVM and 17 or 19 °C (Dunnett's tests, $p > 0.05$). The average molar C:N ratios of copepods ranged 4.2–4.6 and showed significant differences among temperatures (RBD ANOVA, $F(3, 27) = 7.605$, $p < 0.001$). The C:N ratios in DVM (4.6 ± 0.07) were significantly higher than at 14 °C (4.2 ± 0.05) (Dunnett's test, $p < 0.001$), but no significant differences were detected compared to 17 or 19 °C (Dunnett's tests, $p > 0.05$).

The faecal pellet volumes, and the rates of egestion, egg production, and respiration of copepods in the experiments are shown in Table 2. The egestion rates were significantly different among temperature treatments (RBD MANOVA, $F(3, 27) = 2.960$, $p < 0.05$), and increased about 20% from 14 to 17–19 °C ($Q_{10} = 1.4$) (Fig. 1a). However, no significant differences were detected between DVM and the other temperatures (Dunnett's tests, $p > 0.05$) (Fig. 1a). The egg production rates showed significant differences among treatments (RBD MANOVA, $F(3, 27) = 18.723$, $p < 0.001$), increasing with temperature from 60 ± 3.9 eggs cop^{-1} day^{-1} at 14 °C to 91 ± 3.4 eggs cop^{-1} day^{-1} at 19 °C ($Q_{10} = 2.3$) (Fig. 1b). The egg production rates in DVM (85 ± 2.1 eggs cop^{-1} day^{-1}) were significantly higher than those at 14 °C (Dunnett's test, $p < 0.001$), but not statistically different to those at 17 or 19 °C (Dunnett's tests, $p > 0.05$) (Fig. 1b). The respiration rates also showed significant differences among temperature treatments (RBD MANOVA, $F(3, 27) = 9.445$, $p < 0.001$) and increased from 0.129 ± 0.007 µmol O_2 cop^{-1} day^{-1} at 14 °C to 0.179 ± 0.008 µmol O_2 cop^{-1} day^{-1} at 19 °C ($Q_{10} = 2.0$) (Fig. 1c). The patterns of respiration rates were similar to those of egg production: the respiration rates in DVM (0.175 ± 0.010 µmol O_2 cop^{-1} day^{-1}) were significantly higher than at 14 °C (Dunnett's test, $p < 0.001$), but no statistical differences were detected compared to the rates at 17 or 19 °C (Dunnett's tests, $p > 0.05$) (Fig. 1c). When considering the carbon contents of copepods (i.e. weight-specific rates), the dependence on temperature was stronger in all the physiological processes with Q_{10} coefficients of 1.8 for egestion, 2.9 for egg production, and 2.5 for respiration. The egg production to respiration ratios of copepods were 1.24 ± 0.09 in DVM, 1.18 ± 0.08 at 14 °C, 1.10 ± 0.05 at 17 °C, and 1.28 ± 0.07 at 19 °C, and showed no statistical differences among temperatures treatments (RBD ANOVA, $F(3,27) = 0.976$, $p > 0.05$).

The predicted rates of egestion, egg production and respiration in DVM based on the rates observed at 14 and 19 °C and the times spent at each temperature were similar to the actual rates observed in the DVM treatment (Table 3). In the case of egg production and respiration rates, the average predicted values were a bit lower than those observed, although such small differences were not statistically significant (Z tests, $p > 0.05$).

Discussion

The temperature range used in our experiments (14–19 °C) represented the typical thermal conditions that the copepod *C. typicus* may experience during vertical migration in the north-western Mediterranean (Alcaraz 1985; Saiz et al. 1999). The Q_{10} coefficients that we obtained for the rates of egg production and respiration (2.3 and 2.0, respectively) were similar to those reported in previous studies for this species (Fernández 1978; Halsband-Lenk et al. 2002). In the case of the egestion rates, however, the dependence on temperature was lower than expected ($Q_{10} = 1.4$). The pellet production rates in our experiments might appear a bit low according to the values reported in the compilation by Dam and Peterson (1988). However, it is known that the egestion rates of marine copepods can be highly variable across prey types (Traboni et al. 2020). We think that the use of the naked dinoflagellate *O. marina* as prey, which lacks hard body parts, led to lower egestion rates compared to previous studies where other prey organisms with hard body parts (e.g. diatoms) were used as the main food source. This is because hard body parts are difficult to digest by copepods and they lead to a quicker gut filling and shorter gut passage times. Regarding the low Q_{10} value found for the egestion rates of copepods, a temperature difference of 5 °C should be enough to observe differences

Table 2 Faecal pellet (FP) volumes, and rates of egestion, egg production, and respiration of *Centropages typicus* in different temperature treatments

Temperature treatment (°C)	FP volume (µm^3)	Egestion rate (FP cop^{-1} day^{-1})	Egestion rate (µm^3 cop^{-1} day^{-1})	Egg production rate (eggs cop^{-1} day^{-1})	Respiration rate (µmol O_2 cop^{-1} day^{-1})
DVM	124,383 ± 5406 (349)	36 ± 1.3 (8)	4,513,995 ± 152,369 (8)	85 ± 2.1 (8)	0.175 ± 0.010 (8)
14	133,014 ± 9033 (340)	32 ± 1.4 (8)	4,255,466 ± 245,192 (8)	60 ± 3.9* (8)	0.129 ± 0.007* (8)
17	133,374 ± 5211 (343)	39 ± 2.5 (8)	5,232,905 ± 308,786 (8)	77 ± 3.2 (8)	0.175 ± 0.005 (8)
19	123,448 ± 7733 (331)	41 ± 2.6 (8)	5,004,039 ± 317,118 (8)	91 ± 3.4 (8)	0.179 ± 0.008 (8)

DVM: simulation of diel vertical migration (10 h at 14 °C and 14 h at 19 °C). Data from the two experiments were pooled. Means ± SE are provided. Sample sizes are shown in parentheses. Significant differences with DVM are indicated with an asterisk (Dunnett's tests, $p < 0.001$)

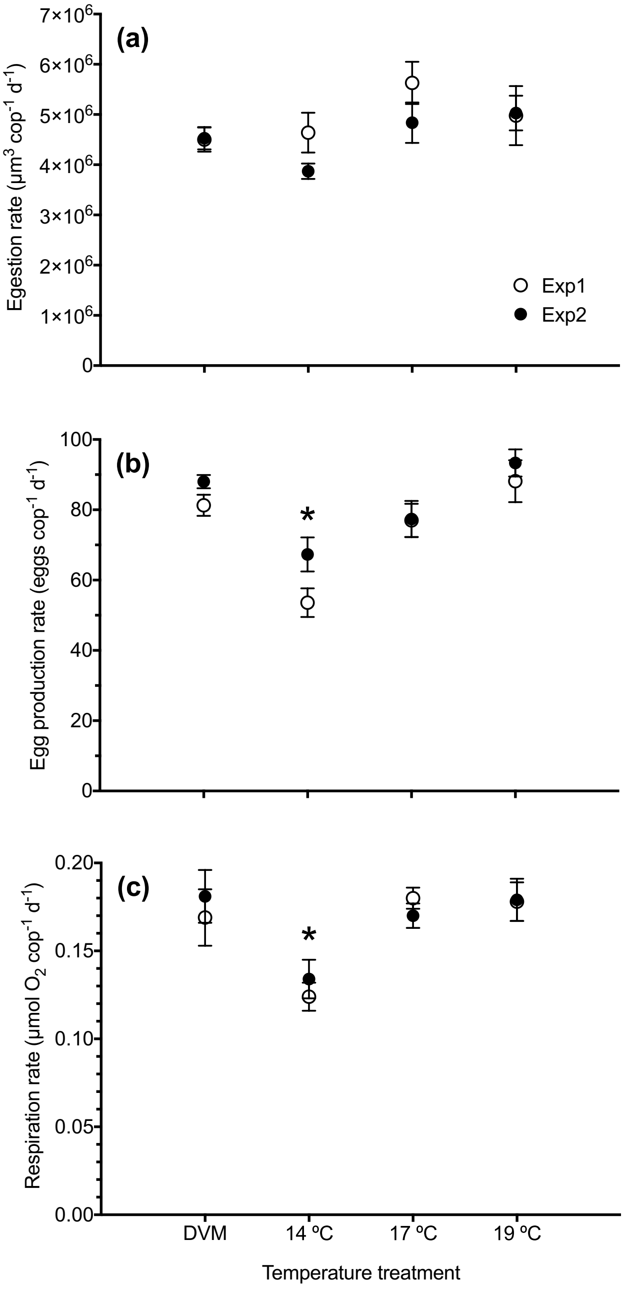

Fig. 1 Rates of egestion (**a**), egg production (**b**), and respiration (**c**) of *Centropages typicus* under different temperature treatments. DVM: simulation of diel vertical migration (10 h at 14 °C and 14 h at 19 °C). Means ± SE bars from the two experiments are shown. Asterisks indicate significant differences with DVM (Dunnett's tests, $p < 0.001$)

in the copepod feeding activity (Sell et al. 2001). It is surprising the little effect found here, as there is an extensive bulk of literature about the significant correlation between temperature and rates of ingestion and gut evacuation in planktonic copepods (Fernández 1978; Kiørboe et al. 1982; Dam and Peterson 1988; Durbin and Durbin 1992). In this sense, the egestion rates of copepods are documented as a good proxy for their ingestion rates (Nejstgaard et al. 2001; Besiktepe and Dam 2002). However, temperature can also affect the absorption efficiency of copepods (i.e. the portion of ingested food that is digested and absorbed; Almeda et al. (2011)), likely affecting the degree of packaging of the non-absorbed food remains. This fact could cause that egestion rates relate to temperature differently than ingestion rates. Therefore, it appears that the ingestion rates would have been a more appropriate parameter to determine the temperature dependence of copepod feeding activity. For that reason, egestion rates are not further considered in the discussion, even though these results do not contradict any of our conclusions.

In our study, we did not detect differences between varying and average temperature effects on copepod performance predicted by Jensen's inequality, as the rates of egg production and respiration of *C. typicus* exposed to fluctuating temperature (10 h at 14 °C and 14 h at 19 °C) were similar to those at 17 °C. Even though Lock and McLaren (1970) also found no evidence of Jensen's inequality when analysing changes in the female lengths of *P. minutus* in the thermal range 8–12 °C, other studies with zooplankton indicate that different outcomes between varying and average temperature regimes may appear upon wider temperature fluctuations (Orcutt and Porter 1983). The existing literature on this matter is still scarce, but it seems that the physiological performance of migrant zooplankton under temperature variations could be estimated through the study of average temperature effects as long as the amplitude of thermal variations is moderate. This finding is particularly relevant considering that studying the effects of constant temperature is simpler and requires less effort than using temperature fluctuations. Moreover, according to our results, average estimates based on the physiological performances at the upper and lower thermal limits and the times spent at each temperature would prove also suitable (even if statistically significant differences between the predicted and observed rates did not emerge due to low replication, both estimates differed on average less than 10%). Although migrant zooplankton may experience diel temperature fluctuations of relatively small amplitude (i.e. up to 5–6 °C) (Saiz and Alcaraz 1990; Cooke et al. 2008; Almén et al. 2014), other diel migrators from both marine and freshwater environments face temperature changes of 10 °C or more when moving between layers (Loose and Dawidowicz 1994; Svetlichny et al. 2000; Al-Mutairi and Landry 2001). In that case, differences between fluctuating and average temperature effects might emerge, and estimating the temperature-dependent performance of migrant zooplankton through the study of fixed temperature effects may become more challenging.

In our experiments, the copepods exposed to the regime of temperature fluctuations experienced through diel vertical

Table 3 Observed and predicted rates of egestion, egg production and respiration of *Centropages typicus* under fluctuating temperature conditions of diel vertical migration

Experiment	Estimate	Egestion rate (μm^3 cop^{-1} day^{-1})	Egg production rate (eggs cop^{-1} day^{-1})	Respiration rate (μmol O_2 cop^{-1} day^{-1})
Exp 1	Observed	4,499,994 ± 241,660 (4)	81 ± 3.0 (4)	0.169 ± 0.016 (4)
	Predicted	4,836,966 ± 381,999 (4)	74 ± 3.9 (4)	0.156 ± 0.007 (4)
Exp 2	Observed	4,527,997 ± 223,187 (4)	88 ± 1.9 (4)	0.181 ± 0.015 (4)
	Predicted	4,547,302 ± 212,647 (4)	82 ± 3.0 (4)	0.160 ± 0.009 (4)

The observed values refer to measurements obtained in the DVM treatment (10 h at 14 °C and 14 h at 19 °C), and the predicted values are calculated according to the rates measured at 14 °C and 19 °C and the number of hours at each temperature in the DVM treatment. Data from the two experiments are shown. Means ± SE are provided. Sample sizes are shown in parentheses. The SE of the predicted values were calculated following error propagation rules

migration showed a better performance (e.g. higher egg production) than those at constant, deep-water temperature (14 °C), but no differences were detected compared to those kept at constant surface temperature (19 °C). Also, the egg production to respiration ratios, as an indicator of physiological cost, were not statistically different among temperature treatments. Our results indicate that copepods do not necessarily suffer physiological costs from daily temperature fluctuations involved in vertical migration, at least those species like *C. typicus* that may experience a moderate range of temperature variation. In this respect, migrant zooplankton may have adaptive physiological mechanisms to compensate diel temperature fluctuations. Recent proteomic analyses indicate that migrant copepods experience distinct physiological shifts derived from their migratory behaviour (Maas et al. 2018). In our study, the carbon and nitrogen contents of copepods under temperature fluctuations did not differ from those at 17 or 19 °C, indicating that any temperature-induced adjustment in the copepod physiology might imply the expression of alternative protein variants, or the modulation of the protein environment (Clarke 2003). In copepods of relatively small size such as *Centropages* spp., changes in the synthesis and accumulation of small amounts of triglycerides might also happen upon temperature variations (Båmstedt 1986), although we think that such modifications in the lipid content would barely affect the copepod carbon: nitrogen ratios. In larger copepods with a greater capacity to accumulate lipid reserves (e.g. seasonal migrators), however, temperature-induced changes in the storage and composition of lipid compounds may play an important role to cope with temperature and pressure variations during vertical migration (Pond et al. 2014). In this regard, Zhou and Sun (2017) reported that diel temperature fluctuations could promote lipid accumulation in *Calanus sinicus*, and Hassett and Crockett (2009) found that *Calanus finmarchicus* was the only copepod among five species that showed changes in cholesterol levels across different temperatures.

Our study demonstrates that the temperature fluctuations involved in diel vertical migration might not imply metabolic disadvantages in marine copepods that experience temperature changes within a moderate range (5 °C). We cannot discard, however, that copepod species conducting larger migrations may suffer physiological costs from wider temperature fluctuations. Also, we did not consider diel changes in other environmental variables besides temperature that can also affect copepod performance. For instance, diel migrators may face important variations in food availability and oxygen saturation through the water column (Saiz et al. 1992; Atkinson et al. 1996; Saltzman and Wishner 1997; Wishner et al. 1998). In this regard, previous studies showed that the copepods *C. typicus* and *Paracartia grani* were capable to deal successfully with short-term fluctuations in food intake (Davis and Alatalo 1992; Calbet and Alcaraz 1996; Olivares et al. 2020). The effects of changing temperature on zooplankton, however, can covariate with those of other environmental variables (Koussoroplis and Wacker 2016), and the joint effects of varying temperature and other parameters during vertical migration might indeed translate into physiological costs compared to non-migrating conditions (Stich and Lampert 1984; Svetlichny et al. 2000). In addition, vertical displacements of diel migrators require an additional energetic investment for swimming activity (Alcaraz et al. 2007), although such energy requirements seem to be highly variable among zooplankton, and could represent from negligible to relatively high costs (Torres and Childress 1983; Morris et al. 1985; Dawidowicz and Loose 1992). Hence, the assessment of metabolic disadvantages of vertical migration in zooplankton goes beyond the study of the effects of diel temperature variations and will require further exploration to determine the overall energetic balance derived from this migratory behaviour.

The absence of physiological costs in *C. typicus* upon short-term temperature fluctuations is especially relevant within a climate change context, as an increased thermal variability in future climates is foreseen (Easterling et al. 2000; Wang and Dillon 2014). In fact, it is argued that higher temperature variability may represent a greater threat to species than global warming itself (Vasseur et al. 2014), although there might be certain groups such as copepods and other zooplankton that could benefit from increasing temperature variations in terms of higher population growth rates (Drake 2005). Still, former research that evaluated climate-driven temperature impacts on terrestrial and aquatic organisms mostly relied on the effects of mean temperatures (Thompson et al. 2013), and the influence of temperature fluctuations on their fitness remain understudied despite their critical role in future climates (Dowd et al. 2015).

As final remarks, our study provides novel evidence about how neritic marine copepods may not suffer physiological costs from diel temperature fluctuations involved in vertical migration. In this sense, marine copepods might have adaptive mechanisms to optimize the trade-offs derived from their migratory behaviour, thus diminishing the energetic costs traditionally associated to vertical migration. This potential capability of marine copepods may be useful to confront the negative impacts of the increased thermal variations expected with climate change.

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Author contributions All the listed authors (MO, AC, ES) contributed to the experimental design, the laboratory work, the data analysis/interpretation, and the manuscript preparation. All the listed authors approved the submitted version of this manuscript.

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Data availability The datasets generated and/or analysed during the current study will be available in the Digital. CSIC repository after publication.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethics approval No approval of research ethics committees was required to accomplish the goals of this study because experimental work was conducted with an unregulated invertebrate species.

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