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Marine meso-herbivore consumption scales faster with temperature than seaweed primary production

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ABSTRACT

Respiration of ectotherms is predicted to increase faster with rising environmental temperature than photosynthesis of primary producers because of the differential temperature dependent kinetics of the key enzymes involved. Accordingly, if biological processes at higher levels of complexity are constrained by underlying metabolic functions, food consumption by heterotrophs should increase more rapidly with rising temperature than photo-autoptrophic primary production. We compared rates of photosynthesis and growth of the benthic seaweed *Fucus vesiculosus* with respiration and consumption of the isopod *Idotea baltica* to achieve a mechanistic understanding why warming strengthens marine plant–herbivore interactions. In laboratory experiments thallus pieces of the seaweed and individuals of the grazer were exposed to constant temperatures at a range from 10 to 20 °C. Photosynthesis of *F. vesiculosus* did not vary with temperature indicating efficient thermal acclimation whereas growth of the algae clearly increased with temperature. Respiration and food consumption of *I. baltica* also increased with temperature. Grazer consumption scaled about 2.5 times faster with temperature than seaweed production. The resulting mismatch between algal production and herbivore consumption may result in a net loss of algal tissue at elevated temperatures. Our study provides an explanation for faster decomposition of seaweeds at elevated temperatures despite the positive effects of high temperatures on algal growth.

1. Introduction

Metabolic rates of organisms are strongly controlled by temperature because the underlying biochemical reactions are governed by the fundamental laws of thermodynamics. Depending on the reactions and enzymes involved metabolic processes display specific responses to changes in temperature. In a physiologically relevant temperature range respiration has been predicted to increase faster with rising temperature than photosynthesis because of the specific temperature-dependency of the kinetics of ATP synthesis in the respiratory complex and Rubisco carboxylation (Allen et al., 2005). The general validity of this prediction is supported by a global analysis of rates of respiration and photosynthesis of diverse organisms from a wide range of ecosystems including marshes, grasslands, forests and shrublands and oceanic plankton (Allen et al., 2005). Accordingly, temperature controls metabolic functions of entire ecosystems, such as the potential of the oceans for capturing CO_2, through its effects on the metabolic rates of the constituent individuals (López-Urrutia et al., 2006).

In addition to the direct metabolic effects temperature can indirectly shape the structure and functioning of ecosystems by altering the outcome of species interactions (Kordas et al., 2001). Metabolic theory of ecology predicts that processes at more complex levels of biological organization are constrained by the rates of underlying metabolic processes and their thermal responses (Brown et al., 2004). Therefore, heterotrophic processes, such as food uptake by consumers, should scale faster with temperature than primary production by photoautotrophs. Accordingly, plant–herbivore interactions provide ideal systems to develop testable hypotheses concerning ecosystem effects of global warming because they allow for directly contrasting herbivore consumption and plant primary production.

Previous studies in the marine environment revealed significant effects of temperature on plant–herbivore interactions but did not confirm a direct temperature effect on herbivore consumption (e.g. Thompson et al., 2004, Morelissen and Harley, 2007). There is strong evidence that floating seaweeds in the North Sea and in the SE Pacific decompose more rapidly in warm waters, presumably because the algae are unable to compensate for enhanced herbivore grazing at elevated temperatures (Vandendriessche et al., 2007; Rothäusler et al., 2009). The authors report on net-changes in algal biomass. However, they do not explicitly compare rates of algal primary production and herbivore feeding in order to mechanistically explain the loss in algal biomass at higher temperatures despite enhanced seaweed growth. Warming was found to increase the per capita interaction strength (i.e. the effect of a consumer on its prey) between the herbivorous amphipod *Ampithoe longimana* and the seaweed *Sargassum filipendula*, which was indicated by a reduced biomass of the seaweed in the presence of the grazer at elevated non-lethal temperature (O'Connor, 2009). Higher

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temperature had a positive effect on algal growth. However, the consumption rate of the grazer was independent of temperature and thus, did not explain the enhanced net-loss of algal biomass at higher temperatures.

Generally, there is only weak evidence for an influence of temperature on the consumption rates of small benthic marine herbivores (meso-herbivores). Accordingly, other factors such as body size and food availability have been suggested to be more important determinants of feeding activity in marine herbivores (Hillebrand et al., 2009; Saiz and Calbet, 2011). Yee and Murray (2004) showed that consumption rates of medium-sized gastropods of the genus *Tegula* from California vary with temperature. However, this result disagrees with the temperature-independent feeding rates of herbivorous amphipods (O'Connor, 2009; Poore et al., 2013) and isopods (Gutow et al., 2014). Strong and Daborn (1980a) found seasonal variations in the feeding rates of the isopod *Idotea baltica* from Nova Scotia (Canada) but did not separate the effects of temperature, body size and potential seasonal variations in seaweed palatability.

We studied the thermal responses of the benthic seaweed *Fucus vesiculosus* and its consumer, the marine isopod *I. baltica*, in order to investigate mechanisms that influence the outcome of a marine plant–herbivore interaction at different temperatures. Both species are common components of coastal marine and brackish ecosystems of the NE Atlantic region. *F. vesiculosus* forms extensive inter- to subtidal canopies on rocky shores and provides food and shelter for a great variety of associated organisms (Wikström and Kautsky, 2007). *I. baltica* is the dominant consumer of *F. vesiculosus* in the Baltic (Engkvist et al., 2000). On floating seaweeds in the North Sea *I. baltica* reaches exceptionally high densities and contributes substantially to the decomposition of algal rafts (Gutow et al., 2015). We studied the influence of temperature on metabolism and related somatic processes of the two species. Based on the predictions of the metabolic theory of ecology we tested the hypotheses that (i) respiration of *I. baltica* increases faster with temperature than photosynthesis of *F. vesiculosus* and (ii) food consumption of the grazer increases faster with temperature than primary production of the seaweed. Laboratory experiments were performed at a temperature range from 10 to 20 °C, which corresponds to natural ambient temperatures in the southern coastal North Sea including incidental maximum values (Wiltshire and Manly, 2004).

2. Material and methods

2.1. Seaweed photosynthesis and growth

F. vesiculosus was collected in January 2013 at low tide from a rocky intertidal groin in the German Wadden Sea (North Sea) near List harbor at the island of Sylt (55°01.02′ N, 008°26.43′ E). One apical piece of about 2 cm length was cut off with a scissor from each randomly selected algal thallus. The pieces were kept humid in a cooler overnight for transport to the laboratories of the Alfred Wegener Institute in Bremerhaven. Upon arrival the distal tips of 1 cm length were cut off the algal pieces and transferred individually into 1 L beakers filled with 800 mL of nutrient enriched (Provasoli, 1968) filtered seawater (0.5 μm). The seawater medium was exchanged completely every 3–4 days to avoid nutrient depletion and accumulation of metabolic waste products. The algae were exposed to a 16:8 h light:dark rhythm at a photon fluence rate of 100 μmol m^{-2} s^{-1} (Osram, L36W/954; München, Germany), which is well above the light-compensation point for *F. vesiculosus* (Bäck and Ruuskanen, 2000; Weinberger et al., 2011). Each beaker was aerated through an air stone. Six replicate algal pieces each were maintained for 21 days at one out of five constant temperatures of 10, 13, 16, 18 and 20 °C in a climatic chamber with a temperature precision of ±0.5 °C. The temperature was controlled every two days. During the first 14 days the wet weight (WW) of the algal pieces was measured every third day (±1 mg). Prior to weighing adherent seawater was carefully removed with tissue paper. During the third week, the algae were left undisturbed except for seawater exchange. Growth of the algal pieces was calculated as

$$G = (M_2\text{-}M_1)/M_1 \cdot t$$

where M_1 and M_2 are the WW at time 1 and time 2, respectively, and t = time in days. Growth was calculated over the entire culturing period excluding the first week to account for potential effects of initial acclimation to the experimental conditions. The growth rate was expressed as $g_{WW} \cdot g_{WW}^{-1} \cdot d^{-1}$.

After 21 days, photosynthesis of each algal piece was measured at the respective culturing temperature. Oxygen evolution was measured using optodes (Microx TX3 with needle type oxygen micro-sensors, PreSens, Regensburg, Germany) in 25 mL chambers filled air-free with seawater at a photon fluence rate of 100 μmol m^{-2} s^{-1}. The oxygen concentration of the seawater was recorded over 30 min at intervals of 10 s (Software TX3, PreSens, Regensburg, Germany). During the first 15 min the algae were kept in darkness to measure dark respiration. During the second 15 min the algae were exposed to light to measure net-photosynthesis. After measuring the photosynthesis, the WW of the algal pieces was measured. At each temperature two control measurements without algae were performed to estimate bacterial respiration. Dark respiration and net-photosynthesis were calculated from the change in the oxygen concentration and corrected for bacterial respiration. Subsequently, gross-photosynthesis was calculated by subtracting dark respiration from net-photosynthesis. The rate of oxygen evolution was expressed as μmol $O_2 \cdot g_{WW}^{-1} \cdot h^{-1}$.

2.2. Herbivore respiration and food consumption

Isopods of the species *I. baltica* were taken from a mass culture maintained in a seawater flow-through system at the Alfred Wegener Institute in Bremerhaven. The cultures are regularly supplemented with individuals from the field, which are predominantly collected from floating seaweeds in the German Bight. 20 randomly selected replicate individuals (adult males and females) each were maintained individually for one week at one out of five constant temperatures (10, 13, 16, 18 and 20 °C) and a day:night rhythm of 16:8 h. Temperatures were recorded daily. The isopods were kept in plastic cups (diameter: 9 cm; height: 3.7 cm) filled with 150 ml filtered seawater (0.5 μm). The seawater was exchanged at least every second day. The body mass of the isopods (measured at the end of the feeding experiments) ranged from 75 to 385 mg (WW).

Thalli of *F. vesiculosus* were freshly collected at low tide from concrete harbor constructions in the Weser estuary at Bremerhaven (53°32.12 N, 008°34.75 E) and pieces thereof were offered ad libitum as food to the isopods. The apical sections of the algae were inspected with the naked eye. Only pieces without visible epiphytes were taken from sections between the 1st and 2nd distal branching of the thallus. The algal food was replaced by fresh pieces every second day.

For determination of the consumption rates of *I. baltica* 100 pieces of freshly collected *F. vesiculosus* were soaked for at least 2 h in filtrated seawater. Subsequently, algal pieces were carefully blotted with tissue paper, weighed (balance: Satorius, A200S) and offered to the isopods. After a feeding period of 24 h, the isopods and the algal pieces were blotted and weighed. Additionally, 20 control pieces were kept under the same conditions but without isopod to estimate the autogenous weight change of the algae during the experiment. The corresponding pieces from the feeding treatment and the control originated from the same algal individuals. The amount of ingested algal tissue (A) was calculated after Cronin and Hay (1996) as $A = F_I \cdot (C_F/C_I) - F_F$ where F_I is the initial and F_F the final WW of *F. vesiculosus* in the feeding treatment. C_I and C_F are the initial and final WW of the control piece. The feeding rate was standardized by the WW of the isopod and expressed as $g_{WW} \cdot g_{WW}^{-1} \cdot d^{-1}$. Isopods that molted during the feeding experiment were excluded from the analysis. Additionally, some individuals did not feed for