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Do yearly temperature cycles reduce species richness? Insights from calanoid copepods

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Abstract The metabolic theory of ecology (MTE) has explained the taxonomic richness of ectothermic species as an inverse function of habitat mean temperature. Extending this theory, we show that yearly temperature cycles reduce metabolic rates of taxa having short generation times. This reduction is due to Jensen's inequality, which results from a nonlinear dependency of metabolic rate of organisms on temperature. It leads to a prediction that relatively lower species richness is found in habitats with larger amplitudes of yearly temperature cycles where mean temperatures and other conditions are similar. We show that metabolically driven generation time of a taxon also relates functionally to species richness, and similarly, its yearly cycles reduce richness. We test these hypotheses on marine calanoid copepods with 46,377 records of data collected by scientific cruise surveys in Mediterranean regions, across which the temperature amplitudes vary dramatically. We test both bio-energetic and phenomenological effects of temperature cycles on richness in 86 1° × 1° latitudinal and longitudinal spatial units. The models incorporated the effect of both periodic fluctuations and mean temperature explained 21.6% more variation in the data, with lower AIC, compared to models incorporated only the mean temperature.

The study also gives insight into the basis of energetic-equivalence rule in MTE determining richness, which can be governed by generation time of taxon. The results of this study lead to the proposition that amplitude of yearly temperature cycles may contribute to both the longitudinal and the latitudinal differences in species richness and show how the metabolic theory can explain macro-ecological patterns arising from yearly temperature cycles.

Introduction

The observation of an increasing gradient in the diversity of species taxa from poles to equator is known as the latitudinal diversity gradient (LDG) (Rohde 1992). There are numerous hypotheses which explain this gradient (Willig et al. 2003, Pimm and Brown 2004, Cardillo et al. 2005). Among those, the metabolic theory of ecology (MTE), which was proposed by Allen et al. (2002), links the temperature to the latitudinal gradient of species richness (α diversity) of terrestrial (e.g., Hawkins et al. 2007), marine (e.g., Rombouts et al. 2011), and freshwater (e.g., Oberdoff et al. 1995) taxa. Temperature has been identified as a principal predictor of the diversity of marine taxa as of today (Tittensor et al. 2010) and also over the past 30 million years (Yasuhara et al. 2012). However, there is lack of consensus as to what exact causal mechanisms determined the underlying patterns (Mannion et al., 2014).

The MTE predicts species richness by biochemical kinetics of metabolism, which is temperature-dependent, with the observation that energy flux through a population per unit area is temperature invariant (Allen et al. 2002). This energy flux per

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population per unit area, estimated as the product of its metabolic rate and abundance, is invariant with respect to the body mass of the species (Damuth 1987) and, thus, is known as the energetic-equivalence rule. Therefore, when temperature is high in an environment, metabolic rate of populations becomes high, and hence, their abundance becomes low, conserving the said rule. Thus, this allows more species to occupy in high temperature environments in order for the total energy flux through the populations in the habitat to be invariant. Thus, Allen et al. (2002) show that species richness increases with the environmental temperature, qualitatively fitting the empirical richness gradient data to the model. A large volume of literature has tested the validity of this theory (Price et al. 2012).

One implicit assumption in MTE (Allen et al. 2002) is that habitat temperature does not vary much within a year. However, monthly mean sea temperature data from the World Ocean Atlas (WOA n.d.) show yearly cycles with amplitudes exceeding 14 °C in some northern temperate regions. If temperature cycled yearly with such large amplitudes, maintaining the same patterns over years, it may have affected the average metabolic rate of, especially, fast-maturing ectothermic populations. This is because the computations in MTE based upon the mean temperature of the year may not be a reasonable approximation to the bio-energetics of a periodic system when the effects of temperature are nonlinear (see Savage 2004, Rajakaruna and Lewis 2017) as metabolic rate is a nonlinear function of temperature (see Allen et al. 2002). Therefore, periodic fluctuations of temperature may also have affected the metabolically driven species richness. Thus, it is reasonable to ask "How does the amplitude of habitat temperature fluctuations affect species richness?"

The MTE does not explicitly explain through which processes the richness, which is theoretically allowed by a given habitat temperature, is mechanized. It only provides a bio-energetic basis to understand the observed correlation between species richness and ambient temperature, but not the mechanisms by which a community conserves the energetic-equivalence rule among populations, allowing more species in high temperature environments, and vice versa. That is, for example, the allowed species richness in an environment, given by temperature, can occur through immigration and emigration from an ecological sense, or speciation (in evolutionary time) and extinction. The species richness distribution observed in habitats at present is an end-product of such processes.

Fossil records of planktonic foraminifera spanning over 30 million years indicate that kinetic effects of temperature can govern the rates of genetic divergence and speciation (Allen et al. 2006). Dowle et al. (2013) further discuss how rates of molecular evolution have been linked to the rates of speciation. A correlation between generation time and the rate of molecular evolution has been shown in some invertebrate taxa

(Thomas et al. 2010). Moreover, the generation time of calanoid copepods is a function of ambient temperature (Huntley and Lopez 1992) (see also Gillooly et al. (2001) and Savage et al. (2004) for the generalization of which for ectotherms.) Thus, generation time of such taxa may also predict species richness, thereby the latitudinal diversity gradient. Thus, the yearly cycles of generation times of fast-maturing taxa, such as copepods, driven by yearly temperature cycles, may also affect the species richness. Such process may also explain the underlying processes by which high temperatures increase species richness from an evolutionary sense, whereby speciation that can result from faster maturation rates (shorter generation times) of populations. Thus, in line with MTE, speciation also can reduce the average abundance per population in a locality conserving the energetic-equivalence rule that was observed.

In this study, we incorporate the effect of yearly temperature cycles into MTE models and investigate the impact of the amplitude of temperature cycles on species richness. We also derive species richness as a function of generation time of taxon (community) on the basis of MTE and show how, in theory, generation times also can explain species richness and also how yearly cycles of which can force an effect on species richness. Our aim here is to gain insight arising from incorporating the periodic temperature fluctuations into the existing metabolic theory, rather than proposing an ideal model incorporating all the plausible external forcing factors that may explain richness distribution.

We calibrate the models for fast-maturing marine calanoid copepod communities in the Mediterranean and adjacent regions using the data from scientific cruise surveys performed by the Institute of Biology of the Southern Seas (IBSS n.d.) and Lebanese University (LU n.d.) in the Mediterranean regions. We use depth-wise sea temperature data from World Ocean Atlas (WOA n.d.). We test the hypothesis arising from the models on the basis of the theoretical predictions that large amplitudes of yearly cycling temperatures cause a reduction in the calanoid copepod richness.

Metabolic rate when temperature cycles

Consider an area, A, with number of species, S, and population density, N_j of species j per unit area, $j = 1..S$. The total number of individuals across all species is $J = \sum_{j=1}^{S} N_j A$. Based on Allen et al. (2002), the metabolic theory of ecology suggests that the metabolic rate, B_j (joules s^{-1}), of an average individual of species j varies with body size M_j, and the ambient temperature T, such that $B_j = b_0 M_j^{3/4} e^{-E/kT}$. Here, b_0 is a normalization constant, independent of body size and temperature ($b_0 \sim 2.65 \times 10^{10}$ Js^{-1} g$^{-3/4}$), and the Boltzmann factor $e^{-E/kT}$ describes the temperature dependence of the

metabolic rate. The quantity, E, is the activation energy of metabolism (~ 0.78 eV), k is the Boltzmann constant (8.62×10^{-5} eV K^{-1}), and T is the temperature in Kelvin (K), such that the mean metabolic rate of an individual in the community is given by

$$\overline{B} = b_0 \overline{M^{3/4}} e^{-E/kT} \tag{1}$$

Here, $\overline{M^{3/4}}$ is the mean derived from the body size distribution of the species constituting the community (taxon) of interest. Note that Eq. (1) is a concave increasing function of increasing T. This suggests that the higher the temperature, the higher the metabolic rate. When temperature T is a periodic function of time t with period t_p, then the average metabolic rate of an individual in a community over a period, starting from time t_0 to $t_0 + t_p$, can be written as $\overline{B}_p = (1/t_p) b_0 \overline{M^{3/4}} \int_{t_0}^{t_0+t_p} e^{-E/kT(t)} dt$. If T can be discretized, for example, at monthly scale, with T_i being considered as the average temperature of month i, for $i = 1,..12$, we can write $\overline{B}_p$ as the average of $\overline{B}$, that is, $\overline{B}_p = b_0 \overline{M^{3/4}} (1/t_p) \sum_{i=1}^{t_p} e^{-E/kT_i}$, where $t_p = 12$ is the period, yielding

$$\overline{B}_p = b_0 \overline{M^{3/4}} \left(\overline{\exp(-(E/k)(1/T))} \right) \tag{2}$$

Here, $\left(\overline{\exp(-(E/k) (1/T))} \right)$ is the arithmetic average of the rates of energy across a year. Note that Eq. (1) is nested within Eq. (2), because when T_i's approximate the mean annual temperature, Eq. (2) approximates Eq. (1). The integral in $\overline{B}_p$ cannot be solved analytically when T is a sinusoidal function of time, which is the case of temperature in temperate marine regions, where the yearly temperature cycles at monthly scales are sinusoidal functions (Benyahya et al. 2007; Patanasatienkul et al. 2014; Rajakaruna and Lewis 2017).

Based on the energetic-equivalence rule (Damuth 1987), Allen et al. (2002) write that average energy flux of a population in the community as

$$\overline{B}_{tot} = \overline{B} \overline{N} \tag{3}$$

Here, $\overline{B}_{tot}$ is a temperature-independent constant. $\overline{N} = (1/S) \sum_{j=1}^{S} N_j$ is the population density averaged over the number of species, S. That is, $\overline{B}_{tot}$ remains constant regardless of the values that $\overline{B}$ (which depends on the temperature of the habitats) takes, because $\overline{N}$ changes reciprocally along with $\overline{B}$ keeping $\overline{B}_{tot}$ constant changing S accordingly. This suggests that S is sensitive to what values $\overline{B}$ takes depending on how we average Eq. (1) when temperature fluctuates. In Allen et al.

(2002), T in Eq. (1) is commonly taken as the mean temperature $\overline{T}$ of the year.

Thus, when temperature fluctuates periodically, we can write,

$$\overline{B}_{tot} = \overline{B}_p \overline{N} \tag{4}$$

As per Allen et al. (2002), the density of individuals of the all species populations per unit area is given by

$$J \big/ A = S \overline{N} \tag{5}$$

Thus, Eqs. (1), (3), and (5) yield

$$\ln S = -(E/k)\left(1/\overline{T} \right) + \ln \left(b_0 \overline{M^{3/4}} J/A \overline{B}_{tot} \right) \tag{6}$$

(Allen et al. 2002). Rombouts et al. (2011) used this model (Eq. (6)) to predict the richness distribution of marine copepods with respect to sea surface temperatures of the habitats.

When temperature is cyclic, and the rate of energy that affects richness is more appropriately the ones averaged over a year, as per the bio-energetics of Eq. (2), rather than the energy as per the average temperature of the year, then we can write similarly from Eqs. (2), (4), and (5)

$$\ln S = \ln \left(\overline{\exp(-E/kT)} \right) + \ln \left(b_0 \overline{M^{3/4}} J/A \overline{B}_{tot} \right) \tag{7}$$

In other words, the above equation is also given by integrating both sides of the exponentially transformed Eq. (6), giving $t_p S / \left(b_0 \overline{M^{3/4}} J/A \overline{B}_{tot} \right) = \int_0^{t_p} \exp(-E/kT(t)) \, dt$ as S is a time-independent constant fixed at the state in which the richness has reached its capacity w.r.t. the habitat temperature, and the quantity $\left(b_0 \overline{M^{3/4}} J/A \overline{B}_{tot} \right)$ is assumed to be a temperature- and time-independent constant as $\overline{B}_{tot}$ remains a temperature-independent constant according to Eq. (3), and we assume temperature-invariance for the total individual abundance per area, J/A, and the means derived from body size distributions, $\overline{M^{3/4}}$ as per Allen et al. (2002) and Rombouts et al. (2011) and Record et al. (2012) specific to copepods.

Relationship between species richness and generation time

Here, we show that species richness can also be written as a function of generation time of taxon, and how yearly cycles of which impact richness.

Savage et al. (2004) showed, following Gillooly et al. (2001), that generation time, g_j, of an ectothermic population j, having mean individual body size, M_j, is proportional to

temperature, given by $g_j \propto M_j^{1/4} \exp^{E/kT}$. Hence, we can write $g_j = g_0 M_j^{1/4} \exp^{E/kT}$, with g_0 (days $g^{-1/4}$ when g_j is days) as the proportionality constant. It has been shown that generation time equations can be empirically generalized for marine taxa such as copepods (Huntley and Lopez 1992) and pelagic tunicates (Deibel and Lowen 2012). Thus, the mean generation time for the copepod community at temperature T can be written as

$$g_T = g_0 \overline{M^{1/4}} \exp^{E/kT} \qquad (8)$$

Here, $\overline{M^{1/4}}$ is the mean derived from the body size distribution of the species constituting the taxon (community). Note that Eq. (8) is a convex decreasing function of T. This means that the higher the temperature, the shorter the generation time, suggesting that a community expends energy more rapidly at higher temperatures. This model is fundamentally based on the Boltzmann-Arrhenius function, which predicts that maturation rates increase monotonically with temperature (Gillooly et al. 2001). Commonly, T is taken as the mean annual temperature $\overline{T}$ of the habitat, such that, we replace the notation g_T with $g_{\overline{T}}$ to symbolize generation time with respect to mean temperature, $\overline{T}$. When temperature T is a periodic function of time t with period t_p, the average generation time of the (taxon) community over a period starting from time t_0 to $t_0 + t_p$ can be written as

$$\overline{g}_T = (1/t_p) \int_{t_0}^{t_0+t_p} g_{T(t)} dt \qquad (9)$$

Equation (8) cannot be solved analytically when $g_{T(t)}$ is a nonlinear function of monthly temperature, $T(t)$, which, in turn, is a sinusoidal function of time as it was the case in the temperate regions. Thus, we can take the arithmetic average, $\overline{g}_T$, of g_{T_i} given for temperatures at months, i, for $i = 1,..,12$, yielding $\overline{g}_T = (1/t_p) \sum_{t_0}^{t_0+t_p} g_{T_i}$. Arithmetic mean is more appropriate when averaging times.

Equations (1), (3), (5), and (8) can be rearranged to yield

$$g_{\overline{T}} S = \left(g_0 b_0 \overline{M^{3/4} M^{1/4}} J / A\overline{B}_{tot} \right) \qquad (10)$$

for the case when habitat temperature is a constant throughout the year, or the annual temperature is a good approximation to the full system. Note that the product $g_{\overline{T}} S$ is a constant that varies with the taxon. In other words, *a constant mean energy flux for populations* means that species richness is inversely proportional to the generation time, i.e., $S \propto 1/g_{\overline{T}}$, once the relationship between the metabolic rate Eq. (1) and the generation time Eq. (8) is taken into account. Taking the log-transformation of Eq. (10), which is commonly used for scaling species richness in

statistical modeling, we write the log-linear form of the equation as

$$\ln S = -\ln g_{\overline{T}} + \ln \left(g_0 b_0 \overline{M^{3/4} M^{1/4}} J / A\overline{B}_{tot} \right) \qquad (11)$$

When temperature T fluctuates in a cycle over a year, we can write,

$$\overline{g}_T S = \left(g_0 b_0 \overline{M^{3/4} M^{1/4}} J / A\overline{B}_{tot} \right), \qquad (12)$$

noting that $S \propto 1/\overline{g}_T$, with $\overline{g}_T$ is dependent on the type of the temperature-time profile of the habitat. Equation (12) yields

$$\ln S = -\ln \overline{g}_T + \ln \left(\eta b_0 \overline{M^{3/4} M^{1/4}} J / A\overline{B}_{tot} \right) \qquad (13)$$

In other words, this is given by integrating both sides of Eq. (10) over the period t_p (year) as same as the case of deriving Eq. (7), yielding $S = \left(b_0 \overline{M^{3/4}} J / A\overline{B}_{tot} \right) / \left((1/t_p) \sum_{t_0}^{t_0+t_p} g_{T_i} \right)$, s.t., $\overline{g}_T = (1/t_p) \sum_{t_0}^{t_0+t_p} g_{T_i}$. In essence, here, we converted a periodically fluctuating, time-dependent system into a time-independent system by time-averaging the system over a year; thus, effectively capturing the effect of cyclically varying metabolism on species richness. Also, note that $\overline{g}_T$ converges monotonically to $g_{\overline{T}}$ as temperature variation diminishes to zero. Thus, Eq. (11) can be viewed as an approximation to Eq. (13) for habitats with low amplitude temperature fluctuations.

Summary of models and theoretical predictions

For statistical simplicity, we rephrase the models as

Model 1: $\ln S = -\gamma \left(1000/\overline{T} \right) + c_1$; based on Allen et al. (2002) from Eq. (6)

Model 2: $\ln S = -\ln(\exp(\gamma 1000/T) + c_1$; (Eq. 7) based on time-averaging Eq. (6) over temperature cycles

Model 3: $\ln S = -\phi \ln g_{\overline{T}} + c_2$; (Eq. 11) based on generation time relation derived from Eq. (6)

Model 4: $\ln S = -\phi \ln \overline{g}_T + c_2$; (Eq. 13) based on time-averaging Eq. (11) over temperature cycles

In above equations, $\gamma = -E/1000k = 9$ K, and $\phi = 1$ ideally based on MTE (Allen et al. 2002), and $c_1 = \log \left(b_0 \overline{M^{3/4}} J / A\overline{B}_{tot} \right)$ and $c_2 = \log \left(g_0 b_0 \overline{M^{3/4} M^{1/4}} J / A\overline{B}_{tot} \right)$ are temperature-independent constants that vary with the taxon of interest. That is, the gradients in Eqs. (6) and (7) should equal 9000 K (Kelvin), and similarly, the gradients in Eqs. (11) and (13) should equal 1. In both cases above, the models assume that habitats have reached the metabolically driven capacity-richness. Thus, the gradients in

models 1 and 2, and 3 and 4 are two hypotheses that we could test against the calanoid copepod data from the Mediterranean regions.

Equation (6) suggests that species richness increases with increasing temperature. This was tested well in the literature using empirical data after Allen et al. (2002). However, when temperature fluctuates, we find that by theory, $\overline{1/T} > 1/\overline{T}$ for $T_i > 0$ for $i = 1,..,12$, due to Jensen's inequality (1906), which states that if T are positive numbers, then for the convex function f(T) = $1/T$, we get $E[f(T)] \geq f(E[T])$, s.t., $E[f(T)]= \overline{1/T}$ and $f(E[T]) = 1/\overline{T}$. The application of Jensen's inequality is also found in Ruel and Ayres (1999) and Rajakaruna and Lewis (2017). This inequality is reverse when the function is concave. Therefore, we predict lnS in Eq. (7), or model 2, with a fluctuating temperature habitat, to be less than lnS in Eq. (6), or model 1, with a non-fluctuating temperature habitat, assuming that other quantities are constants between them. This can be also seen in terms of the metabolic rate $\overline{B}$ in Eq. (1), which is a concave increasing function of increasing T. That is, when temperature fluctuates, $\overline{B}$ given by the mean temperature of the period (Eq. 1) is always greater than $\overline{B}$ given by the time-averaged $\overline{B}$'s of the respective temperatures over the period, i.e., $\overline{B}_p$ (Eq. 2). On the basis of Jensen's inequality, from Eqs. (3) and (4, species richness, S, should be lesser for $\overline{B}_p$ than that for $\overline{B}$ to have $\overline{B}_{tot}$ a constant in similar habitats, where the degree of temperature fluctuation is the only difference.

Equation (11) (model 3) suggests that the shorter the mean generation time of taxon in a community, or the shorter the mean life cycles, the larger the species richness. In other words, because the mean energy flux through a community, $\overline{B}_{tot}$, in Eq. (3), is temperature-independent, a large temperature results in an increase in the average individual metabolic rate, $\overline{B}_T$, decreasing the $\overline{N}$. Therefore, this should result in an increase in S as we hold J per A constant in Eq. (3). Furthermore, according to Eq. (8), g_T decreases exponentially as T increases, because the positive exponent of the equation is an inverse function of T. Thus, we predict that g_T calculated on the basis of the mean annual temperature, $\overline{T}$, i.e., $g_{\overline{T}}$, should be less than that calculated based on the arithmetically time-averaged g_T over the period, i.e., $\overline{g}_T$, which captures the within year variation. As before, this effect is also due to Jensen's (1906) inequality. Therefore, as a whole, we predict that time-averaged inverse-temperature model 2, and time-averaged generation time model 4 should fit to the data of habitats with a range of amplitudes in temperatures better than mean temperature model 1 and mean generation time model 3, and thus, the larger the amplitude of periodic fluctuations of temperature, the lesser should be the predicted species richness.

In addition to the above theoretic bio-energetic models, we also fitted the following phenomenological models to test whether the species richness is related to annual peak-to-peak amplitude U and mean $\overline{T}$ of yearly habitat temperature cycles regardless of the bio-energetic mechanisms:

Model 5: $lnS = \kappa U + c$

Model 6: $lnS = \rho \overline{T} + c$

Model 7: $lnS = \rho \overline{T} + \kappa U + c$

Here, T and U are in Kelvin, κ, ρ are parameters, and c is a constant. We tested which models fitted to the calanoid copepod data, collected from the Mediterranean and adjacent marine regions, the best, to understand if periodic fluctuations impact the species richness. All these models eventually assess if MTE is a good explanatory theory of species richness.

Fitting data to models and testing hypotheses

Sampling units, data, and assumptions

We used 46,377 records of calanoid copepod species distribution data, by depth, collected between 35:45 N latitude, and − 7: − 42 longitude (Mediterranean and adjacent marine regions) by scientific cruise surveys performed by the Institute of Biology of the Southern Seas (IBSS n.d.) covering Adriatic, Aegean Tunisian Plateau, Ionian, Western Mediterranean, Alboran and Black Seas from 1960 to 1993 and also by Lebanese University (LU n.d.) (1965–2007) covering the Levantine Sea (Fig. 1), giving 86 sampling units of 1°×1° (latitude × longitude) blocks with multiple sampling efforts. We used long-term (1952–2012) monthly mean sea temperature data at the same spatial scale from World Ocean Atlas (WOA n.d.) given by depths 0, 5, 10,..,100, 125, 150,..,500, 550, 600,.., and 1500 m. The monthly mean sea surface temperatures varied dramatically across the sampling units in the range of 5–18 °C, with yearly means of 12–22 °C. To incorporate the effect of yearly cyclic temperatures into the models, we assumed that their patterns have remained constant in the order of over many hundreds of years, during which time the metabolically driven species richness has reached the present heights (see Allen et al. 2006 for the kinetic effect of temperature on speciation). Data and methods of analyses are given in the data repository: https://doi.org/10.6084/m9.figshare.5479750.v1.

It is known that calanoid copepods, in general, colonize the upper water column (Bradford-Grieve 2002). Some species exhibit high densities at warm, mixed, oxygenated surface layers at dusk (Hays et al. 2001) and sink to lower depths during the day (Kiørboe and Sabatini 1994; Hays et al. 2001; Andersen et al. 2004), while some maintain a vertical zonation (Mackas et al. 1993; Bollens and Landry 2000; Andersen et al. 2004). However, there is increasing evidence that copepods and other aquatic taxa show a metabolic suppression at diel migration to lower depths at day and expend most their energy at mixed surface layer depths
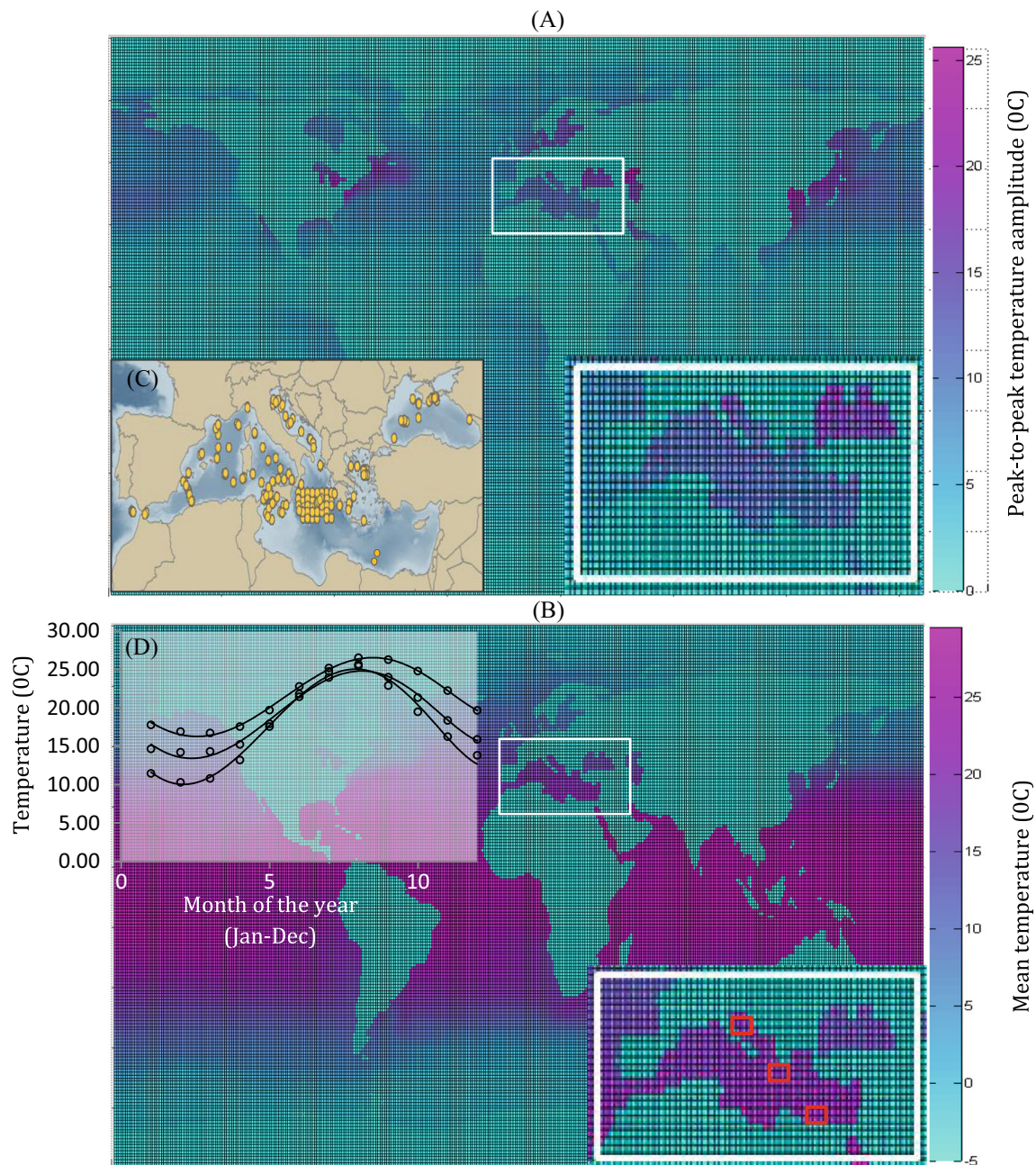
Fig. 1 a Peak-to-peak amplitude and **b** mean of long-term monthly sea surface temperature (per year) estimated at 1° × 1° latitudinal and longitudinal spatial scale based on simple sinusoidal functions for data (1952:2012) from WOA (n.d.). The white box shows the studied Mediterranean region; data (1960–1992: IBSS (n.d.); and 1960–2007: LU (n.d.)) belonging to 86 units of 1° × 1° latitudinal and longitudinal spatial units (**c**). **d** Examples of sinusoidal model fitted to the data from three sampling units (red boxes)

(MLD) in the night. For example, Svetlichny et al. (2000) have shown that metabolically active zone for *Calanus euxinus* is the near-surface layers; about 78.6% of energy is expended about 10 h at the surface layers, while 5.4% of their energy is expended at lower depths, and about 11% of their energy is expended on diel vertical migration. Similar energy budgets have also been observed in other taxa; for example, Seibel et al. (2016) show evidence that metabolic rate of *Euphausiids* (crustaceans) was suppressed by

49~64%, and Maas et al. (2012) show 80~90% in pteropods at lower depths. These suggest that for species showing diel vertical migration, it may be the near-surface mixed layer temperatures that may account for their daily effective rate of metabolism. Therefore, in our study, we assumed that the temperature at mixed layer depth (MLD) as the metabolically germane (effective) temperature of the calanoid copepods dwelling in the upper ocean. In meta-analyses of copepod richness distribution in general, the sea surface

temperature is typically used as their ambient temperature (e.g., Rombouts et al. 2009, 2011).

Figure 2 indicates that MLD, of the sampling units with respect to long-term monthly mean temperatures from WOA (n.d.), extends to about, on average, 100–150 m in the winter-spring months, and a minimum of 10–20 m in the summer-fall months. We calculated the MLD of each month for each unit as the $\|T_{10d} - T_{10(d+1)}| - |T_{10(d+1)} - T_{10(d+3)}\|_{max}$ (in meters) within the top 500 m depth, for vertical depths layers $d = 1,..,57$ for the data, giving a maximum depth of 1500 m. Note that $d = 1,..,21$ are given with 5 m, and, $22,..,38$ are in 25 m, and, $39,..,57$ are in 50 m increments. Note that the amplitudes of the yearly fluctuating monthly temperatures are larger in the MLD compared to that in below the MLD (Fig. 3). In this study, we used the averaged MLD temperatures of each month, i, as the ambient temperatures T_i, for $i = 1,..,12$, of the calanoid copepods in respective sampling units of the region.

We computed the number of species (species richness) (S), in depths <150 m, the number of samples (n), and the surface area (A) (which varied a maximum of 1495.51 km² between units, mean = 9592.18 km²) in the IBSS (n.d.) and LU (n.d.) data for each 1°×1° (latitude × longitude) sampling unit.

We tested the mean and amplitude of temperatures and also the richness data of the 86 spatial units for independence from spatial autocorrelation. We used the inverse of the Euclidian distances between the centers of the units as the weight matrix for the global Moran's I test on residuals (Moran 1950). All three variables yielded p values 0.47, 0.48, and 0.45 respectively for the tests, failing to reject the null hypotheses that the data are not spatially correlated, neither positively or negatively. Here, we used MCMC simulations for computing p values resampling the data with replacement. As the number of samples were ≤ 3 in most units (34 units had only 1 sample, 25 units had only 2 samples, and 18 units have only 3 samples out of 87 units (see Fig. 5a)), we have not tested the independence of data from temporal autocorrelations.

Calibrating generation times g_T

Note that Eqs. (11) and (13), where $S = f(T)$ and $g = f(T)$, result in $S = f(g(T))$. Therefore, predicting S using calibrated

Fig. 2 The average mixed layer depths (MLD) of the 86 sampling units (shown in colors) were a minimum of 20 m (data from WOA (n.d.)). (Red line indicate the approximate bottoms of the MLD of the units from January to December: 100 m; 3 × 125 m; 4 × 20 m; 25 m; 35 m; 50 m)

Depth (1-21: 5 m increments; 22-38: 25 m increments; 39-57:50 m increments)
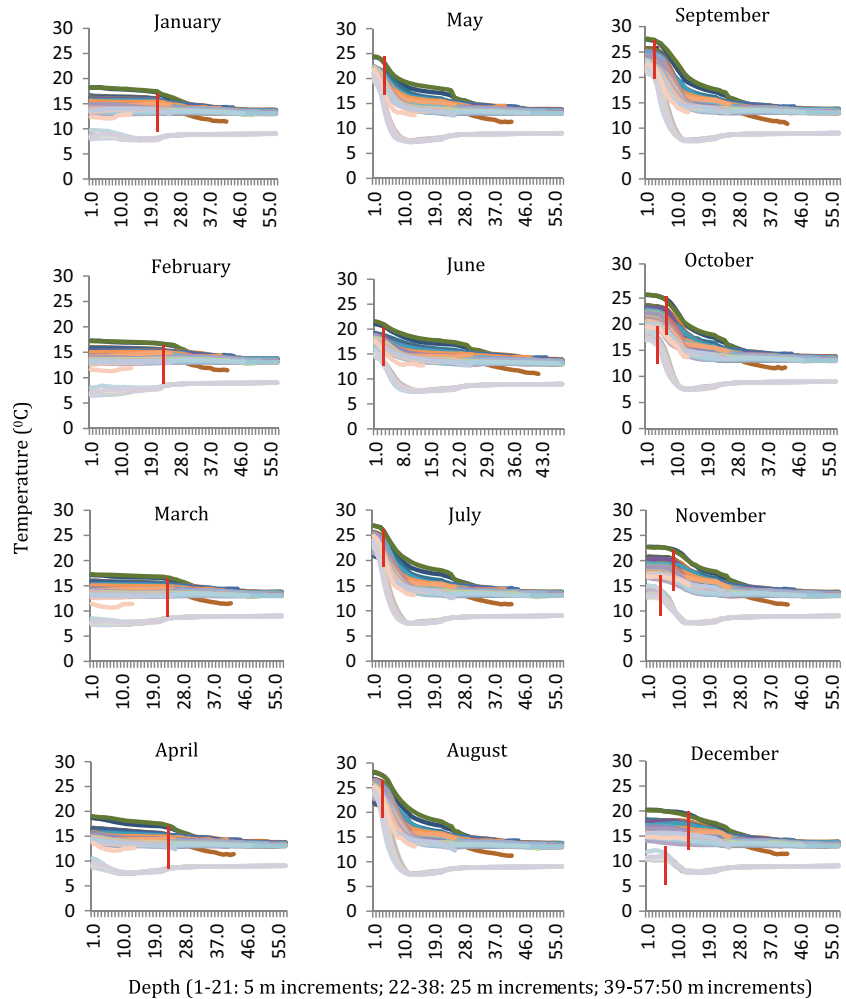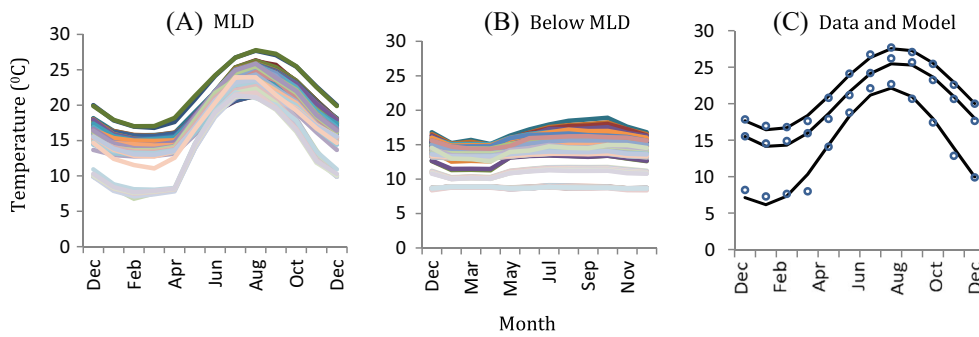
Fig. 3 Temperature from WOA (n.d.) averaged by **a** mixed layer depth (MLD); **b** below MLD, by months, for the 86 sampling units (shown in colors); and **c** examples of monthly MLD temperature data fitted with sinusoidal function. The R^2 of the sinusoidal function were > 0.94 for all sampling units

$S = g(T)$, for a given T's of a tested region, with $g = f(T)$ calibrated as a generalized model for data from elsewhere, will not suffice to conclude that exact generation times of the taxa of the tested region has the predicted relationship to species richness. In order to test such relationship, we will ideally need raw data of generation times of the taxa of the tested region. Although we did not have such data to show the direct relationship between generation time and species richness, here, we will show the effect of temperature and their periodic cycles on species richness through $S = f(g(T))$ function, demonstrating the validity of the theoretical derivations (Fig. 4). Therefore, here, naturally, the fitting of model Eq. (6) to the data will be equivalent to the fitting of model Eq. (11) to the data, and the fitting of Eq. (7) will be equivalent to that of Eq. (13). (See Appendix 1 for model calibrations).

Weighing richness (S) by sampling effort and area of unit

The species richness is correlated with the sampling effort (the number of samples per sampling unit) (Fig. 5a). To neutralize the species richness from sampling effort, we transformed the richness (S), dividing it by $\ln(\alpha n + 1)$. Here, n is the number of samples per unit, and α is a coefficient. The coefficient α was estimated by fitting the regression model $S = 1/\ln(\alpha n + 1)$, and estimating α where R^2 was approximately zero (Fig. 5b). It yielded $\alpha = 3.30$. Furthermore, we rescaled the above-corrected S by calculating it per log km^2 for each sampling unit to neutralize species richness from the area of sampling units, and finally took the log of the corrected S plus 1 for the modeling. From here onward, we use S to represent the transformed values of species richness, unless otherwise stated.

Fitting data to models

Using average MLD temperatures T_i, averaged for each month $i = 1,..,12$, for each sampling unit, we calculated the mean annual temperature, $\overline{T}$, and time-averaged temperature function, in Kelvin, yielding $1000/\overline{T}$ and $\left(\overline{\exp(\gamma 1000/T)}\right)$, respectively, to fit to models 1 and 2, together with the computed bias-corrected log-transformed richness data lnS. (Similarly, we computed $g_{\overline{T}}$ and $\overline{g}_T$ using the calibrated g_T model, using the
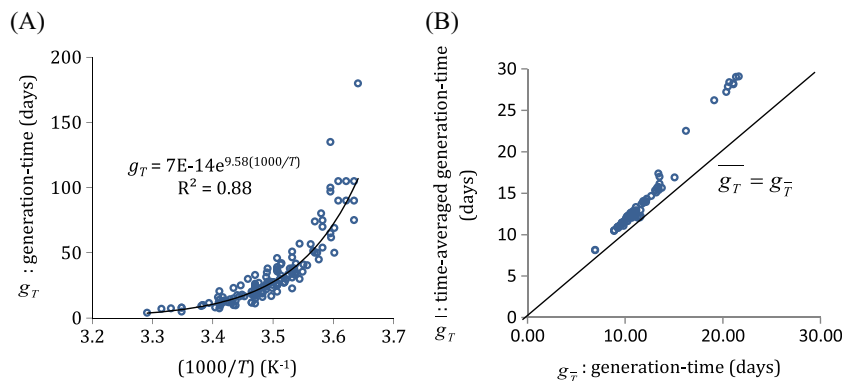

Fig. 4 **a** Generation time g_T of copepods with respect to temperature as modeled by Eq. (8), which yielded $\hbar_1 = 7.97 \times 10^{-16}$, $\hbar_2/1000 = E/1000 \, k = 9.58$ K, and $R^2 = 0.88$, for marine copepod data from Huntley and Lopez (1992). Note that the theoretically expected value of ($E/1000 \, k$) was 9 K. **b** The arithmetically time-averaged generation times ($\overline{g}_T$) in comparison to generation time of mean temperature $g_{\overline{T}}$ for 86 $1° \times 1°$ latitudinal and longitudinal sampling units corresponding to the data from IBSS (n.d.) and LU (n.d.)

Fig. 5 **a** Species richness (S) with respect to number of samples (n) in 86 1° × 1° latitudinal and longitudinal spatial sampling units of data from IBSS (n.d.) and UL (n.d.). **b** After transformation of S weighted by the sampling effort; given by S divided by $\ln(\alpha n + 1)$

(A)

S = 7.09n + 36.15
R² = 0.32

(B)

S= 0.02n + 26.05
R² = 2E-05
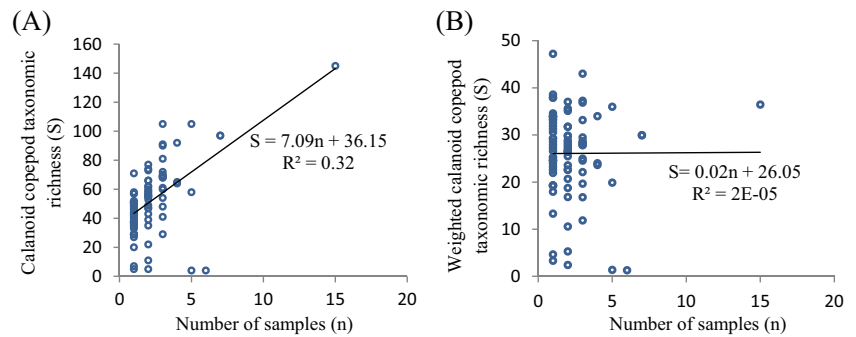
T_i's and the $\overline{T}$, to fit to models 3 and 4 together with the lnS, which should give results similar to fitting models 1 and 2, respectively, as per our discussed under the "Calibrating generation times g_T" section) We used simple linear regression for fitting models to data using Matlab (MATLAB® 2016b), minimizing the sum of squared errors using *fminsearch* procedure.

Furthermore, to fit phenomenological models to data, we calculated the annual peak-to-peak amplitude (U) and the mean annual temperature $\overline{T}$ of the yearly temperature fluctuations by fitting a simple sinusoidal function of the form, $\overline{T} + (U/2)$ $\sin\left[\left(2\pi/t_p\right)t_i + phase\right]$, for t_i for $i = 1..12$, with period $t_p = 12$, to T_i of the averaged MLD's of the sampling units, minimizing the sum of squared errors using *fminsearch* procedure in Matlab (MATLAB® 2016b). In our analyses, based on the periodic system, the phase-shift can be set to zero once the sinusoidal model is calibrated, as we do the calculations for one whole period regardless of the starting month. With $\overline{T}$ and U of the sampling units, together with lnS as calculated as before, we calibrated the phenomenological models 5–7 using simple linear regressions.
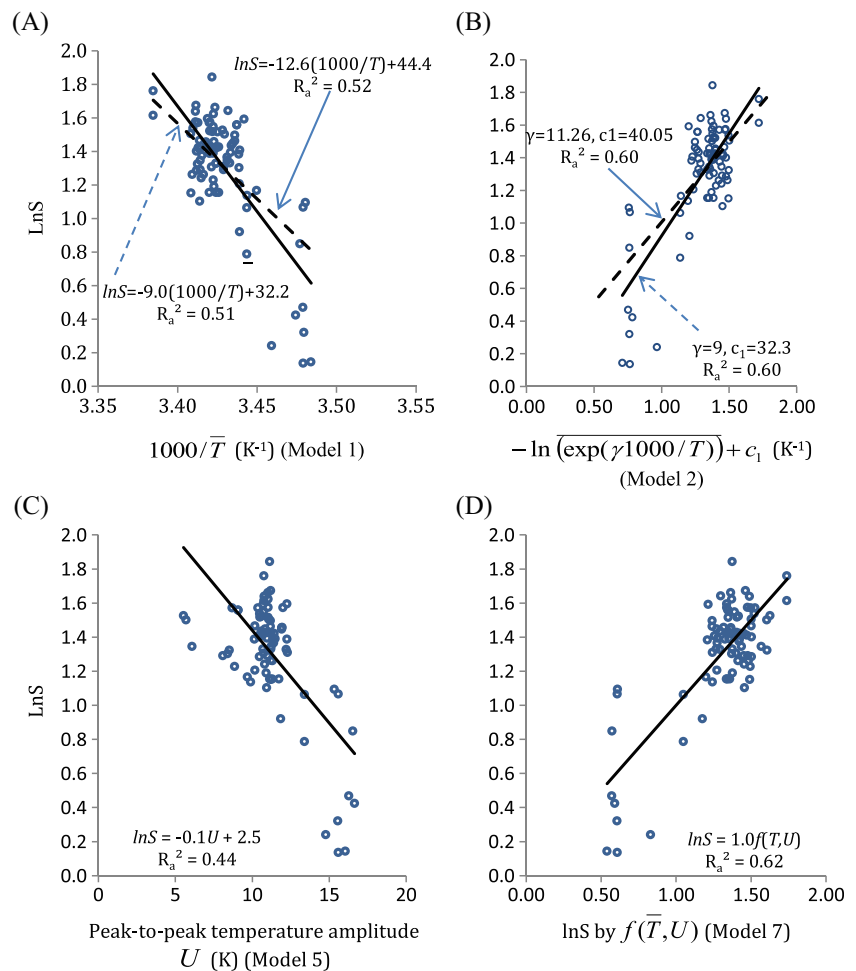
We used adjusted R^2 (denoted by R_a^2) and Akaike information criteria (AIC) for model selection, where R_a^2 is given by $1 - (m-1)(1 - R^2)/(m-q)$ (Kadane and Lazar 2004). Here, q is the sample size (86 units), and m is the number of parameters in the model. The R_a^2 is a criterion for the variation explained and includes a penalty for the number of estimated parameters, while indicates the goodness of fit. Although the predictor variables in models 1, 2, and 3, 4 are functionally nested, they are not nested in the statistical models. This is because, $g_{\overline{T}}$ and $\overline{g}_T$ were calculated from the generation time data of each sampling unit, given their monthly temperatures, independent of the final model regressions. Hence, it leads to the same number of estimated parameters in terms of the degrees of freedom in the bio-energetic models. Bio-energetic models are also not nested with phenomenological models.

Furthermore, we predicted the pattern of calanoid copepod richness along the latitudes by the best-fitted model, incorporating the averages and variances of $\overline{T}$ and U of yearly temperatures, and also accounting for the surface areas, using the sea temperature data from WOA (n.d.) at 1° × 1° latitudinal and longitudinal resolution.

Results

Among bio-energetic models, the largest R_a^2 of 0.60 (lowest AIC, − 262) was yielded by (i) model 2, which correlates the log of time-averaged function $\left(\overline{\exp(\gamma 1000/T)}\right)$ over the yearly cycle, with lnS, for the case where the coefficient of gradient, ϕ was fixed at 1 as theoretically expected (Fig. 6, Table 1). [Without a surprise, model 4 which correlates the time-averaged generation times $\ln\overline{g}_T$ with lnS, fitted to the same data, yielded 0.59 for R_a^2 (AIC, − 261) for the case where the coefficient of gradient γ was fixed at 9 K as theoretically expected (Fig. 6, Table 1).] These results were a contrast to 0.51 for R_a^2 (AIC, − 245) yielded by model 1 as per Allen et al. (2002), which correlated inverse mean temperature $1000/\overline{T}$ with lnS, and 0.53 for R_a^2 (AIC, − 249) yielded by model 3, which correlates log of generation times at mean temperature, $\ln g_{\overline{T}}$, with lnS, for the cases where the coefficients of gradient, ϕ and γ were fixed at 1 and 9 K, respectively, as theoretically expected (Fig. 6, Table 1). For models where coefficients γ and ϕ were estimated, the above models 1 and 2 yielded $\gamma = 12.56$ and 11.26 K, in comparison to theoretically expected $\gamma = 9$ K, and models 3 and 4 yielded $\phi = 1.24$ and 1.12, in comparison to theoretically expected $\phi = 1$. These results suggest that time-averaged temperature model 2 (and similarly, time-averaged generation time model 4) performed better than mean temperature model 1 (and similarly, mean generation time model 3), with respect to the lowest AIC, highest goodness-of-fit R_a^2, and shortest Euclidian distance of the estimation of parameters to theoretically expected values. The model 7, in which the peak-to-peak amplitude U of yearly temperature cycles accounted as a phenomenological factor, in combination with mean annual temperature $\overline{T}$, fitted to log-species richness lnS, yielded 0.62 for R_a^2 (AIC, − 266), improving from 0.54 for R_a^2 (AIC, − 253) yielded by model 6 with the predictor $\overline{T}$ alone. The peak-to-peak amplitude of temperature, U, the sole predictor in model 5, also showed a negative correlation with log-species richness lnS with an R_a^2 of 0.44 (AIC, − 234). All these models were statistically significant yielding $p < 0.001$. In summary, accounting for

Fig. 6 Log taxonomic richness (S) of calanoid copepod species (< 150 m depth) per log km^2, pertaining to Mediterranean regions with respect to **a** $1000/\overline{T}$ (K^{-1}) (Allen et al. 2002; Rombouts et al. 2011), and **b** time-averaged $\left(\overline{\exp(-(E/k)}\right.$ $\left.(1/T)) \right)$ (K^{-1}). The dashed lines are the regression lines where the coefficient of gradients are fixed as theoretically expected, and solid lines are regression lines with gradients estimated. **c** lnS w.r.t. peak-to-peak amplitude of temperature U (per year). **d** lnS modeled by $\overline{T}$ and U. (Species data were from IBSS (n.d.) and LU (n.d.), and modeled temperatures were calculated from the average temperatures in the mixed layer depth (MLD) of the sampling units by month from WOA (n.d.))

(A)

$lnS = -12.6(1000/T) + 44.4$
$R_a^2 = 0.52$

$lnS = -9.0(1000/T) + 32.2$
$R_a^2 = 0.51$

LnS

$1000/\overline{T}$ (K^{-1}) (Model 1)

(B)

$\gamma = 11.26$, c1 $= 40.05$
$R_a^2 = 0.60$

$\gamma = 9$, $c_1 = 32.3$
$R_a^2 = 0.60$

$-\ln \overline{(\exp(\gamma 1000/T))} + c_1$ (K^{-1})
(Model 2)

(C)

LnS

$lnS = -0.1U + 2.5$
$R_a^2 = 0.44$

Peak-to-peak temperature amplitude
U (K) (Model 5)

(D)

$lnS = 1.0 f(T,U)$
$R_a^2 = 0.62$

lnS by $f(\overline{T}, U)$ (Model 7)

variations in temperature over yearly cycles explained an additional 17.1~21.6% of the variation in the species richness data, compared to the fundamental MTE model 1 by Allen et al. (2002) in which the predictor was the mean temperature.

Furthermore, Fig. 7 shows the pattern of calanoid copepod richness predicted by model 7, where the amplitude U and the mean temperature $\overline{T}$ were the predictors, along the latitudes, given their mean and amplitudes of temperatures and topological areas. The species richness predictions along the latitudes, adjusting for the effect of the size of the area, by model 7, showed that there is a hemispheric difference in the mean and the variance in richness, resulting from the variations in the temperature profiles of the northern and southern hemispheres (Fig. 7a). The species richness curve dropped at a faster rate from the tropics, northward, in the northern hemisphere, compared to the drop of the curve southwards in the southern hemisphere, causing the pole-to-pole richness curve to be right-skewed. The skewness of this curve was caused by the apparent faster rate of drop in the mean temperatures (Fig. 7b) and larger amplitudes (Fig. 7c) in the temperate waters in the northern hemisphere, compared to that in the southern hemisphere. Copepod diversity data pertaining to the Atlantic

Ocean in Rombouts et al. (2009), in general, showed a pattern and spread similar to what we show here specific to calanoid copepods. As calanoid copepods usually comprise 55–95% of plankton populations (Mauchline and Mauchline 1998), these patterns may suggest that our predictions on calanoid copepods may be similar.

Discussion

Our study shows that large amplitudes of yearly temperature cycles reduce the average metabolic rates of fast-maturing marine calanoid copepods reducing their species richness. Incorporating the effect of periodic temperature fluctuations into bio-energetics of Allen's et al. (Allen et al. 2002) MTE model, by time-averaging the temperature function, $\exp(\gamma 1000/T)$, across the cycle, improves the predictability of calanoid copepod richness, compared to that by the Rombouts et al. (2011) model as per Allen's et al. The effect of temperature amplitude on species richness was further supported by the phenomenological model, which incorporated the peak-to-peak amplitude of temperature cycles, U, linearly

Table 1 Models of log-species richness, S, estimated by simple linear regressions. $\overline{T}$ —mean, $(\exp(\gamma 1000/T))$ —time-averaged function of T, and U—peak-to-peak amplitude of yearly temperatures (in Kelvin). The g_T(days) is the generation time, given $\overline{T}$, and $\overline{g}_T$ is time-averaged generation time per year

Models	R_a^2, df, AIC		Estimated parameter values (gradients non-fixed)		p values
	Gradient fixed at theoretical values ($\gamma = 9K$; $\phi = 1$)	Gradient estimated			
Bio-energetic models					
1 $\ln S = -\gamma\left(1000/\overline{T}\right) + c_1$	0.51, 1, − 245	0.52, 2, − 251	$\gamma = 12.56$	$c_1 = 44.39$	< 0.001
2 $\ln S = -\ln(\exp(\gamma 1000/T)) + c_1$	0.60, 1, − 258	0.60, 2, − 262	$\gamma = 11.26$	$c_1 = 40.05$	< 0.001
3 $\ln S = -\phi\ln g_{\overline{T}} + c_2$	0.53, 1, − 249	0.55, 2, − 250	$\phi = 1.24$	$c_2 = 4.44$	< 0.001
4 $\ln S = -\phi\ln \overline{g}_T + c_2$	0.59, 1, − 261	0.60, 2, − 260	$\phi = 1.12$	$c_2 = 4.40$	< 0.001
Phenomenological models					
5 $\ln S = \kappa U + c$	–	0.44, 1, − 234	$\kappa = -0.11$	$c = 2.53$	< 0.001
6 $\ln S = \rho \overline{T} + c$	–	0.54, 1, − 253	$\rho = 0.15$	$c = -1.44$	< 0.001
7 $\ln S = \rho \overline{T} + \kappa U + c$	–	0.62, 1, − 266	$\rho = -0.11$ $\kappa = -0.06$	$c = -0.06$	< 0.001

Here, $c_1 = \log\left(b_0 \overline{M^{3/4}} J/A\overline{B}_{tot}\right)$, $c_2 = \log\left(g_0 b_0 \overline{M^{3/4}} M^{1/4} J/A\overline{B}_{tot}\right)$, and c are constants

AIC Akaike information criteria

in combination with the mean temperature $\overline{T}$ of the cycles. The performance improvement of the models, with the incorporation of the effect of periodic temperature fluctuations (cycles), has been substantiated by an increase in the goodness-of-fit of the data of respective models, and lower AIC, and also shorter Euclidian distances of parameters estimated by the data to theoretically expected values with respect to MTE.

Supporting our results, a phytoplankton experiment conducted by Burgmer and Hillebrand (2011) showed that species richness decreased with increased temperature variance (with
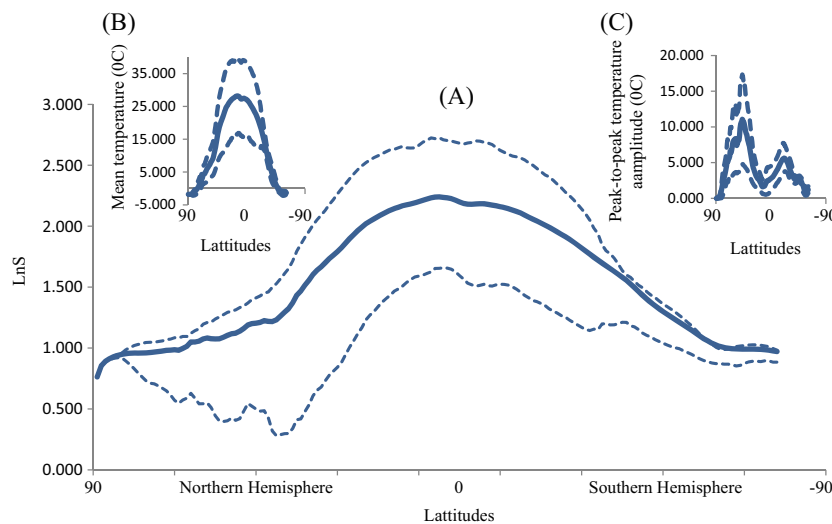

Fig. 7 a Solid lines: log calanoid copepod taxonomic richness predicted by latitude (taking the respective surface area also into account at 1° × 1° spatial scale) using $\ln S = \rho \overline{T} + \kappa U + c$ (model 7), given the average latitudinal mean and amplitude of temperatures, parameterized from IBSS and LU data from Mediterranean regions. Dashed lines: predictions based on ± 1 standard deviation of estimates due to variations in the mean and amplitudes. **b** Yearly mean and **c** peak-to-peak amplitude of latitudinal temperature with ± 1 standard deviation of estimates. Sea temperature data are from WOA (n.d.)

a 2 °C increase of amplitude) as a result of increased rate of species extinction. This experiment has been done over a period of 70 weeks, with temperatures fluctuated as a sinusoidal function, with troughs and peaks at 4 and 20 °C respectively, mimicking winter and summer as in the field, similar to our cases. Another analysis indicated that zooplankton richness is large where the inter-annual variation in bottom-temperature of lakes is high based on the data from 53 temperate lakes (Shurin et al. 2010). This study indicates that temporal scales of temperature fluctuations and the life-history patterns of taxa may also affect the degree to which the fluctuations affect species richness and how.

Our study also indicates, in theory, that reduction of species richness can be related to the average generation time of taxon. Yearly cycling generation times, forced by temperature, reduce the species richness of taxon. That is, time-averaged generation time $\ln \overline{g_T}$ across the cycles is a better predictor of species richness than the generation time $\ln g_{\overline{T}}$ at mean $\overline{T}$ of the temperature cycles. This analysis was a logical deduction demonstrated by the data that we used to test the other models. This effect of generation time on richness hypothesis should be ideally tested with species richness data from habitats with known temperatures, together with their generation times. The hypothesis that shorter generation time of taxon increases species richness may suggest that taxa having faster life cycles in less fluctuating temperatures, such as copepods in tropical and sub-tropical regions, have a greater richness than the same taxa in more fluctuating temperatures with similar mean temperatures and other ecological and environmental conditions.

The observation that relationship $B_{Tot} = \overline{NB}$ (Eq. 3), where B_{Tot} is constant, given by energetic-equivalence rule, seems an end-product of a process rather than the process itself. It means that this relationship can be resulted from two possible processes: For example, (1) when temperature T increases, $\overline{B}$ increases (from Eq. 1), and thus S increases due to $J/A = S\overline{N}$ relationship (where J/A is assumed to be a constant), conserving the $B_{Tot} = \overline{NB}$ relationship as $\overline{N}$ decreases, increasing S by "immigration" or (2) when temperature T increases, $\overline{B}$ increases, and thus S increases by "speciation" due to generation time g decreases (i.e., as maturation rate increases), conserving the same $B_{Tot} = \overline{NB}$ relationship as the end-product, decreasing $\overline{N}$. This is because $B_{Tot} \propto \overline{N}/\overline{g}$ as the theory has shown. As suggested by Allen et al. (2006), kinetic effects of temperature may govern the rates of genetic divergence and speciation. A generation time may govern the rate of molecular evolution (Dowle et al. 2013), which may in turn govern the rates of speciation, because the molecular evolution may govern the rate of speciation as per Thomas et al. (2010). The point is that, the process by which a system conserved the relationship $B_{Tot} = \overline{NB}$ in the end, by getting to the allowed richness, can be either of the above processes. Thus, in summary, the density to body mass relationship leading to

conservation of $B_{Tot} = \overline{NB}$ relationship in MTE can be the end result. That is, for example, with high energy in a locality, species richness can increase due to immigration at shorter time scales in ecological sense, and/or by speciation in evolutionary times due to faster maturation rates.

Hypotheses explaining latitudinal diversity gradient are many, and the underlying causal mechanisms of which can be multifactorial, whereas the temperature can be one. Those include mid-domain effect (Colwell and Lees 2000), geographical area (Terborgh 1973), species energy, climate harshness (Currie et al. 2004), climate stability (Pianka 1966), historical perturbation (Clarke and Crame 2003), effective evolutionary time (Rohde 1992), and biotic hypotheses (Pianka 1966). Our hypothesis that species richness can be linked to generation time, driven by temperature, conserving the energetic-equivalence rule as per MTE, may support the evolutionary rate hypothesis, which states that higher evolutionary rates have caused higher speciation rates and thus increased diversity (Cardillo et al. 2005, Weir and Schluter 2007, Rolland et al. 2014). Higher temperatures may result in higher mutation rates, shorter generation time or faster physiological processes (Rohde 1992, Allen et al. 2006). Faster microevolution rates, which may have resulted in speciation, have been shown for plants (Wright et al. 2006), mammals (Gillman et al. 2009) and amphibians (Wright et al. 2010).

The observation that yearly cyclic fluctuations of temperature and generation time reduce species richness may support the climate stability hypothesis (Pianka 1966), which suggests that fluctuating environment may increase the extinction rate or preclude specialization. Stochastic theory also shows that increased environmental fluctuations, at high frequencies, increase the extinction probability of local populations, in general (Lande et al. 2003). Understanding of elements, such as the rates of extinction in relation to mean temperature or temperature cycles, is important in the overall modeling picture in understanding how richness reduces in fluctuating environments. As mentioned before, experiments on phytoplankton by Burgmer and Hillebrand (2011) supported the idea that temperature variance, similar to the scales that we studied, leads to a reduction in species richness resulted from higher rates of extinction.

The intermediate disturbance hypothesis states that species richness is higher in moderately fluctuating environments (Sommer 1995; Townsend et al. 1997). In contrast, we showed that calanoid copepod species richness was the lowest when amplitude of yearly cyclers of habitat temperature was the highest. Our observation falls in line with Fox (2013) who presented the case in a review that intermediate disturbance hypothesis should be abandoned. There is a possibility that frequency and magnitude of fluctuations and spatial temporal scales of external environmental factors affect different taxa in different ways. High frequency fluctuations can neutralize the

effect of low frequency fluctuations on species richness depending on their magnitudes. The WOA (n.d.) temperature data show that regions, such as northwest Atlantic and northwest Pacific near-coasts, were subject to high frequency fluctuations (daily/weekly) compared to other marine regions (Fig. 1). The effect of yearly temperature cycles, measured at monthly scales, on species richness that we have shown here can be neutralized in such regions. Thus, locality-specific variations can have a large impact on the general trends that we have investigated. Therefore, large confidence intervals in the prediction of species richness may result. The effect size we show here can be less at marine ecoregional scale (Spalding et al. 2007), which is larger than the latitudinal and longitudinal spatial scale. The results can be sensitive to what spatial and temporal scale we conducted the analyses.

In our theory, the amplitude of temperature can be used as a predictor of relative calanoid copepod species richness among regions where the difference in mean temperature is small. Thus, the longitudinal variation in temperature amplitude may also explain the longitudinal variation in calanoid richness on a latitude, along which the mean temperature does not very much. Thus, this may predict an east and west coast difference in calanoid richness on a global scale due to apparent differences in the amplitudes of their temperature-time profiles in general (see Fig. 1).

It has also been shown that salinity is correlated with copepod species richness (Rombouts et al. 2009). The aim of our study was to test whether temperature amplitude has an effect as the MTE suggested. However, it will be important to study multi-factors that affect richness to test which ones explain the patterns better.

Furthermore, in our analysis, we did not have sufficient data to test the assumptions that long-term total individual abundance per area, J/A, and averages derived from the body size distribution, $\overline{M^{3/4}}$ and $\overline{M^{1/4}}$, are independent of the temperature. This same assumption has been made by Rombouts et al. (2011) in their study of the relationship of mean habitat temperatures to marine copepod richness. However, the transect data across the Mediterranean, from north to south, in Nowaczyk et al. (2011), may suggest that total copepod abundance per area in the sampled transect has no significant differences, except for one data point at the station 13 m from the shore.

In theory, the phenomenon of periodic temperature fluctuations reduce species richness may exist, in general, in less migratory, shallow water-dwelling, epipelagic, ectothermic species with short generation times, breeding throughout the year without regard to the seasons (iteroparous organisms), and living in spatially confined habitats having less heterogeneous, but periodic temperature fluctuations. As most coastal dwelling crustaceans have life stages in water, especially their larval stages (Subramoniam 2016), they may also be affected by sea temperature fluctuations. These propositions may also be applicable to taxa in closed aquatic systems, such as lakes.

In summary, the amplitude of periodic temperature has a nonlinear effect on bio-energetics. Although mean annual temperature may be a good predictor of species richness, incorporating the effect of periodic fluctuations into the bio-energetics improves the predictability of richness for taxa that it matters. This may be true for other ectothermic species, more effectively those having shorter generation times, and expose to large yearly temperature fluctuations (cycles). More importantly, the apparent reduction of species richness by yearly temperature cycles may also validate the principles behind the MTE by Allen et al. (2002). Although the effect of temperature amplitudes on species richness is relatively small due to small effect sizes and other confounding factors, it is important to study this phenomenon further because it is supported by a theory. The bio-energetic effect on richness distribution forced by periodic temperature fluctuations stands out the other plausible correlated of seasonal effects along the longitudes and may contribute a dimension in the hyperspace. A mechanism, by which MTE relates to species richness, can be the temperature-driven generation time of the taxon lead by the rates of speciation, or simply immigration, both of which can potentially conserve the energetic-equivalence rule. It may also be important to study the effect of other factors that affect generation times, isolating temperature, and the exact probability distributions of the terms that have been taken as averages here.

Furthermore, by this theory, we may predict that an increase in the amplitude of periodic temperatures could offset some of the effects of global warming (the rise in the mean sea temperatures), possibly balancing-off its net effect on long-term change in species richness of the susceptible taxa. Our hypotheses provide new insights into the understanding the global species richness as an important extension to the MTE. To test these theories and hypotheses further in a broader scale, we need to investigate the changing diversity distribution patterns from Paleoecological perspectives (Louys et al. 2012), for example "hopping hotspots" of marine biodiversity (Renema et al. 2008), and historical biodiversity tracking of the earth's temperature (Mayhew et al. 2012).

Appendix 1: Calibrating generation times g_T

We calibrated the mean calanoid generation time per species, g_T, at temperature T (°C) using generation time data of copepods from Huntley and Lopez (1992) simplifying the model Eq. (8), $g_T = g_0 \overline{M^{1/4}} \exp^{E/kT}$, as $g_T = \hbar_1 \exp[(\hbar_2/1000)(1000/T)]$, with the selection of parameters, $\hbar_1 = g_0 \overline{M^{1/4}}$, $\hbar_2 = E/k$, and using the nonlinear least squares regression method *lsqcurvefit* in Matlab. The generation time data are given for 181 estimates in Huntley and Lopez (1992) of 33 marine copepod species tested at environmental temperatures ranging from -1.7 to 30.7 °C. In our model calibrations, we should get $\hbar_2/1000 \sim 9$K, ideally, as the activation energy E for aquatic taxa is ~ 0.78 eV (Allen et al. 2002). For our study of calanoid, we assumed that g_T calibrated based on marine copepod data, yielding $R^2 = 0.88$ (Fig. 5a), are not deviated largely from that of calanoid copepods, which usually comprises of 55–95% of the plankton samples (see Mauchline and Mauchline 1998). We assumed also that size variation among calanoid species is negligible (most are 0.5–2.0 mm in length: Mauchline and Mauchline [1998]), and the distribution is Gaussian. As it is said that the generation time is a reasonable period for acclimatization of copepods in temperature-related experiments (Landry 1975; Huntley and Lopez 1992), we assumed that metabolism, and, thus, $\overline{g}_T$, responds to temperatures averaged at the generation time or a larger time-scale. As the generation time of marine copepods in the sampling units of the Mediterranean and adjacent seas, computed using the calibrated model as above, on the basis of the mean temperatures of the units, was less than 30 days (Fig. 5b), the assumption that monthly mean temperatures of the habitats is a reasonable scale, at which the copepods respond metabolically to varying temperature, may be justified.

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