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ORIGINAL PAPER

Effects of temperature on carbon circulation in macroalgal food webs are mediated by herbivores

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Abstract

Warming is one of the most dramatic aspects of climate change and threatens future ecosystem functioning. It may alter primary productivity and thus jeopardize carbon sequestration, a crucial ecosystem service provided by coastal environments. *Fucus vesiculosus* is an important canopy-forming macroalga in the Baltic Sea, and its main consumer is *Idotea balthica*. The objective of this study is to understand how temperature impacts a simplified food web composed of macroalgae and herbivores to quantify the effect on organic carbon storage. The organisms were exposed to a temperature gradient from 5 to 25 °C. We measured and modeled primary production, respiration, growth and epiphytic load on the surface of *Fucus* and respiration, growth and egestion of *Idotea*. The results show that temperature affects physiological responses of *Fucus* and *Idotea* separately. However, *Idotea* proved more sensitive to increasing temperatures than the primary producers. The lag between the collapse of the grazer and the decline of *Fucus* and epiphytes above 20 °C allows an increase of carbon storage of the primary productivity at higher temperatures. Therefore, along the temperature gradient, the simplified food web stores carbon in a non-monotonic way (reaching minimum at 20 °C). Our work stresses the need of considering the combined metabolic performance of all organisms for sound predictions on carbon circulation in food webs.

Introduction

Future predictions on global carbon cycle estimate the rise of atmospheric carbon concentration due to anthropogenic CO_2 emissions, the magnitude of which increases even further when the ocean-atmosphere models are integrated with the responses of primary producers to climate change (Cox et al. 2000). The carbon fixation through photosynthesis and the release of carbon through respiration determine whether the system is a sink or a source of carbon (Valentini et al. 2000). Warming may decrease net primary production due to steeper increase of respiration than photosynthesis to rising temperature (Tait and Schiel 2013). This mechanism leads to a reduction in carbon fixation by primary producers, thus jeopardizing global carbon sequestration (Mystakidis et al. 2016).

In coastal marine systems, canopy-forming seaweeds are responsible for a substantial proportion of total carbon storage (Golléty et al. 2008). For example, in the Australian coast, the estimated storage in living macrophytes biomass is 2200×10^6 grams of carbon per square kilometer (Hill et al. 2015). However, changes in the temperature regime (e.g. fluctuations and warming) threaten key macroalgae populations and their functioning (Wernberg et al. 2010; Wahl et al. 2015; Arias-Ortiz et al. 2018). In general, temperature-driven individual- and community-level shifts of physiological responses (Vasseur et al. 2014) and trophic interactions (Gilbert et al. 2014) can impact ecosystem functioning, such as carbon flow within the food web (Duarte and Cebrian 1996).

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Under climate change scenarios, grazing plays an important role in maintaining balanced food webs. For instance, mesograzers consume epiphytic and free floating algae thus increasing light penetration and releasing habitat-forming macrophytes from competition (Alsterberg et al. 2013). Mesograzers also prey upon small herbivores that feed on benthic microalgae resulting in top-down control (Alsterberg et al. 2013). However, mesograzers may pose a risk to primary producers (Gutow et al. 2016). Provost et al. (2017) demonstrated that besides direct effects of warming, indirect effects such as increase in herbivory represent additional threats to kelps exposed to higher temperatures. The strength of trophic interactions varies with temperature due to changes in physiological responses (Brown et al. 2004), e.g. consumers experience an increase in metabolic rates with rising temperature that results in individual and population growth and intensification of feeding rates (O'Connor et al. 2009).

Individual thermal performances are usually hump-shaped, indicating that biochemical reaction rates accelerate until the optimum temperature (Pörtner and Farrell 2008; Harley et al. 2012). The metabolic intensification, which occurs until the optimum temperature, increases loss of energy through respiration resulting in higher energy demand. All the organisms that compose a food web are vulnerable to the increase of energy demand resulting in the amplification of consumption in all trophic levels. Thus, the amount of energy produced by the lowest trophic level, which is already reduced by physiological response to temperature, becomes the limiting factor that determines the structure of the biological community (Kordas et al. 2011). The ensuing alterations of the food web structure depend on the specific tolerance to warming and the effective trophic level of the interacting organisms involved. A possible scenario is that herbivores cope with their rising energy demand by increasing grazing rates (O'Connor 2009). An alternative scenario is related to the loss of herbivores that do not tolerate warming. This loss might alleviate the pressure on the base of the food web, thus resulting in thriving primary producers (Petchey et al. 1999). The combination of both scenarios means that the rise in temperature enhances the metabolic activity of herbivores, thus triggering the top-down control on primary producers until the optimum temperature of the grazers is attained. If the temperature continues to rise above the optimal thresholds of herbivores, they will reduce their consumption (i.e. the declining part of the hump-shaped curve) until reaching their upper temperature tolerance limit, thus releasing the primary producers from top-down control (Mertens et al. 2015).

Fucus vesiculosus plays important roles in ecosystem functioning since it provides a habitat to numerous species (Wikström and Kautsky 2007) and contributes to nutrient binding, oxygen production and carbon fixation in coastal food webs (Worm et al. 2000). The *Fucus* populations in the Baltic Sea have already experienced steep decline since the 1970s, which was attributed mainly to high input of nutrients (Nilsson et al. 2004). The increase of nutrients may cause a phytoplankton bloom that, due to decreased water transparency, restricts the macroalgae population to shallower depths (Kautsky et al. 1986). Another side effect of nutrient load is the excessive growth of filamentous algae (Nilsson et al. 2004). The filamentous algae may affect *F. vesiculosus* in different ways. The first one is the increase of competition for hard surfaces during the recruitment stage (Berger et al. 2003, Kraufvelin et al. 2007). The second one is that epiphytic filamentous algae may attract grazers that consume both epiphytes and host algae, i.e. "co-consumption", although they may also protect *F. vesiculosus* from direct predation, i.e. "protective coating" (Wahl and Hay 1995; Karez et al. 2000; Råberg and Kautsky 2008). In the Baltic Sea, the isopod *Idotea balthica* exerts strong control on primary producers and is the main consumer of *F. vesiculosus* (Engkvist et al. 2000).

In this work, we studied the impact of temperature on carbon fluxes together with the interaction between the macroalgae system, i.e. the *Fucus*-epiphytes assemblage (Thornber et al. 2016) and the mesograzer *I. balthica*. We aimed to (a) investigate how single physiological responses of the *Fucus*-epiphytes assemblage and *I. balthica* are modulated by different temperatures and (b) quantify the amount of carbon transferred through the trophic interaction between the grazer and the macroalgae assemblage along the temperature gradient. We expect temperature to regulate the carbon balance directly by affecting the physiology at individual-level and indirectly due to its effect on grazing rates. Modeling the carbon balance from a system perspective might challenge the interpretation based on the performance of single species.

Materials and methods

Material collection

Individuals of *F. vesiculosus* were collected in the Kiel Fjord (54°38′N, 10°20′E) on 17 Oct 2016 and transported within 20 min to the facilities of GEOMAR while maintained in the seawater from the sampling site. The algae were collected together with attached cobbles, as naturally occur in the field. The *Fucus* individuals were placed in tanks inside a climate chamber at field temperature (15 °C) for 24 h with continuous flow through of seawater. The tanks were equipped with a combination of LED lights providing an irradiance level of 165 µmol photons m^{-2} s^{-1} (eco+ LED-Leiste SUNSET 3500 K 34 W and eco+ LED-Leiste DAY 5500 K 34 W, LEDAquaristik UG, Hövelhof, Germany).

The organisms were kept under 12:12 h light: dark cycle, which corresponded to field conditions when the material collection took place. After the initial 24 h, all individuals of *F. vesiculosus* were submerged in freshwater for 20 s, a procedure ensuring the removal of all motile organisms associated with the thalli (Holmlund et al. 1990) and the *F. vesiculosus* were then placed in the experimental setup. The organisms removed with freshwater were retained in a sieve and 18 *I. balthica* individuals of approximately 1.2 cm were collected. Each individual was kept isolated inside a 200 mL glass jar with food ad libitum and continuous aeration for temperature acclimation.

Experimental design

The experiment was conducted in the climate chamber from 17 Oct to 30 Nov 2016. The macroalgae were kept in 10 L buckets that were maintained in thermobaths. The buckets were equipped with a mosquito net (mesh size 1.5 mm, installed vertically dividing each bucket into two equal sized halves). In each half of the bucket, one *F. vesiculosus* individual of comparable biomass (mean wet weight = 11.2 g, sd = 5.5 g) was placed. The buckets were supplied with continued aeration and received a flow through of 13 L sand-filtered seawater per day pumped from the Kiel Fjord. There were three replicate buckets per temperature treatment.

The target temperatures for the experiment were 5, 10, 15, 20, 22 and 25 °C. Since we expected *I. balthica* to decline at 25 °C, we added 22 °C for keeping a higher resolution of the hump-shaped curve of the thermal performance. These temperatures were reached by gradually increasing or decreasing 1 °C per day the initial temperature of the tanks (15 °C). In order to have identical rates of temperature change, the starting points of warming and cooling differed in time. After 10 days all tanks attained the target temperatures. Once the target temperatures were reached, in only one of the two halves of each bucket we introduced one individual of *I. balthica* in order to assess the effect of grazing on *F. vesiculosus*. The temperature treatment ran for 4 weeks. We started the experiment in October since field temperature matched the mean temperature of the selected gradient (15 °C). Moreover, carrying out the study during this month kept at minimum the amount of energy invested by *F. vesiculosus* for reproduction (Graiff et al. 2017).

Every week the macroalgae were separated from the grazers for 2 days. Both were maintained in thermobaths at the corresponding temperatures; the macroalgae were kept in the buckets and each isopod was transferred to a 200 mL-glass jar for egestion quantification before the respiration measurement. This separation process imposed transient starvation on the grazers. However, moderated starvation periods have little or no effect on lipid content and survival of adult *I. balthica* (Gutow et al. 2007).

Incubations

Every week we incubated the *Fucus*-epiphytes assemblage (i.e. the brown algae together with associated epiphytes) for photosynthesis and respiration measurements and each *I. balthica* individually for respiration measurements.

The photosynthesis and respiration of the *Fucus*-epiphytes assemblage were measured in 6 L gas-tight cylindrical chambers equipped with a stirrer and a non-invasive oxygen sensor spot PSt3 (PreSens Precision Sensing GmbH, Regensburg, Germany). The seawater used for incubations was filtered through a 1 µm polypropylene sediment filter. After sealing the chamber, the change in oxygen concentration was logged during 1 h using the Multi-channel Fiber Optic Oxygen Meter Oxy-10 mini (PreSens Precision Sensing GmbH, Regensburg, Germany). The incubation chambers were kept in thermobaths respecting the corresponding temperatures. The photosynthesis (net primary production, NPP) incubations were performed under light conditions (165 µmol photons m^{-2} s^{-1}). The respiration measurements were performed in the dark after a black cover was temporarily placed over the tanks. During every incubation, a control chamber containing only filtered seawater was measured for correcting possible changes in oxygen concentration.

The respiration of *I. balthica* was measured in 100 mL Winkler bottles. The measurements were carried out with the PreSens system described above and logged during 1 h, after sealing the bottle. The water used for incubation was filtered through 0.2 µm Whatman mixed cellulose ester filter (GE Healthcare Life Sciences, Germany) and kept in bottles inside thermobaths overnight to reach the temperature of the respective treatments before the incubations. Control incubations of filtered seawater were carried out for detecting possible changes in oxygen concentration due to reasons unrelated to the respiration of *I. balthica* (e.g. temperature compensation). All the respiration incubations were carried out in thermobaths, in order to maintain the experimental temperature conditions.

The oxygen consumed or produced was calculated as the difference between final and initial concentrations; this value was corrected by the control incubations and standardized by incubation time, biomass (wet weight - ww, g) of the *Fucus*-epiphytes assemblage or length (mm) of *I. balthica*.

Growth of the Fucus-epiphytes assemblage

The macrophyte biomass was quantified (ww) weekly. The relative growth rate (RGR) was calculated according to Eq. 1:

$$\mathrm{RGR}(\%) = 100 \cdot \frac{\ln\left(b_t\right) - \ln\left(b_{t-1}\right)}{\Delta t} \quad (1)$$

where b_{t-1} refers to initial biomass, b_t indicates final biomass and Δt is the number of days between the two measurements.

Biomass of epiphytes

In order to avoid disturbing certain properties of the *F. vesiculosus* surface, e.g. bacterial composition (Wahl et al. 2010), during the experiment we did not remove the epiphytic filamentous algae growing on the host brown algae. Therefore, biomass quantification and incubations for photosynthesis and respiration refer to both the host brown algae and epiphytes (i.e. *Fucus*-epiphytes assemblage). At the end of the experiment, the epiphytes were removed from a piece of *F. vesiculosus* with a cell scraper, washed with distilled water and kept in 20 mL glass vials. The samples were frozen at − 80 °C. They were thawed and dried at 40 °C for 48 h and the dry weight was quantified. The dry weight was normalized by the wet weight of the piece of *F. vesiculosus* from which the epiphytes were removed.

Egestion and growth rates of *I. balthica*

Weekly, the grazers were isolated from the *F. vesiculosus* for 48 h (period in which the macroalgae incubations were carried out). After this period, we collected the fecal pellets produced with disposable transfer pipettes and froze them at − 20 °C. For dry weight (dw) determination, the pellets were thawed, placed in pre-muffled and pre-weighed Whatman glass microfiber filters (GF/C–GE Healthcare Life Sciences, Germany), freeze-dried and weighed. After each incubation, the isopods were photographed and their body length (from cephalon to telson, excluding antennas) was measured using ImageJ software (Schneider et al. 2012). After all measurements were completed, the individuals were placed back in the buckets. The body length was converted to body mass according to the Eq. 2 (author's unpublished data; see supplementary information 1, SI.1):

$$\log(m) = 2.56 \cdot \log(l) - 1.86 \quad (2)$$

where m is body mass in dry weight (mg) and l is body length (mm). Finally, using weekly measurements of body mass we determined growth rates (Eq. 3):

$$G = \frac{(m_t - m_{t-1})}{\Delta t} \quad (3)$$

where G is growth rate, m_t and m_{t-1} are final and initial body mass, respectively, and Δt is the time interval between initial and final measurements (in our case, 7 days).

Carbon consumption of *I. balthica*

The measurements of egestion (E), respiration (R) and growth (G) rates of *I. balthica* were converted to carbon (SI.1 and SI.2). The values were summed to determine the carbon consumption per individual per day (C), according to Eq. 4 (Crisp 1971).

$$C = G + R + E \quad (4)$$

In order to quantify the energy used from the carbon storage of the primary producers, we calculated the ratio between *I. balthica* consumption and the NPP of *Fucus*-epiphytes assemblage. The ratio presents the proportion of carbon mobilized from NPP of the assemblage, thus the higher the ratio the lower the amount of carbon stored in the primary producers. The oxygen production was converted to carbon using a photosynthesis quotient of 1.2 (Kotta et al. 2000) and a respiration quotient was 0.85 (Hawkins and Bayne, 1985) (see SI.3). NPP of the *Fucus*-epiphytes assemblage and consumption of *I. balthica* were expressed as milligrams of carbon per day. To obtain a more realistic outcome, we scaled experimentally quantified NPP and consumption with field data of *I. balthica* density in relation to 1 kg dry weight of *F. vesiculosus* biomass to the respective temperatures (Anders and Möller 1983) (see SI.4).

Assimilation efficiency of *I. balthica*

We calculated the assimilation efficiency of *I. balthica* after Lang et al. (2017). Assimilation efficiency (ε) is obtained dividing the energy assimilated (respiration plus growth) by the total consumption:

$$\varepsilon = \frac{R + G}{C} \quad (5)$$

Assimilation efficiency is always included in the interval $0 \leq \varepsilon \leq 1$; without knowing the relative importance of the three consumption components (i.e. egestion, respiration and growth) it can be calculated with the following equation:

$$\varepsilon = \frac{e^{E_\varepsilon \frac{(T-T_0)}{kTT_0}} m^{\alpha_\varepsilon}}{1 + e^{E_\varepsilon \frac{(T-T_0)}{kTT_0}} m^{\alpha_\varepsilon}} \quad (6)$$

where E_ε is the activation energy for assimilation efficiency, T is the temperature in Kelvin (K) and T_0 the temperature normalized to 20 °C (293.15 K), k is the Boltzmann's constant (8.62×10^{-5} eV K^{-1}), m is the body mass in grams and α_ε is the allometric exponent for assimilation efficiency. Many studies report that the allometric exponent of various types of consumers (i.e. detritivores, herbivores and carnivores) is 3/4 while the activation energy ranges between 0.6 and 0.7 eV (Brown et al. 2004; Lang et al. 2017). Here we aimed at quantifying the exact values of these constant parameters for *I. balthica*.

Statistical analysis

The focus of our analysis was to assess the effect of temperature on the carbon transfer along the *Fucus*-epiphytes-grazer system. Therefore, the weekly repeated measurements obtained for every response variable were summarized in a single mean value per replicate and temperature level. Measurements obtained from the second week onwards were considered, excluding the first week when acclimation to the target temperatures took place. In case of growth of *I. balthica*, mean daily values as biomass were used along the 3 weeks to avoid stochastic variations due to the molting of single individuals, which occurred during different moments. The effect of the temperature gradient over the response variables of *Fucus*-epiphytes assemblage (i.e. NPP, respiration, growth and epiphytic load) was modeled using linear regression analysis. The adequacy of the selected models was evaluated through diagnostic plots of residuals. The models were selected according to the best fit provided by the Akaike Information Criterion (AIC). Respiration, growth, egestion, consumption and ratio consumption:NPP of *I. balthica* were modeled using nonlinear least squares. The Gaussian equation fitted to these *I. balthica* responses to temperature was based on Angilletta (2006). The assimilation efficiency was fitted using nonlinear least squares and it follows a logistic model (Lang et al. 2017). The analyses were performed with the R package *stats* (R Core Team 2017).

Results

NPP, respiration and growth rates of Fucus-epiphytes assemblage

NPP and respiration increased linearly with temperature (Fig. 1a and b; Table 1). On average, the increase of NPP with temperature was marginally significant from 130.41 µmol O_2 [g ww *Fucus*]$^{-1}$ day^{-1} at 5 °C to 189.66 µmol O_2 [g ww *Fucus*]$^{-1}$ day^{-1} at 25 °C. Respiration increased from 63.27 µmol O_2 [g ww *Fucus*]$^{-1}$ day^{-1} at 5 °C to 158.28 µmol O_2 [g ww *Fucus*]$^{-1}$ day^{-1} at 25 °C. The best fit for growth rates was a quadratic polynomial (Fig. 1c) although the relationship with temperature was not siginificant (Table 1). The modeled maximum growth rate occurred at 15 °C (2.05% day^{-1}) and the minimum at 25 °C (−2.04% day^{-1}).

Biomass of epiphytes

Biomass of epiphytes changed with temperature following a quadratic polynomial trend (Fig. 1d; Table 1). The epiphytic load was low at 5 °C (average 6.15 mg dw epiphytes [g ww *Fucus*]$^{-1}$), reaching the highest fouling density at 15 °C (20.54 mg dw epiphytes [g ww *Fucus*]$^{-1}$). Beyond the peak, the epiphytes biomass declined to 3.79 mg dw epiphytes [g ww *Fucus*]$^{-1}$ at 25 °C.

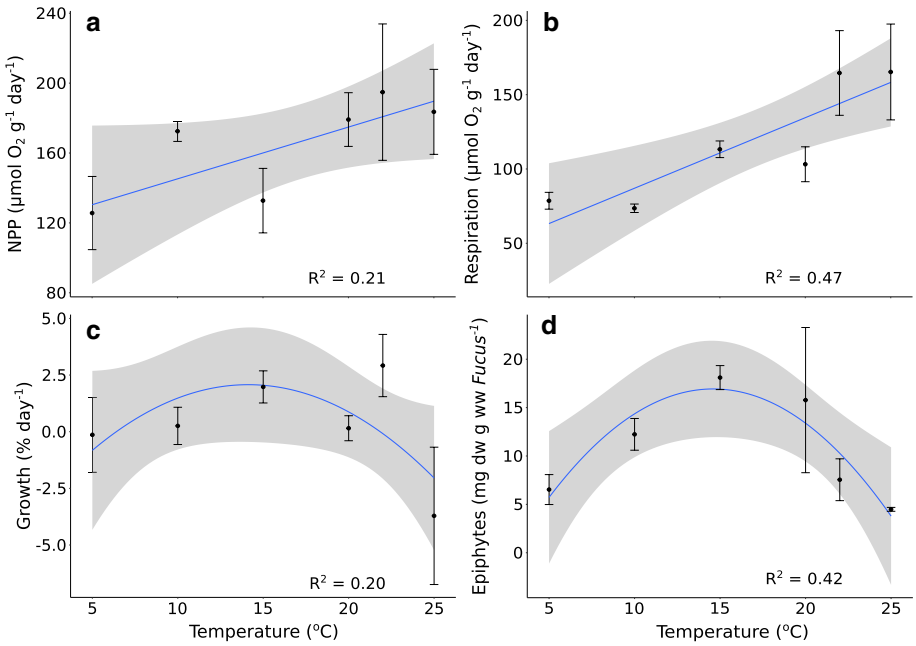

Fig. 1 Relationship between temperature and net primary production (NPP) (**a**), respiration (**b**), growth (**c**) of the *Fucus*-epiphytes assemblage and macroepiphytes load on *F. vesiculosus* surface (**d**) (blue lines: mean trends, grey areas: 95% confidence intervals). The circles correspond to mean values and the bars to standard error of the mean ($n = 3$)

Table 1 Linear model results of the response variables of *Fucus*-epiphytes assemblage exposed to temperature gradient

Response variable	Model	Term	Estimate	Std. Error	*t* value	*p* value
NPP	Linear ($R^2=0.214$, $F_{1, 14}=3.803$, $p=0.071$)	*a*	115.597	28.042	4.122	0.001
		b	2.962	1.519	1.950	0.071
Respiration	Linear ($R^2=0.465$, $F_{1, 14}=12.180$, $p=0.003$)	*a*	39.514	25.129	1.572	0.138
		b	4.750	1.361	3.490	0.003
Growth	Quadratic ($R^2=0.202$, $F_{2, 15}=1.897$, $p=0.184$)	*a*	0.243	0.716	0.339	0.739
		b	−1.782	3.037	−0.587	0.566
		c	−5.641	3.037	−1.857	0.083
Epiphytic load	Quadratic ($R^2=0.417$, $F_{2, 14}=4.997$, $p=0.023$)	*a*	11.149	1.423	7.830	<0.001
		b	−0.614	5.871	−0.105	0.918
		c	−18.549	5.871	−3.159	0.006

The linear models follow the equation $y=a+bx$ and the quadratic function follows the equation $y=a+bx+cx^2$. The element *y* corresponds to the response variable (NPP—net primary production, respiration, growth and epyphites load), *x* is the temperature (independent variable) and the parameters *a*, *b* and *c* refer to the terms presented

Respiration, egestion, growth and carbon consumption rates of *I. balthica*

The respiration, growth, egestion and carbon consumption rates of *I. balthica* were modeled with Gaussian fitting (Table 2). Respiration increased from 5 to 20 °C (4.55 and 20.83 µmol O_2 [mm *Idotea*]$^{-1}$ day^{-1}, respectively), followed by a decrease reaching 15.29 µmol O_2 [mm *Idotea*]$^{-1}$ day^{-1} at 25 °C (Fig. 2a). Growth rates also increased from 5 to 20 °C (0.08 to 5.43 mg dw day^{-1}, respectively), and decreased above this temperature to 2.45 mg dw day^{-1} at 25 °C (Fig. 2b). Egestion rate observed at 5 °C was 0.15 mg dw day^{-1}, followed by an increase towards the maximum value at 15 °C (0.32 mg dw day^{-1}); after this peak, egestion decreased to 0.19 mg dw day^{-1} at 25 °C (Fig. 2c). The amount of carbon consumed by the isopod was low at 5 and 10 °C (0.10 and 0.38 mg C day^{-1}, respectively), increased and peaked at 20 and 22 °C (0.89 and 0.81 mg C day^{-1}, respectively), followed by a final decline at 25 °C (0.59 mg C day^{-1}) (Fig. 2d; Table 2).

Ratio consumption: NPP

The ratio of organic carbon consumed in relation to the NPP informs about how much useful carbon produced by *Fucus*-epiphytes assemblage is lost to grazing instead of being potentially available for growth, reproduction and exudate (e.g. as dissolved organic carbon) of the macroalgae. The ratio responded to temperature following a Gaussian trend (Fig. 3; Table 2). From 5 to 22 °C the proportion increased from 0.001 to 0.024 decreasing at 25 °C to 0.017. Gutow et al. (2006) found that *I. balthica* is able to destroy algae patches rapidly due to sloppy feeding behavior, which we did not take into account for the proportion calculated. Thus, despite the low percentage we found in this study, this might be an underestimation of the carbon removal of the macroalgae assemblage by *I. balthica*.

Table 2 Gaussian model results summarizing the response variables from *I. balthica* exposed to temperature gradient

Species	Response variable	Term	Estimate	Std. Error	*t* value	*P* value
I. balthica	Respiration ($D^2=0.42$)	Mu	18.710	1.729	10.821	<0.001
		Sigma	7.828	2.089	3.747	0.002
	Growth ($D^2=0.70$)	Mu	18.910	0.677	27.910	<0.001
		Sigma	4.747	0.813	5.833	<0.001
	Egestion ($D^2=0.34$)	Mu	15.899	1.302	12.204	<0.001
		Sigma	8.579	1.961	4.374	<0.001
	Consumption ($D^2=0.65$)	Mu	18.843	0.990	19.030	<0.001
		Sigma	6.673	1.178	5.663	<0.001
Ratio consumption: NPP ($D^2=0.59$)		Mu	19.822	1.342	14.770	<0.001
		Sigma	5.930	1.508	3.931	0.001

The term mu refers to mean value and the term sigma stands for standard deviation of the Gaussian function fitted

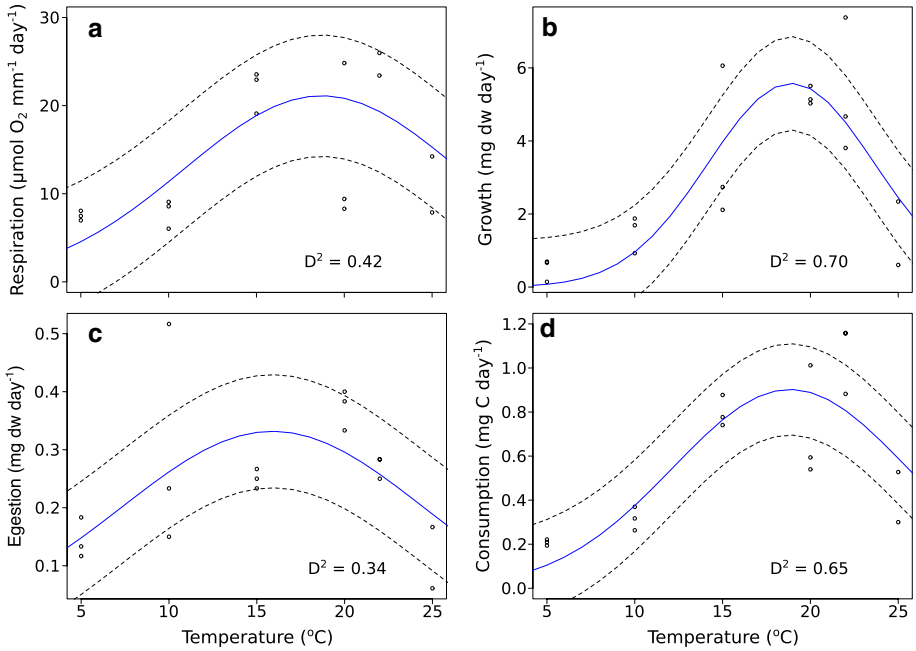

Fig. 2 Relationship between temperature and respiration (**a**), growth (**b**), egestion (dw of fecal pellets produced per day) (**c**) and carbon consumption (**d**) rates of *Idotea balthica*. The circles correspond to the replicates ($n=3$), the blue line refers to mean trend and dashed lines define the thresholds of the 95% confidence intervals

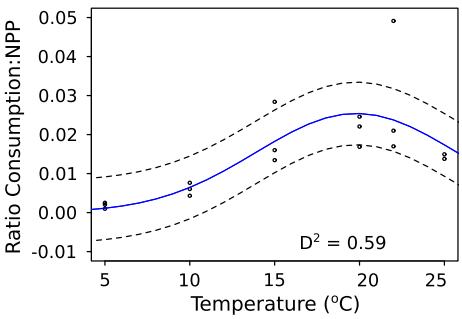

Fig. 3 Relationship between temperature and ratio of *Idotea balthica* consumption to *Fucus vesiculosus* NPP. The circles correspond to the replicates ($n=3$), the blue line refers to mean trend and dashed lines define the thresholds of the 95% confidence intervals

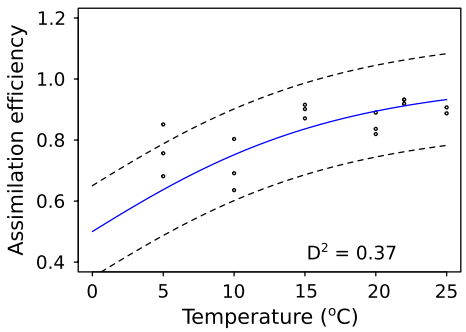

Fig. 4 Relationship between temperature and assimilation efficiency of *Idotea balthica*. The circles correspond to the replicates ($n=3$), the blue line refers to mean trend and dashed lines define the thresholds of the 95% confidence intervals

Assimilation efficiency

The assimilation efficiency of *I. balthica* followed a logistic trend that tends to saturation with increasing temperature (i.e. especially, starting from 15 °C; Fig. 4). By applying the Eqs. 5 and 6 to our data, we fitted a logistic curve and obtained the value of the constant parameters representing the allometric exponent ($\alpha_\varepsilon = 0.77$) and the activation energy ($E_\varepsilon = 0.74$ eV) for the assimilation efficiency of *I. balthica*. These values comply with those of the metabolic theory (Brown et al. 2004) as illustrated by Lang et al. (2017), i.e. $\alpha_\varepsilon = 0.75$ and $0.6\text{ eV} \leq E_\varepsilon \leq 0.7$ eV.

Discussion

In this work we measured individual-level metabolic responses of two consecutive trophic levels exposed to a temperature gradient and combined them to quantify the potential carbon storage in the primary producers of this simplified food web. The NPP rate of *F. vesiculosus* presented an increase (marginally significant) and respiration rates of the macroalgae increased linearly under the temperature gradient to which they were exposed (Fig. 1). The respiration and growth rates of the mesograzers reached maximum values at ca. 20 °C, while egestion rate peaked at 15 °C (Fig. 2a–c). The proportion of carbon consumed by the isopods to the NPP of the *Fucus*-epiphytes assemblage (Fig. 3) followed the individual carbon consumption

trend of *I. balthica* (Fig. 2d) with both peaking around 20 °C. The carbon balance of the trophic interaction between the *Fucus*-epiphytes assemblage and *I. balthica* was regulated by temperature. The combination of metabolic processes with different functional responses (i.e. the modeled trends) illustrates that conclusions on carbon balance differ when considering single species in isolation versus a system perspective.

F. vesiculosus is able to withstand a wide range of environmental changes, since the species is exposed to different temperatures along the seasons (Takolander et al. 2017). Graiff et al. (2015) demonstrated that the temperature for maximum photosynthesis capacity (expressed as maximum relative electron transport rate) was 24 °C. Takolander et al. (2017) found that temperatures beyond 26 °C jeopardize the photosynthetic activity of the macroalgae. In our study, the rates of NPP did not decrease along the temperature gradient and respiration of the *Fucus*-epiphytes assemblage increased linearly with temperature (Fig. 1a and b). Our experimental temperature did not exceed 25 °C, which could be the reason we did not detect a collapse in NPP rates. In addition, we were not able to directly disentangle the contribution of *F. vesiculosus* to NPP and respiration from that of epiphytes. However, Binzer and Middelboe (2005) demonstrated that the photosynthetic performance per thallus surface area of *Fucus* in isolation is higher than that of epiphytic filamentous algae. Graiff et al. (2015) showed that the highest rates of *F. vesiculosus* growth ranged between 15 and 20 °C. In our work, although the growth rate trend (Fig. 1c) was comparable with the previous study, it did not respond significantly to temperature (Table 1). In light of these results and the similiarities of our trends to those obtained by previous studies (Graiff et al. 2015; Takolander et al. 2017), we suggest that in our work *F. vesiculosus* was the main responsible for NPP changes. Noticeably, the NPP rate was relatively low at 15 °C, the temperature in which the epiphytic load peaked (Fig. 1d). This pattern could indicate that epiphytes negatively affected the photosynthetic activity of *F. vesiculosus* due to shading (Vogt and Schramm 1991; Rohde et al. 2008).

Differences in the trends displayed by the physiological responses of *I. balthica* in relation to temperature were detected. Our study shows that all metabolic variables considered for *I. balthica* responded to temperature following a non-monotonic curve, exhibiting increasing values up to the optimum (Strong and Daborn 1980). Respiration and growth rates peaked at ca. 20 °C, beyond which they decreased, showing considerably lower values at 25 °C (Fig. 2a and b). Similarly, Panov and MacQueen (1998) observed that high temperatures are responsible for low growth rates of amphipods. In case of respiration, our model corroborates the findings of Gutow et al. (2016) between 10 and 22 °C. Our results demonstrate that beyond 22 °C, the respiration rate declines, revealing the upper limit for this response variable for *I. balthica*. Clarke and Fraser (2004) suggested respiration rates as an appropriate indicator for basal metabolism (i.e. energy necessary for maintaining essential metabolic activities) in invertebrates because the respiration is related to the synthesis of ATP. Therefore, a temperature of 20 °C can be regarded as the limit of *I. balthica* metabolism capacity since the respiration rates attain their maximum. Differently, egestion rate peaked at lower temperature (15 °C; Fig. 2c). Although the amount of algae consumed directly by the grazer was not quantified in our experiment, Gutow et al. (2006) found that *I. balthica* egests about 90% of the ingested algae. The high percentage is attributed to the herbivore feeding, i.e. the algae are available in excess and such diet is poor in nitrogen and proteins thus the feeding rate must be intensified in order to supply the isopod's demands.

As an analogy to ecosystem functioning, the fitness of individuals should be considered as multidimensional (Laughlin and Messier 2015). Thus, in order to have a better perspective of how the grazers interfere in the carbon balance, we integrated the physiological response variables that result in energy expenditure (i.e. respiration, growth and egestion) for calculating carbon consumption. Our outcomes on the individual responses demonstrate that the carbon consumed by *I. balthica* was modulated by temperature (Fig. 2d). The *I. balthica* consumption changed very little at low temperatures (between 5 and 10 °C) and increased from 10 to ca. 20 °C, followed by a drastic decrease beyond this threshold. Respiration is usually the most important determinant of an individual's carbon budget (López-Urrutia et al. 2006) but our results show that both growth and respiration can mostly explain the changes of this response variable for *I. balthica*.

Allen et al. (2005) suggested that the carbon stored in the individuals can be scaled up to calculate the storage capacity of ecosystems. Therefore, we focused on the proportion of NPP consumed by *I. balthica* to understand how the carbon storage in the simplified food web of the experiment was modulated by the temperature gradient. Although the NPP rate increased linearly with temperature, the ratio of carbon consumed by *I. balthica* in relation to NPP increased up to 20 °C and decreased at 25 °C (Fig. 3). This outcome can be explained by the mesograzer's carbon consumption and is coherent with the increase of grazing on the primary producers that was previously found to occur in temperatures up to 20 °C (Gutow et al. 2016). The change in the ratio is due to the reduction of the metabolism of *I. balthica* (Fig. 2) at temperatures above 22 °C. Werner et al. (2016) also found that warming affected the metabolism of grazers at lower temperatures than that of the primary producers. This pattern confirms the finding of Mertens et al. (2015) that the daily interaction strength per capita increased up to 20 °C.

Between 22 and 24 °C the strength declined significantly, i.e. the primary producers outperformed the grazers under higher temperatures. Our results show that the decline of potential carbon storage is driven by *I. balthica* within the temperature range of its maximum consumption (from 15 to 20 °C; Kotta et al. 2006). Therefore, the carbon storage in this simplified food web is regulated by top-down control only at temperatures between 15 and 20 °C, while above such interval the decline in the consumption of the grazers was severe enough to attenuate the effect on the NPP.

Although the grazer's consumption in relation to NPP may be regarded as negligible (up to 2.5%), the secondary production is a relevant link to higher trophic levels in the food web (Waters 1977). Secondary production is defined as the formation of biomass by heterotrophic organisms (Benke and Huryn 2010) and is directly dependent on assimilation efficiency, which is modulated by temperature (Lang et al. 2017). In our study, the assimilation efficiency increased with temperature (Fig. 4) and, according to the values of Lang et al. (2017), at higher temperatures the assimilation efficiency of *I. balthica* was comparable to that of carnivores. The authors detected differences in the assimilation efficiencies of detritivores, herbivores and carnivores, attributing the dissimilarities between the feeding modes to digestibility. Jormalainen et al. (2005) found that phlorotannin produced by *F. vesiculosus* was responsible for lowering assimilation efficiency in *I. balthica* since this compound decreases digestibility. However, temperatures higher than 20 °C inhibit the production of phlorotannins by brown algae (Cruces et al. 2012), which supports high assimilation efficiency of the grazers. In our study such pattern is further corroborated by the egestion rates of the isopod, which decreased at 20 °C, thus suggesting higher digestibility. Therefore, the secondary production in the present work was a product of the synergistic response of autotrophs and heterotrophs to temperature.

Warming is expected to intensify the loss of carbon stored within the living systems (Allen et al. 2005). Here we show that at temperatures higher than 20 °C the *Fucus*-epiphytes assemblage presents higher capacity to store carbon while the grazers display a decline in all metabolic responses. The combination of the linear NPP trend of the macroalgae (Fig. 1a) together with the Gaussian distribution of *I. balthica* consumption (peak at 18.8 °C; Fig. 2d; Table 2) resulted in a Gaussian response (ratio consumption: NPP; Fig. 3) that attains its maximum at 19.8 °C (Table 2). These outcomes emphasize how integrating the study of the physiological responses of single species with herbivory is crucial to quantify functioning and services provided by primary producers under global warming scenarios.

Conclusions

In this work, we showed that the strength of the interaction between the *Fucus*-epiphytes assemblage and *I. balthica* is modulated by species-specific physiological responses to temperature. The decline of the herbivore's physiological performance causes an increase in carbon storage at the level of the primary producers. Therefore, the interaction strength between primary producers and herbivore plays an important role in driving the carbon balance of the system in times of ocean warming. The inclusion of primary producers has been shown to be an essential feature to yield accurate carbon cycle estimates using ocean-atmosphere models (Cox et al. 2000). Here we demonstrate that trophic interactions should not be neglected if the goal is to generate realistic predictions of carbon storage and circulation in food webs.

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Author contribution MI and MW conceived and designed the study. MI, MS, MF, FRB and BB conducted the experiment. MI, MS, MZ, FRB and TGH analyzed the data. MI wrote the first draft of the manuscript. All authors significantly contributed to the preparation and revision of the manuscript.

Data availability The data is archived at PANGEA database. https://doi.pangaea.de/10.1594/PANGAEA.901658

Compliance with ethical standards

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

Ethical statement All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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