Does heat tolerance vary with rates of oxygen production in photosymbiotic cnidarians?

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Abstract

Oxygen acquisition and delivery to tissues is believed to be a key factor in heat tolerance, but testing this link has been challenging due to methodological limitations in separating processes related to oxygen acquisition and oxygen delivery. In this study, we altered tissue oxygenation by manipulating light intensity using cnidarians that host endosymbiotic algae as a model. We first verified that light intensity determines net photosynthetic rates, showing that all species produced oxygen at the highest light intensity, and that chemical inhibition successfully inhibited oxygen production. We then tested the prediction that heat tolerance would be higher at higher light intensity and lower in chemically inhibited specimens. Overall, photosynthetic specimens had a higher heat tolerance than inhibited specimens and increased light intensity improved heat tolerance for two of the three species we examined. Because inhibited specimens had lower heat tolerances, we conclude that oxygen dynamics are involved in shaping heat tolerance. Interestingly, light intensity also affected oxygen uptake and heat tolerance in some of the chemically inhibited specimens, indicating that light modulates aspects of cnidarian metabolism that are related to thermal tolerance, but extend beyond oxygen dynamics and the photosynthesis occurring in their algae.

Introduction

Assessing the vulnerability of organisms to global warming frequently employs experimental measurements of their heat tolerance. With thermal isoclines being major correlates of patterns in species distribution, it is perhaps not too surprising that patterns in heat tolerance are related to geographic distribution ranges of species and their habitat use [1–3]. In aquatic (i.e. marine and freshwater) ectotherms, such linkages between heat tolerance and geographic distribution appear to be stronger than for terrestrial ectotherms [4].

One mechanism that has long been hypothesized to explain the decrease in performance and eventual mortality in ectotherms exposed to stressfully high temperatures is a shortage of oxygen [5]. Elevated temperatures lead to exponential increases in biological rates, with concomitant increases in metabolic demand for energy and hence oxygen [6]. According to the oxygen limitation hypothesis, beyond some upper temperature threshold, animals have insufficient capacity for extracting and transporting oxygen such that oxygen delivery can no longer keep up with elevated tissue demand for oxygen [7]. Although the hypothesis was originally proposed to be a universal explanation for heat tolerance limits under normoxia, experimental support for this hypothesis is mixed and appears to be stronger, but not universal, for aquatic ectotherms than for terrestrial ectotherms [8]. Note that although less oxygen dissolves in warmer water, maximum rates of diffusion can still increase due to an increase in oxygen diffusivity [9]. However, extracting oxygen from water in general is much more challenging than from air, which likely contributes to the greater susceptibility to oxygen limitation in water breathers [3].

In addition to measurements of aerobic and anaerobic metabolism to characterize thermal limits, manipulative approaches to testing the oxygen limitation hypothesis comprise altering either ambient oxygen availability or the capacity of organisms to extract and transport oxygen [10,11]. While experiments often show strong reductions in heat tolerance when measured in hypoxic water (i.e. water in which oxygen levels are reduced below 100% saturation), improvements in heat tolerance when measured in hyperoxic water are typically much less pronounced, or absent [8]. Experiments with hyperoxia alleviate potential oxygen deficiencies and are therefore seen as a stronger test of the oxygen limitation hypothesis. However, alleviating oxygen limitation can simply result in a process other than oxygen delivery to become limiting. If the temperatures at which both processes fail are similar, no substantial improvement in heat tolerance is expected, but oxygen may still be limiting under normoxia. Note also that if organisms only infrequently experience hyperoxic conditions, they are unlikely to have evolved the capacity to exploit periods of hyperoxia [12]. In a similar vein, a few studies have manipulated the capacity of an organism for oxygen transport and then tested if this affected their heat tolerance. These found subtle changes [e.g. 13], but due to the effects being small, it has remained difficult to falsify the hypothesis.

Here we circumvent these experimental difficulties by noninvasively altering tissue oxygenation without manipulating the oxygen levels in the water, or an organism's capacity to transport oxygen by examining three different photosynthetic cnidarian species spanning diverse clades (Anthozoa, Scyphozoa and Hydrozoa) under different light intensities. The gastrodermal tissue of these cnidarians is filled with single-celled dinoflagellates that can photosynthesize to produce sugars and oxygen in a light-dependent manner. If oxygen is limiting under normoxia, these species should exhibit improved heat tolerance with increasing light intensity as more and more oxygen is generated internally as a byproduct of photosynthesis (providing the amount of light does not exceed the amount needed to induce photoinhibition and

photodamage). In previous work on a sea slug that retains functional chloroplasts from the algae it feeds, we observed improved heat tolerance under high light intensity [14]. Here we expand on this work, studying three different species, and as an additional test, we chemically inhibited photosynthesis to investigate whether photosynthesis, not light, determines heat tolerance.

Materials and Methods

Three different cnidarian species (n= ~54/species) were collected from the same mangrove habitat (Spaanse Water) on Curacao (Fig 1). The anthozoan, *Bunodeopsis antilliensis* Duerden, 1897 was found on, *Thalassia testudinum* and *Halophila stipulacea* seagrass at a depth of 0.5-1.5 meters. The hydrozoan, *Myrionema hargitti* (Congdon, 1906) was attached to mangrove roots at 0-1m deep, while the scyphozoan, *Cassiopea* cf. *xamachana* Bigelow, 1892 was found amongst the seagrass rhizoid and on bare patches of silt at 1-2m depth. The light intensity at the collection site was measured using a SQ-500-SS Full-spectrum Quantum sensor with a 30 cm cable and a microCache Bluetooth micro-logger (Apogee Instruments) as described in Burgués Palau et al. [15]. All specimens were transported to the laboratory at the Caribbean Research and Management of Biodiversity Institute (CARMABI) for experimentation.

In the lab, specimens were housed in 20L plastic tanks containing aerated seawater maintained at 26°C to match the water temperature in the field. They were provided with a light intensity of 1600µmol $m^{-2}s^{-1}$ (OSRAM 30W full spectrum LED, OSRAM GmbH, Germany), matching the light intensity measurements taken at 2m depth in the field at midday on the day samples were collected. Specimens were allowed to adjust to laboratory conditions for at least 3 hours before experimentation began. Half of these specimens remained capable of photosynthesis during experimentation (i.e. untreated). The other half of the specimens were treated with a 2µg ml^{-1} solution of monolinuron (Algol, JBL GmbH & Co. KG, Germany) in seawater for 2 hours before they were measured [16]. Monolinuron selectively inhibits photosystem II activity by blocking the electron transport chain [17], which also blocks O_2 formation. Exposure to 2µg ml^{-1} has demonstrated effectiveness in chloroplasts, even when they are incorporated in animal tissues [16,18].

Oxygen production/consumption

To measure the metabolic rate of each specimen, it was placed in a respiratory chamber (glass jar), containing aerated seawater (with or without monolinuron) and a PSt3 optical sensor (Presens GmbH, Germany). A Fibox 4 Trace (Presens GmbH, Germany) was used to record the oxygen saturation every 6 minutes for an hour. Before experimentation, the Fibox was calibrated using 2-point calibration (100% O2 saturated seawater and 0% oxygen: nitrogen gas). Oxygen saturation was converted to concentration following the protocol outlined in [14] and detailed in Supplementary File 1.

Critical Thermal limits

Nine specimens from each species were randomly selected for each treatment according to a 3x2 experimental design (3 light conditions x monolinuron-treated or not monolinuron-treated, Supplementary Table 1). Light intensity was manipulated by placing 30W LED panels (OSRAM GmbH, Germany) at different heights above the specimens, resulting in the provisioning of 100µmol $m^{-2}s^{-1}$, 700µmol $m^{-2}s^{-1}$, and 1600µmol $m^{-2}s^{-1}$ of light matching natural conditions. Specimens were placed in individual jars at one end of a large plastic container. The water temperature was increased by 1°C every 15 minutes adding small amounts of boiling water to the other end of the container. Vigorous aeration ensured rapid water mixing.

Two behavioral changes were used to denote each species' Critical Thermal limits (CT1 and CT2). In *B. antilliensis*, unstressed specimens were attached to the substrate via their pedal discs and they often had their tentacles extended into the water column (Fig 1A). CT1 was defined as the temperature at which each anemone partially and suddenly retracted all of its tentacles at once, a stress response they also demonstrated when being moved from their substrate (Fig. 1B). CT2 was defined when *B. antilliensis* detached from the substrate (Fig. 1B). In *C.* cf. *xamachana*, unstressed specimens pulsed their bells 40-60 times per minute (Fig. 1C). When thermally stressed, they reduced this rate to <10 times per minute (CT1). After additional warming, jellyfish no longer reacted to a soft jet of water from a pipette by pulsing their bells rapidly, indicating they were no longer able to try to flee the stressor (CT2,Fig. 1D). In *Myrionema hargitti*, unstressed specimens were observed with their polyps fanned out in the water. CT1 was defined as the temperature at which each specimen retracted the first polyp(s) (Fig. 1E) and CT2 was defined as the point at which it retracted all of its polyps (Fig. 1F).

Data analysis

Both oxygen production/consumption and the critical thermal limits were analyzed in R-Studio [19] based on R version 4.2.0 [20] using linear models. Best fit models were identified using Akaike Information Criterion values. The model that best fit our O_2 data explained 85% of the variation and included the fixed effects, light intensity, monolinuron, species and their interactions. Since CT1 and CT2 were positively correlated (Pearson $r = 0.694$; $t_{1,159} = 12.17$; $P < 0.0001$), they were pooled and the resulting model explained 84% of the variation. In both analyses, light intensity was log transformed to allow curvilinear relationships to be fitted. Since we found significant three-way interactions between light, species and monolinuron for both sets of data, we proceeded to fit simplified models to evaluate their effects for each species separately. We did this by sub-setting the data by species and running the same model excluding species and its interactions (Table 1). Significance levels were then based on a Type III ANOVA, unless the interaction between light and monolinuron was not significant, in which case we used a Type II

ANOVA (detailed in Supplementary Tables 2-3 and the code provided). The packages ggplot2 [21], dplyr [22], broom [23] and visreg [24] were used for data handling and visualization.

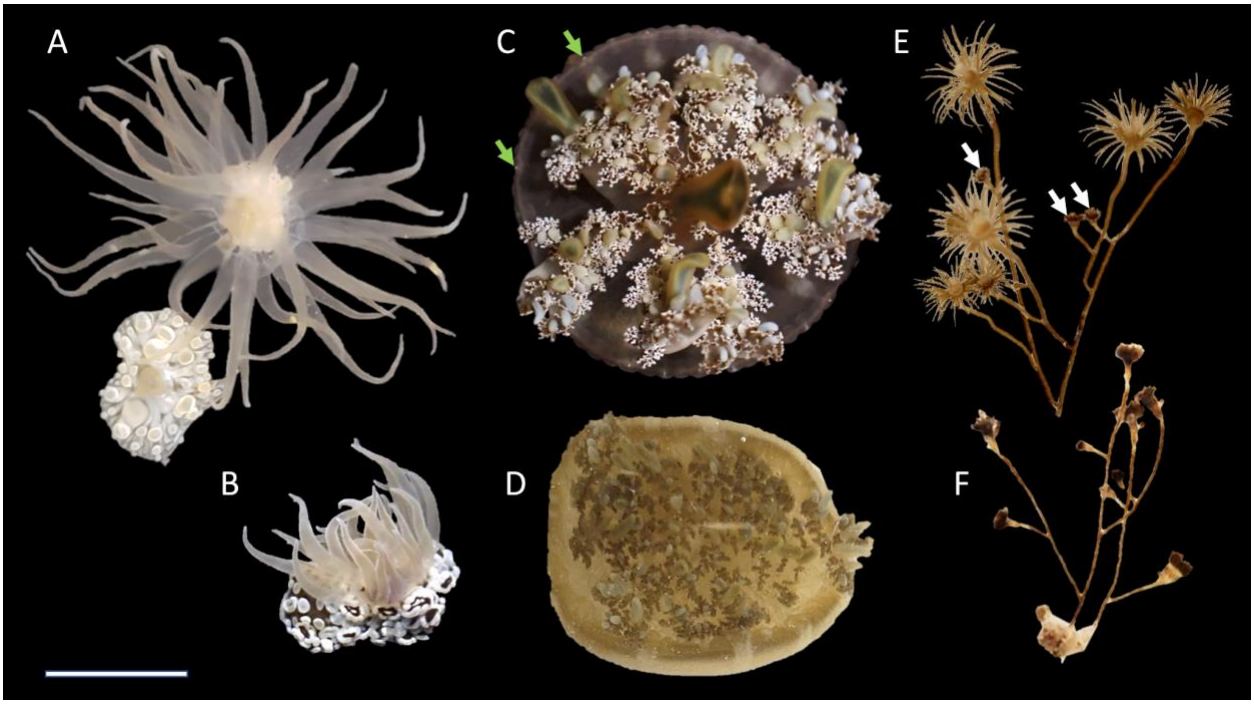

Fig. 1 The species used in this study and the behaviors used to define CT1 and CT2. A) *Bunodeopsis antilliensis* (oral view) fully extended and completed contracted (lower left). Specimens were observed in both of these states in the field and the holding tank, but they always had tentacles completely extended after transfer to the jars used in the CT trials. B) the partial contraction of all tentacles in one sudden movement (CT1) and the point at which the pedal disc detached from the respirometry chamber wall or bottom (CT2). C) *Cassiopea* cf. *xamachana* - oral view during bell relaxation and D) during a bell pulse. The green arrows indicate rhopalia –light sensing organs. E) A *Myrionema hargitti* specimen that simultaneously retracted three small polyps demonstrating (CT1,see white arrows) and H) a specimen, with all of its polyps retracted (CT2). Scale bar is ~2mm for A, ~4mm for B, ~15mm for C-D and ~10mm for E-F.

Results and Discussion

Light intensity at the collection site decreased with depth from 1986.58 ± 154.72 μmol m^{-2} s^{-1} at the water's surface to 1624.45 ± 207.74 μmol m^{-2} s^{-1} at 2m depth and 1277.62 ± 149.70 μmol m^{-2} s^{-1} at 4m depth (Supplementary Table 3). Since specimens were collected at 1-2m depth, the highest light intensity treatment in this study (1600 μmol m^{-2} s^{-1}) was not considered an environmental stressor for these species, despite the fact that it is higher than the light intensities used in most photophysiological studies, reinforcing the notion that most photophysiological studies chronically underestimate the light intensities found in nature [15,25]. Furthermore, if exposure to this intensity was a stressor, we would expect a decrease in O_2 production rates at higher light intensities due to photoinhibition [e.g. 31], however this was not observed.

In *M. hargitti*, thermal tolerance stayed consistent across light conditions, suggesting their thermal tolerance was not governed by light, even though photosynthetic specimens consistently outperformed chemically inhibited specimens. This observation could suggest that chemical inhibition has unintended effects on thermal tolerance in this species, but investigating this will require further study.

All three cnidarian species oxygenated the surrounding seawater when allowed to photosynthesize and provided with 700 or 1600 µmol $m^{-2}s^{-1}$ light, as evidenced by positive O_2 production rates. Under low light (50 µmol $m^{-2}s^{-1}$), *B. antilliensis* consumed more O_2 than was produced via photosynthesis, contrasting *C.* cf. *xamachana* and *M. hargitti*. The amount of O_2 that was produced by each species increased at higher light intensities for all three species (Fig. 2A-C; $t > 4.68$; $P < 0.001$).

Table 1 ANOVA results for each species. P-values indicated in bold are < 0.05 and thus considered significant.

		Light		Monolinuron		Monolinuron * Light		Type of Anova
	Species	F-value	P-value	F-value	P-value	F-value	P-value	
MO_2	*B. antilliensis*	28.95	**<0.0001**	105.71	**<0.0001**	1.56	0.22	II
	C. cf. *xamachana*	24.20	**<0.0001**	7.78	**0.0075**	35.28	**<0.0001**	III
	M. hargitti	39.20	**<0.0001**	1.92	0.172518	23.63	**<0.0001**	III
CT	*B. antilliensis*	14.51	**0.00024**	2.04	0.15593	6.07	**0.015**	III
	C. cf. *xamachana*	137.48	**<0.0001**	34.56	**<0.0001**	0.51	0.48	II
	M. hargitti	6.42	**0.013**	44.19	**<0.0001**	0.014	0.91	II

Monolinuron successfully inhibited photosynthesis, resulting in a net uptake of O_2 from the surrounding seawater, which yielded negative O_2 production values (i.e. oxygen consumption, Fig. 2A-C, Supplementary Table 2). Rates of O_2 consumption were either weakly related to light intensity (*B. antilliensis*), did not respond to light intensity (*M. hargitti*), or were negatively related to light intensity (*C.* cf. *xamachana*). The fact that light still modulated their rates of O_2 consumption suggests that animals are able to perceive and respond to light resulting in metabolic change. Nevertheless, our observations indicate that photosynthesis was successfully inhibited in our study species, enabling us to manipulate internal O_2 levels in their tissues, which will be higher in photosynthetic individuals.

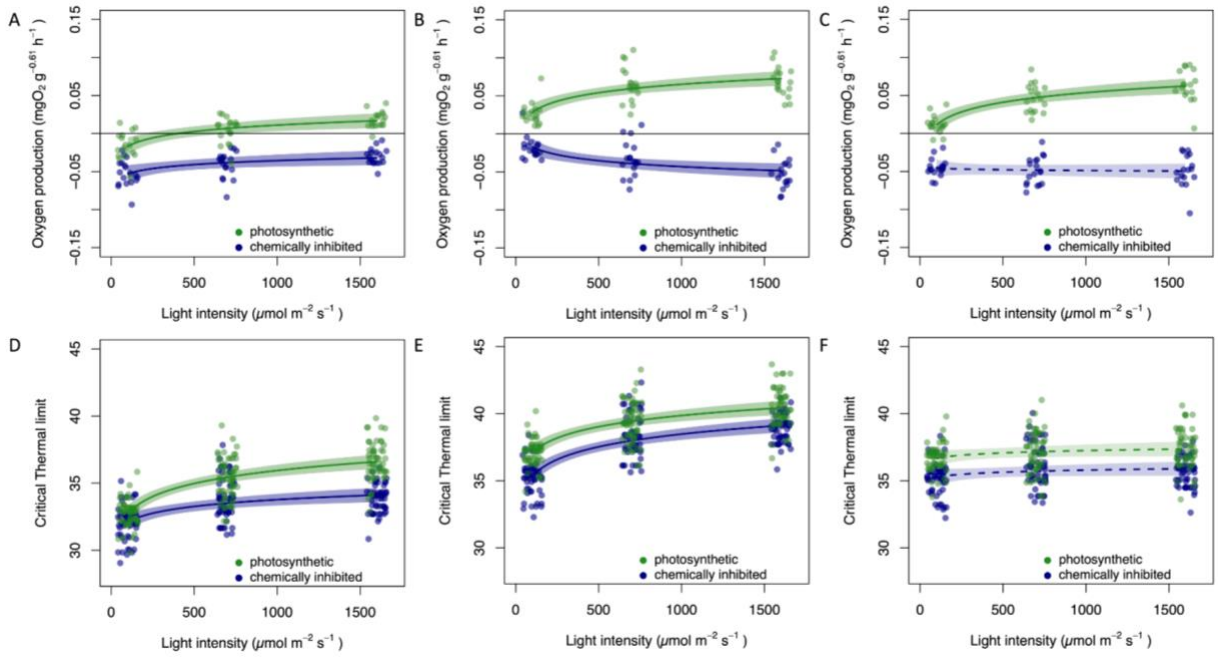

Fig. 2 Rates of oxygen production/consumption (panels A-C) and heat tolerance (panels D-F) in relation to light intensity for each of the species examined here. In each panel, we distinguish between specimens capable of photosynthesis (green points and shading), and those incubated with monolinuron to inhibit photosynthesis (blue points and shading). For panels A-C, positive values indicate (net) oxygen production, while negative values indicate (net) oxygen consumption. All panels depict partial residual plots, which illustrate the relationship between the response variable and an independent variable while accounting for the effects of other independent variables in the model (Tables S3, S4). The lines are regression lines and the shaded bands are 95% confidence intervals. Dashed lines and lighter shaded bands indicate that no significant relationship exists between the points connected by that line.

In general, we observed that photosynthetic specimens displayed a greater ability to withstand heat stress than chemically-inhibited specimens (Fig. 2D-F). Furthermore, with increasing light intensity, heat tolerance improved in photosynthetic *B. antilliensis* and *C. cf. xamachana* ($t > 7.29$; $P < 0.0001$), while a trend of increasing heat tolerance was found for *M. hargitti* ($t = 1.86$; $P < 0.066$). We expected that in specimens for which photosynthesis was chemically inhibited, we would no longer find an effect of light intensity on heat tolerance, and our results for *B. antilliensis* fit this expectation best. In this species, we found a significant interaction between monolinuron and light intensity ($F = 6.07$; $P = 0.015$), such that in monolinuron treated specimens' light intensity had a much smaller effect on heat tolerance than in untreated photosynthetic specimens. Taken together, these results support the hypothesis that heat tolerance can be limited by insufficient oxygen [7,11,14], since boosting tissue oxygen levels via photosynthesis improved heat tolerance, while inhibiting photosynthesis reduced heat tolerance.

Our results also highlight that mechanisms other than oxygen production are likely at play. An effect of light intensity on heat tolerance was found in chemically inhibited *B. antilliensis* and *C. cf. xamachana* specimens. Since visual systems and visually-guided behaviors are common in cnidarians

[27,28], a link between light exposure and various physiological processes including thermal tolerance is plausible. In this light (pun intended), it is interesting that *C. cf. xamachana*, the only species with a well-developed visual system and light-dependent behaviors during non-larval ontogenetic stages [29] displayed the strongest increase in oxygen consumption when exposed to high light (Fig 2B), and showed the strongest response to light in heat tolerance when inhibited. Thus, perhaps this species anticipates warmer water when perceiving light, leading to physiological changes that improve heat tolerance and increase metabolic energy demand. Understanding why light influences heat tolerance in our study species will require further study, but it does indicate that light can affect heat tolerance via mechanisms unrelated to oxygen. This is an important caveat for studies that have documented relationships between light-induced diel fluctuations in oxygen levels and improved heat tolerance in aquatic fauna [30].

Photosynthesis not only provides animals with oxygen, but also photosynthates such as glucose. A lack of oxygen and hence energy during experimental ramping trials can be partly compensated via anaerobic metabolism and upregulation of pathways such as the pentose phosphate pathway, which constitutes a major metabolic hub with connections to glycolysis and the TCA cycle [11], and which also helps to explain effects of starvation on heat tolerance [14]. However, in our study, consistent differences across specimens in rates of photosynthesis and hence glucose storage prior to experimentation is unlikely because animals were allocated to different light intensities after the inhibition of photosynthesis and just before we started the respiration and thermal tolerance trials.

In conclusion, we show that heat tolerance is modulated by light intensity in two of the three species studied. The reduced heat tolerance following chemical inhibition of photosynthesis indicates a role for tissue oxygen levels and lends support to the hypothesis that oxygen limitation can affect heat tolerance. Since, these patterns differ across species, and light perception and mounting anticipatory responses are likely also involved, there is a high probability that mechanisms unrelated to oxygen are also key factors in determining heat tolerance.

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Data accessibility

All data is available by reasonable request from EMJL.

Ethics statement

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

Author contributions

Both authors conceived of the study, analyzed the data, prepared the figures, wrote the first draft of the manuscript and edited subsequent drafts. EMJL conducted the preliminary experiments, tested the equipment, collected the specimens and data in the field, and acquired funding to conduct this research.

Competing interests

The authors declare they have no competing interests.

Supplementary Materials for "Does heat tolerance vary with rates of oxygen production in photosymbiotic cnidarians?" by EMJL Laetz and WCEP Verberk (submitted in 2024).

- **Supplementary Info 1** Detailed methods for measuring oxygen consumption / production
- **Supplementary Table 1** Overview of treatments and number of specimens used.
- **Supplementary Table 2** Summary statistics from the O_2 experiments.
- **Supplementary Table 3** Summary statistics from the Critical Thermal limit experiments.

Supplementary Info 1: Detailed methods for measuring oxygen consumption / production

To measure the metabolic rate of each specimen, it was placed in a respiratory chamber (glass jar), containing aerated seawater (with or without monolinuron) and a PSt3 optical sensor (Presens GmbH, Germany). A Fibox 4 Trace (Presens GmbH, Germany) was used to record the oxygen saturation in each respiratory chamber, which was measured every 6 minutes for an hour. Before experimentation, the Fibox was calibrated using 2-point calibration (100% O2 saturated seawater and 0% oxygen: nitrogen gas). Both *B. antillinesis* and *M. hargitti* were measured in 2ml chambers, whereas the larger *C.* cf. *xamachana* was measured in 22ml chambers. Once the specimen was in the chamber, the entire chamber was placed back in the tank where the animal had been housed for 30 minutes, with the lid off to ensure the water in the chamber could mix with the rest of the aerated water in the tank. This provided each specimen some time to recover from the stress of moving to a new environment, and, for the anemones, time to reattach their pedal discs to the chamber wall as a new substrate, without affecting the oxygen saturation in the chamber. After this recovery period, the chambers were closed, ensuring no air bubbles were contained within the chamber and that water could no longer mix. Each chamber was then placed in a larger water bath to maintain a stable temperature.

To examine oxygen uptake or release during the respirometry experiments, specimen volumes were first subtracted from the total chamber volume (2ml or 22ml) resulting in the actual amount of water (and hence oxygen) in the chamber (i.e. larger specimens take up more space so less water is therefore contained in these chambers). Measuring the volume of water displaced by *B. antilliensis* and *M. hargitti* was not possible due to their small size, so it was estimated using a density proxy (1.14 g/l) that was empirically derived from very large *B. antilliensis* specimens (pedal disk diameter 3-4cm) found at the same location as the smaller ones used in this study. The initial and final oxygen saturations (%) were converted to O_2 concentrations in $mgO_2\ L^{-1}$ by determining how much oxygen (mg) is found in 1L of seawater at 26°C and 35 PSU using an online calculator: https://water.usgs.gov/water-resources/software/DOTABLES/ - U.S. Geological Survey, 2018, and then calculating the amount of O_2 actually inside the chamber. The final O_2 concentration was then subtracted from the initial, yielding the change in O_2 concentration during the experiment. Then the background (microbial) respiration was subtracted. This value was then divided by the time the experiment ran resulting in an amount of O_2 that was produced/consumed by each specimen in one hour (mg O_2 produced/consumed h^{-1}).

Since rates of oxygen uptake scale allometrically with body mass [1,2], we could not express rates of oxygen uptake on a per gram basis. Instead, we corrected rates of oxygen uptake using a scaling exponent (0.61) that was derived empirically based on the mass of the specimens and the metabolic rates measured in this study. Therefore, metabolic rates are presented as mg O_2 produced/consumed $g^{-0.61}\ h^{-1}$. This accounts

for the effect of mass on metabolic rate and ensures that the remaining variation explained in our statistical analyses is due to our treatments rather than variation in mass across our specimens.

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Supplementary Table 1 Overview of treatments and number of specimens used. The high-light treatment matches the light intensity measured in the field.

	high light 1600 µmol $m^{-2}s^{-1}$	moderate light 700 µmol $m^{-2}s^{-1}$	low light 100 µmol $m^{-2}s^{-1}$
Non-monolinuron-treated (photoysnthetic)	n=9 of each species	n=9 of each species	n=9 of each species
monolinuron-treated	n=9 of each species	n=9 of each species	n=9 of each species

Supplementary Table 2 Summary statistics from the O_2 production/consumption experiments. Since "Light intensity" had three levels, we log transformed it to account for non-linear effects. The best-fit model allowed interactions between the predictors, "Species", "log10Light" and "Monolinuron".

term	estimate	std.error	t value	p value
(Intercept)	-0.072	0.018	-3.93	**0.00013**
SpeciesCassiopea_xamachana	0.027	0.026	1.028	0.31
SpeciesMyrionema_hargitti	-0.00048	0.026	-0.018	0.99
log10Light	0.028	0.0067	4.13	**6.05E-05**
Monolinuron_y	-0.015	0.026	-0.59	0.56
SpeciesCassiopea_xamachana : log10Light	0.0091	0.0095	0.96	0.34
SpeciesMyrionema_hargitti : log10Light	0.014	0.0096	1.49	0.14
SpeciesCassiopea_xamachana : Monolinuron_y	0.096	0.037	2.61	**0.0098**
SpeciesMyrionema_hargitti : Monolinuron_y	0.049	0.037	1.33	0.18
log10Light : Monolinuron_y	-0.010	0.0095	-1.10	0.27
SpeciesCassiopea_xamachana : log10Light:Monolinuron_y	-0.053	0.013	-3.91	**0.00014**
SpeciesMyrionema_hargitti : log10Light:Monolinuron_y	-0.035	0.014	-2.58	**0.011**

Supplementary Table 3 Summary statistics from the Critical Thermal limit experiments. The best fit model included interactions between the predictors “Species”, “log10(Light)” and “Monolinuron” as well as an interaction between “CT_type” and “Species” and additive effects from “CTtype”.

term	estimate	std.error	t value	p value
(Intercept)	28.74	1.012	28.39	**7.38E-88**
CTtype	3.16	0.13	23.85	**7.05E-72**
SpeciesCassiopea_xamachana	0.30	1.43	0.21	0.83
SpeciesMyrionema_hargitti	5.50	1.43	3.84	**0.00015**
log10Light	1.68	0.37	4.52	**8.83E-06**
Monolinuron_n	-2.43	1.43	-1.70	0.091
CTtype : SpeciesCassiopea_xamachana	-1.87	0.19	-9.99	**1.54E-20**
CTtype : SpeciesMyrionema_hargitti	-1.30	0.19	-6.91	**2.86E-11**
SpeciesCassiopea_xamachana : log10Light	1.47	0.52	2.80	**0.0054**
SpeciesMyrionema_hargitti : log10Light	-1.16	0.52	-2.21	**0.028**
SpeciesCassiopea_xamachana : Monolinuron_n	4.90	2.025	2.42	**0.016**
SpeciesMyrionema_hargitti : Monolinuron_n	3.73	2.03	1.84	0.067
log10Light : Monolinuron_n	1.53	0.52	2.92	**0.0037**
SpeciesCassiopea_xamachana : log10Light:Monolinuron_n	-1.89	0.74	-2.55	**0.011**
SpeciesMyrionema_hargitti : log10Light:Monolinuron_n	-1.48	0.75	-1.99	**0.048**