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RESEARCH ARTICLE

Ecophysiology of two mesophotic octocorals intended for restoration: Effects of light and temperature

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Abstract

Light and temperature are driving forces that shape the evolution and physiology of mesophotic organisms. On the Mississippi-Alabama continental shelf, octocorals dominate the mesophotic seascape and provide habitat for many fish and invertebrate species. Gaps in knowledge regarding the fundamental physiological responses of these species to light and temperature are of particular interest to restoration activities following the *Deepwater Horizon* oil spill. To address these gaps, the photobiology and thermal tolerance of *Swiftia exserta* and *Muricea pendula* were assessed in the field and laboratory. Pulse amplitude modulated fluorometry, histology, light microscopy, and epifluorescence imaging revealed low densities of photosynthetic endobionts in samples of *S. exserta* and none in samples of *M. pendula* collected near the determined bottom of the euphotic zone (51.45 m). Response to the recorded monthly mean habitat temperature range (18.5–25.4°C) was assessed using respirometry and polyp activity data from live corals exposed to temperatures between 18°C and 26°C. There was no significant difference in oxygen consumption for either species between 18°C and 26°C, and calculated Q_{10} values were not significantly different from 1, thus suggesting that both species have a low sensitivity to the local thermal environment. However, a negative correlation between temperature and polyp activity suggests that *M. pendula* is more sensitive to higher temperatures than *S. exserta*. This study improves the understanding of the effects of light and temperature on mesophotic octocoral physiology and lays the foundation for future work to explore the thermal thresholds of each species and the endobiont–host relationship in *S. exserta*.

Coral reefs are subject to a suite of chronic and acute stressors that have resulted in an unprecedented decline in their overall health and abundance (Pandolfi et al. 2003; Bellwood et al. 2004; De'ath et al. 2012). Mesophotic coral ecosystems are no exception to this decline, with an increase of stressor events, such as thermal bleaching within the upper mesophotic zone (30- to 50-m depth) (Smith et al. 2016). One of the most recent catastrophic events to affect a mesophotic coral ecosystem was the *Deepwater Horizon* oil spill in 2010 with 3.2 million barrels of crude oil released onto the Mississippi-Alabama continental shelf over 87 d (USA v. BP 2015). The *Deepwater Horizon* oil spill caused high incidence of injury to gorgonian octocorals, which are some of the most ubiquitous structure-forming organisms in mesophotic habitats on the Mississippi-Alabama shelf (Silva et al. 2016). In the wake of the *Deepwater Horizon* oil spill, there has been interest in using laboratory-based propagation as a method of active restoration for gorgonian corals at impacted mesophotic habitat sites.

Assessing physiological responses to abiotic factors is critical to optimizing restoration efforts for success. Growth rate and survivorship are the most common criteria assessed for determining the suitability of a species for active restoration

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(Bostrom-Einarsson et al. 2020). Techniques important to propagating corals in the laboratory, such as enhancing growth rate and spawning, are often influenced by light and temperature (Rodolfo-Metalpa et al. 2008; Kaniewska et al. 2015; Merck et al. 2022). As such, understanding an organism's physiological relationship with light and temperature is crucial to informing aquaria conditions for laboratory-based propagation and field-based outplanting.

Understanding mesophotic gorgonian habitat preferences and their relationship with temperature and light levels can provide key insights into their ecophysiology, which is critical to guide restoration actions. Light and temperature are known to shape mesophotic coral ecosystems, leading to high amounts of endemic and rare species (Hinderstein et al. 2010). These abiotic factors change with depth, forming gradients in the water column. As depth increases, temperature decreases and light intensity declines exponentially, creating enrichment in blue-green wavelengths (Kirk 2011; Slattery et al. 2024). Dense assemblages of gorgonian octocorals provide shelter, feeding areas, and nurseries for many commercially important species and are common worldwide (Lasker et al. 2003; Sánchez et al. 2019). However, while some gorgonian species are depth generalists that span shallow to mesophotic depths, others are depth specialists that occur in only limited light and temperature conditions (Kahng et al. 2010). To best inform laboratory-based propagation, understanding the ranges of the abiotic factors on mesophotic coral habitats and the corals' physiological responses is crucial.

The method of energy acquisition is another important factor to consider for successful coral propagation activities. Evaluating the role of light in metabolism has been generally inferred rather than empirically tested in many mesophotic corals. Mississippi-Alabama continental shelf mesophotic species *Swiftia exserta* and *Muricea pendula* are presumed to rely solely on heterotrophy for energy acquisition (Sánchez et al. 2019). However, some mesophotic corals can also acquire energy through autotrophy via mutualistic symbiosis with intracellular algae in the family Symbiodiniaceae (LaJeunesse et al. 2018). Other mesophotic octocorals previously assumed to be asymbiotic have been found to possess Symbiodiniaceae (Wagner et al. 2011; Vicario et al. 2024). These endobionts depend on photosynthetically active radiation (PAR) to obtain energy for photosynthesis, which is often used to meet the metabolic demands of the host (Muscatine 1990). Efficient use of low photon flux densities allows for many algae-hosting corals to survive in dimly lit environments where irradiance can be as low as 1% of the surface irradiance (Kahng and Kelley 2007; Pyle et al. 2016; Backstrom et al. 2024). Studies have also found that Symbiodiniaceae can be mixotrophic at depths below the photic zone with plastic transcriptomic responses to growth in complete darkness when supplied with prey of bacteria and microalgae (Jeong et al. 2012; Xiang et al. 2015; Backstrom et al. 2024). Evidence of a symbiotic relationship is imperative to successful laboratory propagation as well as overall health and survivorship of the species.

A species' metabolic response to temperature provides key information on its sensitivity to thermal stressors. Thermal stress events are increasingly common and severe, with increased incidence of large-scale shallow-water coral mortality occurrences (Heron et al. 2016; Sánchez et al. 2014). These thermal events may also pose a threat to mesophotic corals (Smith et al. 2016; Gugliotti et al. 2019; Diaz et al. 2023). It had previously been assumed that depth creates a buffer from warm-water anomalies; however, temperatures are increasing in mesophotic coral ecosystems (Frade et al. 2018). Increases in water temperature have been associated with changes in metabolic demand (Lesser 1997) and reproductive output (Michalek-Wagner and Willis 2001), or it can induce bleaching if Symbiodiniaceae are present (Diaz et al. 2023). This in turn could negatively impact its growth rate and spawning capabilities. Understanding its thermal tolerances within the temperature ranges it currently experiences provides information on its sensitivity to temperature, which can be used to optimize growth in nurseries.

The objective of this study was to determine key ecophysiological characteristics of *S. exserta* and *M. pendula*, two mesophotic gorgonian corals that were adversely impacted by the *Deepwater Horizon* oil spill and that are intended to be propagated for restoration activities. This information is needed to optimize aquarium conditions for laboratory-based propagation and field-based outplanting. The first aim of this study was to determine the lower limit of the euphotic zone and characterize the complete range of temperatures where these species are abundant. The second and third aims of this study were to investigate the presence of endobionts in the octocorals and understand the physiological response of octocorals to their experienced temperature range. An understanding of the ecophysiological relationship of *S. exserta* and *M. pendula* with light and temperature is essential for optimizing their growth and characterizing their potential for active restoration activities in response to the *Deepwater Horizon* oil spill.

Materials and methods

Study sites

Samples of *S. exserta* (Duchassaing and Michelotti, 1864) and *M. pendula* (Verrill, 1864) were collected from mesophotic sites on the Mississippi–Alabama continental shelf, and additional samples of *S. exserta* were collected at Edisto Reef offshore the South Carolina coast (Fig. 1; Supporting Information Table S1). Light and temperature were characterized at the collection and adjacent sites on the Mississippi–Alabama shelf, and temperature was characterized on Edisto Reef.

Irradiance on the Mississippi-Alabama shelf was measured at six sites with a high abundance of *S. exserta* and *M. pendula*

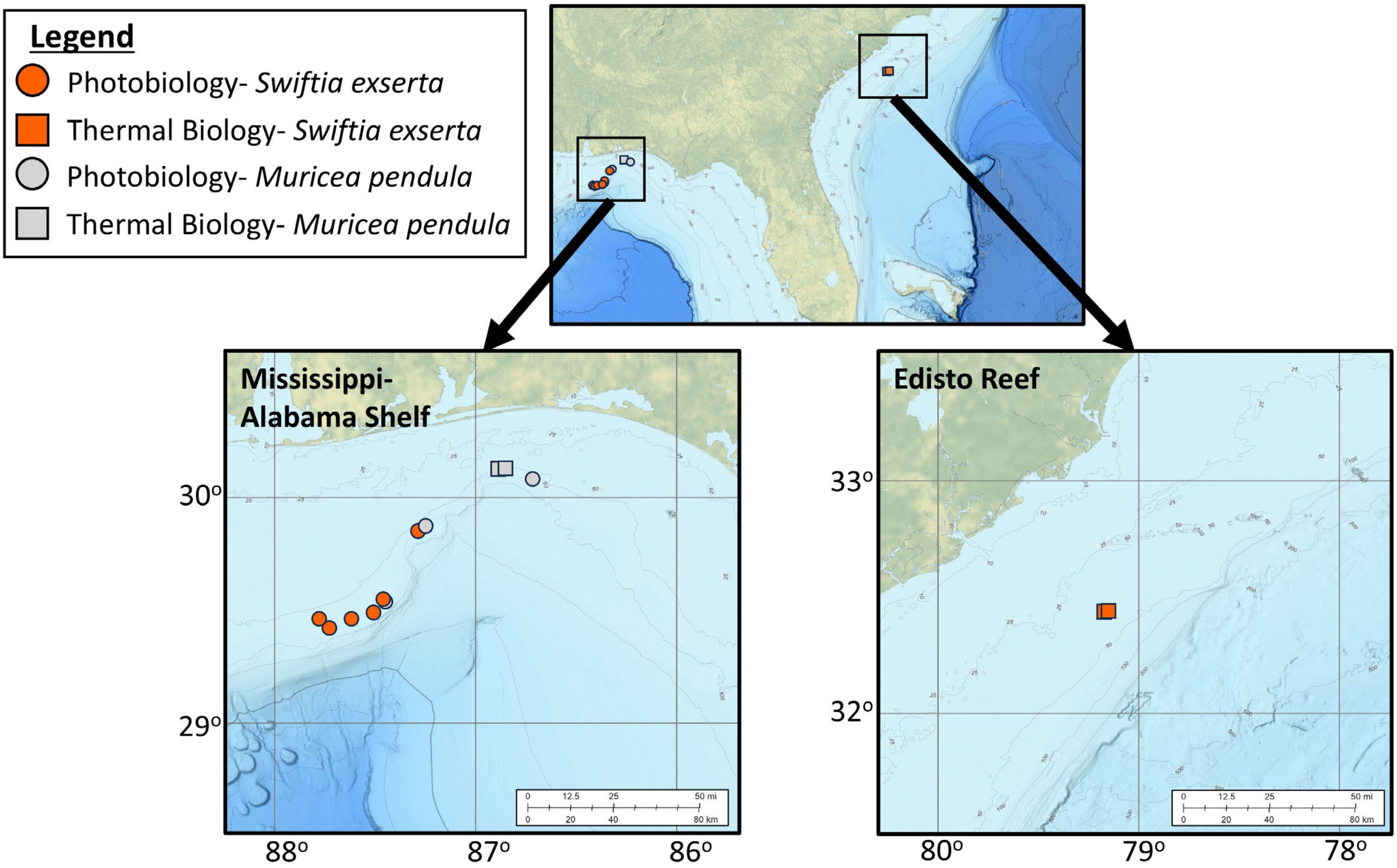

Fig. 1. Collection sites of octocorals. Circles indicate sites where samples were collected for photobiology, and squares indicate sites where samples were collected for thermal biology. *Swiftia exserta* samples are denoted in orange, and *Muricea pendula* samples are denoted in gray.

during October 2022 (Supporting Information Table S2). A conductivity, temperature, and depth (CTD) rosette with a calibrated PAR Biospherical LI-COR LI-192 quantum sensor (LI-COR, USA) was lowered to coral depth (50–114 m) midday on calm, clear days with the vessel oriented to avoid shadows. The scalar irradiance (E_0; Kirk 2011) was measured at a rate of 24 scans per second from the water surface to the ocean bottom. The vertical attenuation coefficients for scalar irradiance (K_0) from the downcasts of the CTD profiles were calculated using Beer's Law (Kirk 2011). The logarithmic scalar irradiance values were plotted against depth to verify the uniformity of the water column ($R^2 > 0.98$). The mean lower limit of the euphotic zone—the 1% surface irradiance—was calculated by dividing the constant of 4.6 described in Kirk (2011) by the calculated mean vertical attenuation coefficient from the six casts. Temperature at mesophotic depths on Mississippi-Alabama shelf sites (Supporting Information Table S3) was assessed using continuous UTBI001 temperature loggers (HOBO, Onset, USA) deployed from June 2022 to May 2023 ($n = 2$) and May 2023 to August 2024 ($n = 4$) with sampling intervals of 15 min at sites between 55 and 65 m. Loggers were deployed over the side of the vessel and then repositioned to coral habitat of the two species of interest by the remotely operated vehicle (ROV).

Temperature was characterized on Edisto Reef; however, the light environment has not been assessed. Conductivity, temperature, and depth data from the Southeast Area Monitoring and Assessment Program South Atlantic (SEAMAP) of the National Marine Fisheries Service was received from the South Carolina Department of Natural Resources to determine the bottom temperature range on Edisto Reef patches (49–64 m) from 2013 to 2023.

Respirometry

Specimens of *M. pendula* ($n = 6$) were collected on the Mississippi-Alabama shelf in October 2021 from 50 to 65 m using the ROV *Mohawk* (University of North Carolina Wilmington [UNCW]). Branched samples (length = 0.1–0.2 m) were collected from the distal portion of large source colonies (height = 0.5–1 m) using a five-function manipulator arm (ECA Hytec, ARM Micro 5E, France). Due to the difficulty of acquiring samples for experimentation, specimens of *S. exserta* ($n = 6$) were collected from Edisto Reef off the South Carolina coast in March 2021 from 50 to 65 m also using ROV *Mohawk*

(UNCW) and the R/V *Point Sur* (Fig. 1; Supporting Information Table S1). Edisto Reef's ecosystem has similar species assemblages and characteristics to the Mississippi-Alabama shelf habitats (NOAA Deep Sea Coral and Sponge Portal, https://www.ncei.noaa.gov/maps/deep-sea-corals/mapSites.htm, accessed February 2, 2023), and Edisto Reef and Mississippi-Alabama shelf populations of *S. exserta* are similar genetically with the same prominent haplotype (Frometa et al. 2021).

Live samples from both expeditions were stored aboard the ship for 1–2 d in a chest freezer held at −18°C with water changes every 12 h using bottom water from CTD Niskin bottles. Upon deboarding, live samples were immediately shipped back in 3.7-L jars filled with seawater in an insulated container at 18–22°C. Samples arrived within 48 h to Hollings Marine Laboratory in Charleston, SC, and immediately were acclimated and transferred to a 200-gal mesocosm. The system was supplied with artificial seawater (Red Sea Coral Pro). Water temperature, pH, and salinity were recorded daily, while ammonia, nitrite, nitrate, calcium, and phosphate levels were recorded weekly. Corals were mounted to aragonite Aquadome (ReefSmart, USA) bases using Coral Glue (EcoTech Marine, USA) and positioned upright oriented in the direction of flow to emulate their posture in their natural habitat. Each colony was target-fed 5 mL from a mixture of 400 mL seawater containing: one 1-g cube of frozen baby *Artemia* spp., one 1-g frozen cube of *Calanus* spp., and 1 tsp. of Reef-Roids® (Polyp Lab®, USA) once daily. Fragments of *S. exserta* and *M. pendula* were held in aquaria for 17 and 10 months, respectively, prior to experimentation.

A total of six 6-cm fragments each of *S. exserta* and *M. pendula* were used to assess thermal performance within their observed habitat temperature range from 18°C to 26°C. Closed-system respirometry was used to measure oxygen consumption at 18°C, 22°C, and 26°C within a temperature-controlled environment at Hollings Marine Laboratory. Oxygen saturation in the closed systems ranged from 80% to 100%. To maintain standardized conditions across trials and to ensure full oxygen saturation at the onset of new measurement, the respirometry chambers were flushed after each individual trial at each of the three experimental temperature treatments. Fragments were initially acclimated for 5 d at 18°C prior to pO_2 ($mg\,L^{-1}$) measurement. The temperature was then raised by 0.5°C daily and held at the next target temperature for another 5-d acclimation period. All measurements were taken in the dark to account for possible metabolic activity of photosynthetic endo- or epibionts.

Respirometry chambers were constructed using a 250-mL glass jar with an elevated platform to position the coral fragment and a stir bar beneath to ensure homogeneous mixing throughout the chamber. The lid was modified with a sealed cord grip to accommodate the fiber optic O_2 sensor. Background activity was measured for 15 min in the sealed chamber with ambient tank water prior to the first fragment being moved into the chamber, and the rates were determined to be negligible at each temperature. Continuous measurements of pO_2 ($mg\,L^{-1}$) were made using an Oxy-4 Mini oxygen-sensing system (PreSens, Germany) every 15 s for 12 h, and then the chamber water and fragments were replaced. Measurements on each individual fragment were repeated at 18°C, 22°C, and 26°C.

To calculate the oxygen consumption rate, the volume of the coral was first measured prior to beginning respiration measurements using a water displacement method that avoided handling effects. Then coral oxygen consumption rate ($\mu mol\,h^{-1}\,mL^{-1}$) was calculated following the methods of Krueger (2019). Additionally, Q_{10} values were determined for each species. This value describes how the rate of a physiological process changes with a 10°C rise in temperature and is often used to describe the dependence of metabolism on temperature (Mundim et al. 2020). Q_{10} values were calculated using the following equation:

$$Q_{10} = \left(\frac{R_2}{R_1}\right)^{\left(\frac{10}{T_2 - T_1}\right)} \tag{1}$$

In this equation, R_1 is the oxygen consumption rate for an individual at T_1 (18°C), and R_2 is the oxygen consumption rate for the same individual at T_2 (26°C).

Polyp activity with temperature

Polyp activity and temperature were recorded once daily during the duration of the respirometry experiment. The polyp activity was monitored continuously throughout a 1-h window (11:00 AM–12:00 PM) each day. Fragments received a score of "0" if < 50% of the polyps opened during the monitoring period, and "1" if > 50% of the fragment's polyps were open at any point during the monitoring period. The proportion of measurements with > 50% of polyps open at a given temperature was then calculated. The number of sample points at a given temperature varied from 6 to 60, dependent on how many days the coral was held at each temperature throughout the respirometry experiment, with the most datapoints derived from acclimation periods.

Pulse amplitude modulated fluorometry

To test for the presence of photosynthetic endobionts in *S. exserta* and *M. pendula*, photosynthetic activity was measured using a pulse amplitude modulated (PAM) fluorometer (Junior-PAM, Walz, Germany). Samples of *M. pendula* ($n = 5$) and *S. exserta* ($n = 5$) were collected from 50- to 70-m depths on the Mississippi–Alabama shelf in June 2022 (Fig. 1; Supporting Information Table S1) using the ROV *Mohawk* (UNCW). Branching samples (length = ~ 0.2 m) were collected with the lights off, and only one individual was collected per dive to be brought to the surface using a dark-adapted holding chamber on the ROV. Upon retrieval, the sample was immediately brought into a dark wet lab on the R/V *Point Sur* for PAM fluorometry measurements.

Dark-adapted measurements of fluorescence were taken on five colonies of each species using a blue excitation beam (460 nm, Gain = 2, Freq. = 3, Int. = 9). The variable fluorescence was calculated using the minimum (F_0) and maximum (F_m) fluorescence values through the equation $F_v = F_m/F_0$ (Ralph and Gademann 2005; Padilla-Gamiño et al. 2019). The presence or absence of a maximum quantum yield value of photosystem II (F_v/F_m; unitless) indicated photosynthetic material within *S. exserta* and *M. pendula*. On each colony, 20–22 haphazard, spatially separated (at least 3 cm) yield measurements were taken to account for spatial variation in coral physiology. If a fragment of either *S. exserta* or *M. pendula* displayed a consistent positive maximum quantum yield, that specimen was further investigated using histology and epifluorescence microscopy.

Histology

Subsamples of *S. exserta* ($n = 5$) and *M. pendula* ($n = 5$) collected for PAM measurements were promptly preserved upon collection in June 2022 in 10% buffered formalin. After 24 h, the samples were transferred to 70% ethanol for shipment back to Hollings Marine Laboratory for further processing. Samples were decalcified using RDO Rapid Bone Decalcifier (Globe Scientific, USA) and then dehydrated in a graded ethanol series to absolute ethanol and cleared with toluene. Samples were then transferred into paraffin using a HistoCore Pearl automatic processor (Leica Biosystems, USA) and embedded in wax blocks. A rotary microtome was used to cut 6-μm thick sections, which were then mounted on slides and stained using hematoxylin and eosin. Slides were examined for the presence or absence of endobionts under a compound microscope at 40× magnification. When present, the diameter of a subset of the endobionts (identified opportunistically; total $n = 5$) was measured using the average Feret's diameter in ImageJ (Schneider et al. 2012).

Endobiont determination

Two pieces of tissue (2 cm) were excised each from three healthy *S. exserta* fragments collected from 65 to 70 m depths on the Mississippi-Alabama shelf in October 2022 using the ROV *Mohawk* (UNCW; Fig. 1; Supporting Information Table S1). Polyps and coenchyme were micro-dissected from each branch and observed separately. First, all samples were observed under an epifluorescent microscope (Zeiss Axioskop 2 FS, Zeiss, Germany; 534/59 nm excitation and 630–69 nm emission) to determine the presence of endobionts. Endobiont density within these tissues was visualized and enumerated with a hemocytometer (Strehlow et al. 2016) following multiple centrifugations and washing steps. Polymerase chain reaction (PCR) amplification of isolated algal cells was attempted numerous times with multiple published primer sets and protocols (Hume et al. 2018) to genetically identify the endobiont. Polymerase chain reaction products were verified by electrophoresis and an Agilent 2100 Bioanalyzer (Agilent, USA) for correct target size and then sequenced. Results were nucleotide blasted through the National Center for Biotechnology Information database (http://blast.ncbi.lnm.nih.gov).

Statistical analyses

Comparisons of endobiont densities and maximum quantum yield were each performed using a one-way ANOVA and Kruskal–Wallis test, respectively. A two-way ANOVA was performed to compare oxygen consumption rate between species and temperatures. Normality was assessed using Shapiro–Wilk tests, and homogeneity of variances was tested using Levene tests prior to all analyses. Endobiont density and oxygen consumption data were normalized using logarithmic transformations to obtain normality and homogeneity of variances as needed, and a Kruskal–Wallis test was used for the maximum quantum yield data when the transformation was not successful. Comparisons of oxygen consumption rates at the three temperatures for each species were performed using a nonparametric Friedman test with temperature to reduce error variance by measuring an individual fragment's response between the different temperature treatments. To test if the Q_{10} values were significantly different from 1, data were normalized using a cube root transformation, and then a t test was run. A Spearman nonparametric correlation test was used to test if there was a correlation between temperature and the proportion of colonies with open, active polyps. Statistical differences were defined as significant when $\alpha < 0.05$. All analyses were performed in R Studio version 2021.09.01. The datasets generated and/or analyzed during the current study are included and the code used in analyses is publicly available on GitHub at https://github.com/kassidylange/Ecophysiology-of-two-mesophotic-octocorals-code-and-data/tree/main.

Results

Site characterization

The mean (± SE) temperature across sites 55–65 m on the Mississippi-Alabama shelf was 21.25 ± 1.39°C, and the range in monthly mean temperatures was about 7°C—with the monthly mean temperature as high as 25.4 ± 1.7°C in September 2023 and as low as 18.5 ± 0.5°C in February 2024. The highest observed temperature was 29.1°C in September 2023, and the lowest observed temperature was 12.6°C in September 2022. A line fitted to the data displays a gradual increase in temperature into September–November when it begins to decline until February (Supporting Information Fig. S1A,B). Acute thermal stressor data was also observed from loggers deployed in 2022 when temperatures sharply dropped at both 55 and 65 m by 6–8°C over the course of 36 h when Hurricane Ian moved over the habitat. The monthly mean temperature on Edisto Reef similarly ranged from 18.8°C to

25.2°C over the course of 2013–2023 CTD data (SEAMAP-SA Data Management Work Group 2024).

The vertical attenuation coefficients (K_0) on the Mississippi–Alabama shelf ranged from -0.081 to -0.105 m^{-1} with a mean K_0 of -0.0894 ± 0.005 m^{-1} (± SE). The mean K_0 was used to calculate the 1% surface irradiance, or bottom of the euphotic zone, to be 51.45 m (Supporting Information Table S2). The measured irradiance at the bottom of the euphotic zone was 13.06 ± 1.86 μmol photons cm^{-2} s^{-1} (± SE).

Respirometry and polyp activity

There were no significant differences in respiration rate among the three temperature regimes—18°C, 22°C, and 26°C—for either species (Friedman test, $p = 0.846$ for *S. exserta*; $p = 0.447$ for *M. pendula*, Fig. 2; Supporting Information Table S4). This was further supported by calculated Q_{10} values, which were 1.240 ± 0.59 and 1.202 ± 0.57 for *S. exserta* and *M. pendula*, respectively. The Q_{10} values were not found to be significantly different from 1 (*t*-test, $p = 0.683$ for *S. exserta*; $p = 0.482$ for *M. pendula*). There was a significant difference in metabolic rates between the two species (two-way ANOVA, $p = 0.014$; Fig. 2; Supporting Information Table S5).

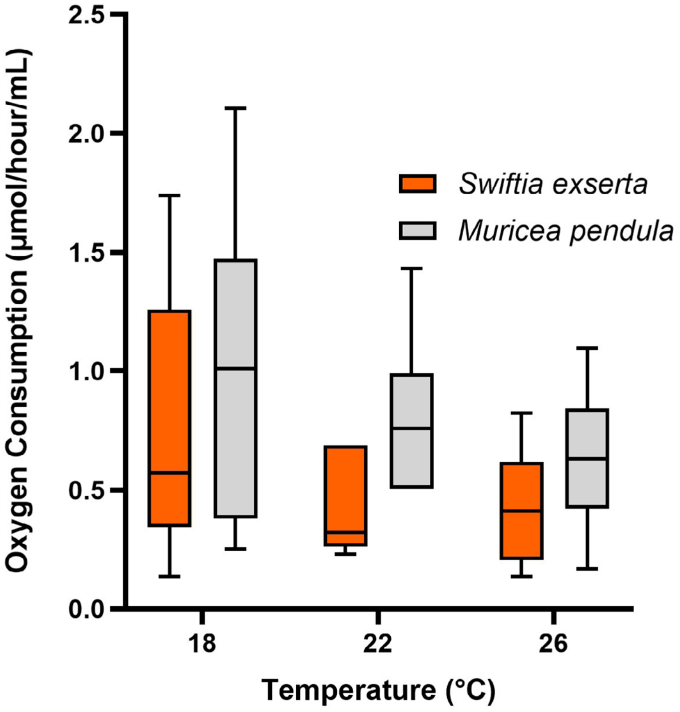

Fig. 2. Comparison of oxygen consumption rates across temperatures for *Swiftia exserta* ($n = 6$) and *Muricea pendula* ($n = 6$). Boxplot displays median and upper/lower quartile with whiskers including the complete range of values. There was a significant difference between the two species (two-way ANOVA; $p = 0.014$) but no significant difference in metabolic rate between the three temperature regimes (Friedman test; $p_{Swiftia} = 0.846$; $p_{Muricea} = 0.447$).

The effect of temperature on polyp activity was observed in *M. pendula*, but it was not observed in *S. exserta*. The correlation coefficient of *S. exserta* between polyp activity and temperature was not significant (Spearman correlation test, $R = 0.217$; $p = 0.4025$, Fig. 3a). However, *M. pendula* had a strong negative correlation (Spearman correlation test, $R = -0.624$; $p = 0.0074$, Fig. 3b), suggesting that the polyp activity significantly decreased as temperature increased.

Pulse amplitude modulated fluorometry

Low levels of photosynthetic activity were observed in *S. exserta*, and negligible amounts were detected in *M. pendula*. *Swiftia exserta* had maximum quantum yield values (mean ± SE) of 0.28 ± 0.03. All measurements in *S. exserta* were greater than zero. Maximum quantum yield values of *S. exserta* were significantly different from values of *M. pendula* (Kruskal–Wallis, $p < 0.001$; Fig. 4). Measurements in *M. pendula* were variable, with 44% of the values equaling zero, suggesting a total absence of photosynthetic material or a negligible abundance of endo- or epibionts.

Endobiont visualization and density

Scattered endobiont cells were identified in *S. exserta* sections in the outer epithelial polyp tissue of all five samples (Fig. 5). Five identified endobiont structures were measured to be approximately 8.964 ± 0.015 μm (mean ± SE) in diameter.

Additionally, Symbiodiniaceae-like structures of expected size (~ 10 μm), golden/brown, and coccoid morphology were visualized using light and epifluorescence microscopy in samples of *S. exserta* in both the polyps and coenchyme (Fig. 6a). Endobiont densities (mean ± SE) were significantly (one-way ANOVA, $p < 0.001$) greater in their coenchyme ($7.2 \pm 1.7 \times 10^4$ cells mg^{-1}) than in their polyps ($2.1 \pm 0.4 \times 10^4$ cells mg^{-1}) (Fig. 6b). No Symbiodiniaceae-like structures were identified in *M. pendula*. Polymerase chain reaction amplification of isolated algal cells from *S. exserta* was attempted numerous times; however, results were inconclusive, resulting in sequences having a high identity to uncultured *Symbiodinium*, but only at 33% coverage. Often, returned results also revealed identities to other soft corals and stony corals.

Discussion

Thermal tolerance, metabolism, and polyp activity

On the Mississippi-Alabama shelf, mesophotic habitats experienced a temperature fluctuation of up to 16.4°C over 2 yr of continuous temperature data from 2022 to 2024. This study found a mean monthly temperature range of 18.5–25.4°C, which includes temperatures higher than the upper thermal limits of similar mesophotic gorgonians experiencing wide in situ temperature ranges including *Eunicella singularis* and *Corallium rubrum* from the Mediterranean Sea and *Adelogorgia phyllosclera* from the Channel Islands (Torrents et al. 2008; Ezzat et al. 2013; Gugliotti et al. 2019). The broad range of temperatures on the Mississippi-Alabama shelf

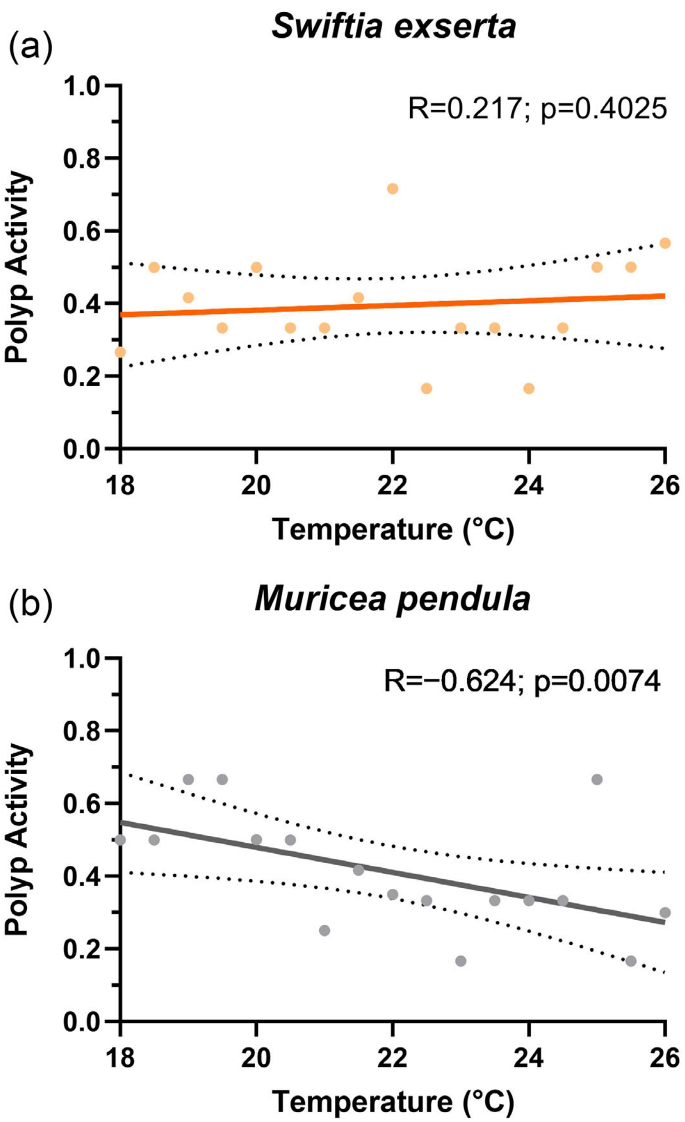

Fig. 3. The correlation between temperature and the proportion of colonies with active polyps (1 = open and feeding; 0 = closed and not feeding) for *Swiftia exserta* (**a**) and *Muricea pendula* (**b**). A Spearman correlation test found no strong correlation in *S. exserta* ($R = 0.217$; $p = 0.4025$) but a significant negative correlation in *M. pendula* ($R = -0.624$; $p = 0.0074$).

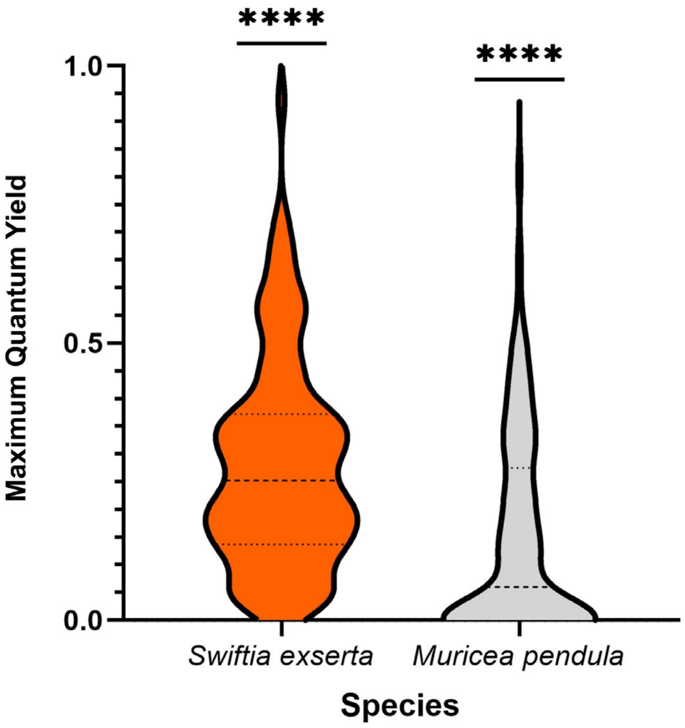

Fig. 4. Pulse amplitude modulated fluorometry measurements on octocoral species found that the maximum quantum yield was significantly higher (Kruskal–Wallis, $p < 0.001$) in *Swiftia exserta* ($n = 5$) than in *Muricea pendula* ($n = 5$) (20 measurements were taken per individual). The large distribution (44%) of maximum quantum yield values equaling zero is depicted for *M. pendula*.

prompted the questions to test physiological response: (a) are *S. exserta* and *M. pendula* within their optimal thermal performance range? and (b) is there a change in their respiration rate throughout the 18–26°C experienced range in temperature?

As with most Octocorallia, physiological response to temperature changes still remains poorly studied despite the increase in thermal stressor events in the mesophotic (Smith et al. 2016; Gugliotti et al. 2019; Diaz et al. 2023). This study found no significant metabolic change based on oxygen consumption in either species between 18°C and 26°C. Furthermore, calculated Q_{10} values were not found to be significantly different from 1, indicating a lack of temperature-dependent metabolism detected in the temperature range utilized. These results suggest that both *S. exserta* and *M. pendula* have a low sensitivity to the local thermal environment of 18°C and 26°C, likely due to a thermotolerance encompassing the local temperature gradient. This supports the climate variability hypothesis, which states that populations exposed to more fluctuating thermal environments tend to be less sensitive to temperature than those from more stable habitats due to evolutionary adaptation or physiological acclimation to greater temperature variability (Oliver and Palumbi 2011; Godefroid et al. 2023a; Godefroid et al. 2023b).

No known studies exist assessing thermotolerance of mesophotic octocorals on the Mississippi-Alabama shelf; however, similar work has been done in other regions. The studies that have evaluated the sensitivity of corals to their local thermal environment have reported varying levels of thermotolerance. High thermal sensitivity in four gorgonian species was demonstrated by Previati et al. (2010), who found that both oxygen consumption and polyp activity peaked between 18°C and 20°C, but declined at temperatures above and below 18°C or 20°C, suggesting sensitivity to the local thermal environment of 14–22°C. In two mesophotic Antipatharia coral species,

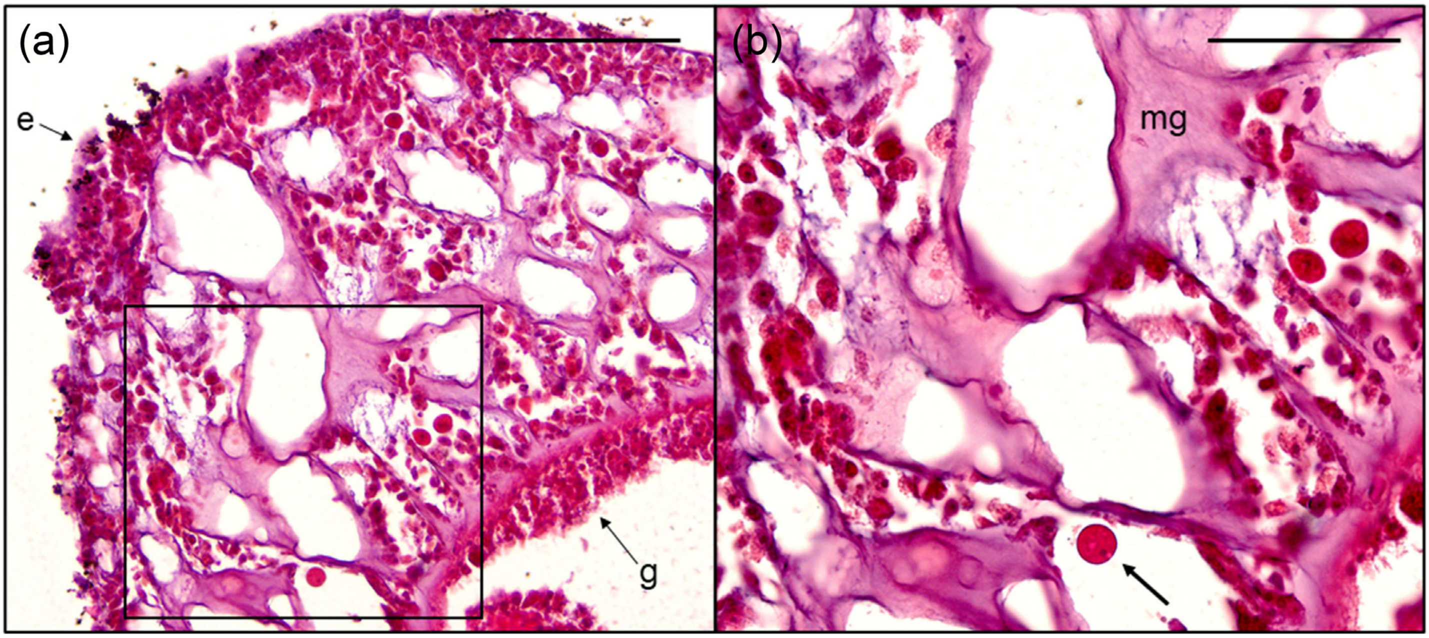

Fig. 5. Endobionts in a histological section of *Swiftia exserta* tissue. (**a**) Cross section of *S. exserta* tissue showing epidermis (e) and gastrodermis (g), and a low density of endobiont cells (*see* inset, b, for greater detail). This section is 7 μm thick and was stained with hematoxylin and eosin. Scale bar is 100 μm. (**b**) Higher magnification of the area indicated by the black box in (a), showing greater detail of an endobiont (arrow) and its location within the tissue. mg = mesoglea; scale bar is 50 μm.

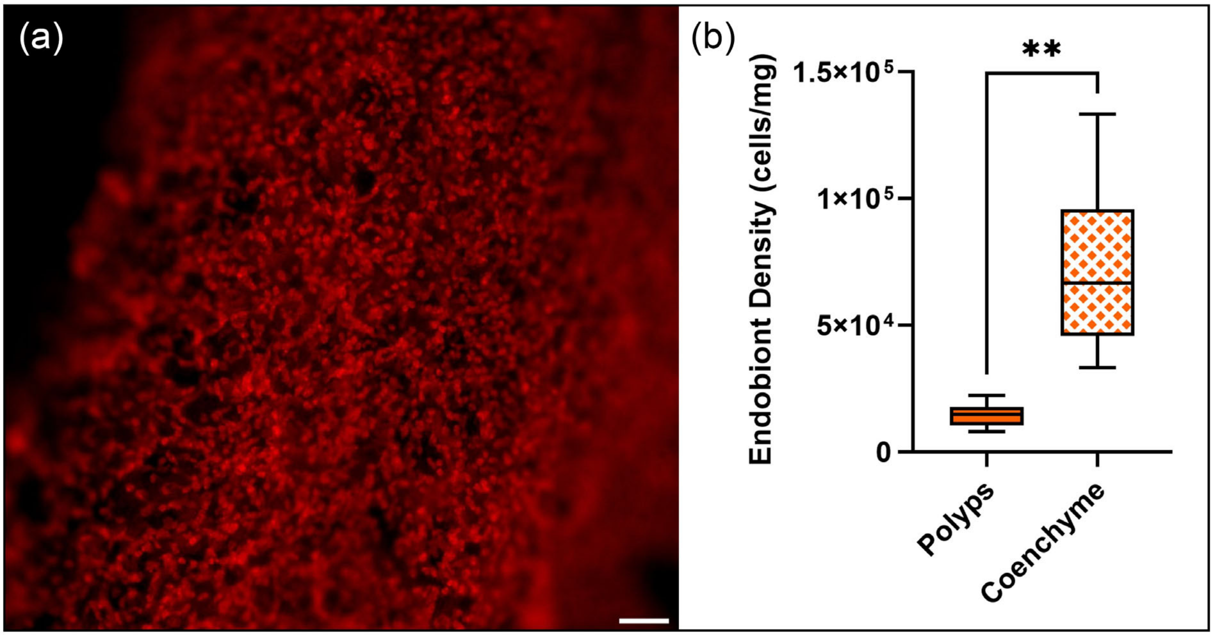

Fig. 6. Endobiont presence and density within *Swiftia exserta* tissue. (**a**) Epifluorescent microscopy image of *S. exserta* coenchyme, displaying the autofluorescence of internal photosynthetic spherical red cells. Scale bar is 100 μm. (**b**) Density of endobionts present within excised coenchyme and polyp tissues.

Godefroid et al. (2023b) demonstrated that colonies exposed to greater thermal variability across depth (*Antipathella wollastoni*, Gran Canaria) and between regions (*Stichopathes gracilis*, Lanzarote vs. Mo'orea) exhibited lower thermal sensitivity in their oxygen consumption rates, supporting the climate variability hypothesis that predicts higher thermal tolerance in populations from more fluctuating thermal environments. Similarly, this study found no significant differences in oxygen consumption for either species between 18°C and 26°C, suggesting that these corals are thermally tolerant and well adapted to their wide in situ temperature range.

Polyp activity is also reflective of respiration and metabolism in gorgonians. Expansion of the polyps can maximize both the diffusion/consumption of oxygen in the tissue and the feeding efficiency (Sebens and DeRiemer 1977; Shick 1990; Fabricius et al. 1995). Hence, decreased polyp activity has been characterized as a negative response in studies assessing thermal tolerance in gorgonians as it decreases when it reaches values close to their thermal tolerance limits (Gugliotti et al. 2019; Torrents et al. 2008; Previati et al. 2010). Previati et al. (2010) found that polyp activity increased up to 18°C or 20°C in all four species assessed and declined as each species reached its critical thermal maximum (CT_{max}). *Muricea pendula* polyp activity significantly declined as temperature increased from 18°C, suggesting that *M. pendula* may be approaching its CT_{max}. *Swiftia exserta* displayed consistent activity patterns in polyp expansion and contraction across temperatures, potentially suggesting that it may have a higher thermal limit than *M. pendula*. Future studies including additional temperatures above and below this current study's range can enable the construction of a comprehensive thermal performance curve and test the hypothesis that *M. pendula* is more stenothermal than *S. exserta*.

Slower-growing organisms often exhibit lower metabolic rates, reflecting reduced energy acquisition and allocation toward somatic growth and reproduction (Auer et al. 2018). Although *M. pendula* displayed significantly higher respiration rates than *S. exserta*, both species demonstrated low overall oxygen consumption compared to other octocorals, regardless of symbiont presence (Borrelli et al. 2021). These low respiration rates suggest inherently slow metabolic processes, consistent with the slow growth rates reported for these species (Lange and Etnoyer 2024a). As such, large (> 0.5 m) colonies of *S. exserta* and *M. pendula* are likely to be slow-growing, long-lived individuals; however, additional studies are needed to directly measure the age of these species.

Photobiology

The calculated lower limit of the euphotic zone (51.45 m) suggests that photosynthesis is possible at mesophotic depths on the Mississippi–Alabama shelf at the sampling time point in October 2022. These findings should be interpreted with consideration for seasonal and annual variability, which extends beyond the data's temporal scope in this study. Other studies in the region during the spring and summer have found the lower limits of the euphotic zone as deep as 72 m due to the higher water clarity during these seasons (Lange and Etnoyer 2024b).

Corals are known for complex symbiotic interactions with a wide range of microorganisms. The most well-studied symbionts are intracellular dinoflagellates of the family Symbiodiniaceae (Bourne et al. 2016; LaJeunesse et al. 2018). Typically, when these species are obligate symbionts of octocorals, they are found in high densities (2.0×10^6–8.0×10^6 cells cm^{-3}; McCauley and Goulet 2019) within the gastrodermis, where they photosynthesize and absorb nutrients, providing the host with their metabolic products (Muscatine 1990). However, the density of endobionts in the tissues of *S. exserta* was orders of magnitude lower ($0.8 \pm 0.4 \times 10^4$ cells cm^{-3}) than in shallow-water Caribbean gorgonians (Ramsby et al. 2014). Very low densities of Symbiodiniaceae in mesophotic and deep-sea corals at depths up to 655 m have been observed previously (Kaiser et al. 1993; Wagner et al. 2011; Pupier et al. 2021; Vicario et al. 2024). The mean maximum quantum yield values of *S. exserta* were also low (0.28) in comparison to other mesophotic corals. For example, Padilla-Gamiño et al. (2019) reported that *Leptoseris* spp. from 65- to 125-m depths had maximum quantum yield values at over twice the efficiency (0.65–0.67). Hence, the metabolic contribution of the photosynthetic endobionts in *S. exserta*, if any, is presumed to be negligible.

Symbiodiniaceae are the most studied anthozoan associates; however, there have also been numerous studies documenting the widespread prevalence of apicomplexan corallicolids (phototropic alveolate coral symbionts) in the tissues of shallow- and cold-water corals (Janouškovec et al. 2012; Kwong et al. 2019; Vohsen et al. 2020). Vohsen et al. (2020) reported that corallicolids with the plastotypes 7, 8, and 9 were documented in both mesophotic *M. pendula* and *S. exserta* collected from the same region on the Mississippi–Alabama continental shelf. However, some evidence suggests that these corallicolids cannot be involved in photosynthesis due to their lack of photosystem genes and the presence of light-independent protochlorophyllide oxidoreductase subunits in deep-water corals (Kwong et al. 2019; Vohsen et al. 2020). Therefore, PAM fluorometry and epifluorescence microscopy would not detect these corallicolids. The findings of this study suggest that photosynthetic endobionts are present in *S. exserta* tissue; hence, the identity does not align physiologically with corallicolids.

The low abundance and apparent preference for location outside of the gastrodermis makes the type of relationship between *S. exserta* and its endobionts unclear. This study found a significantly higher density of algal cells within the coenchyme compared to the polyps. Further, histology suggested that the endobionts are found in the outer epithelial tissue of the polyps in low densities. The endobionts did not visually display the stressed characteristics such as swelled cytoplasmic vacuolation that were observed in Landsberg et al. (2020), suggesting these endobionts are healthy. However, the abundance and location of the endobionts suggest that they are likely not significantly contributing to the host metabolic processes. In order to improve understanding of this endobiont–host relationship, additional metrics, including accurate identification of the type of endobiont present, as well as stable isotopes and lipid analysis, can help evaluate if metabolic energy transfer is occurring.

Conclusions and applications

Restoration efforts following the *Deepwater Horizon* oil spill include field-and laboratory-based coral propagation, with *S. exserta* and *M. pendula* identified as key octocoral candidates due to their ecological importance and documented decline (Silva et al. 2016). This study addresses knowledge gaps in their physiology by examining their responses to in situ temperature and light conditions, which can be utilized to calibrate tank systems to continue to support healthy, spawning corals for restoration work. Both species showed similar oxygen consumption across seasonal temperatures in the mesophotic. However, reduced polyp activity in *M. pendula* suggests it may be more sensitive to higher temperatures. Inclusion of a broader range of temperatures would provide data to construct a complete thermal performance curve and pinpoint an optimal temperature for both species. While endobionts were confirmed in *S. exserta*, much remains to be resolved about the nature of the relationship between the identified endobionts and their host, including their identity. By characterizing mesophotic habitats on the Mississippi–Alabama shelf and evaluating coral thermal responses, this work contributes critical insights to optimize propagation techniques and inform broader coral ecosystem management.

Author Contributions

Kassidy Lange was responsible for conceptualization, data curation, formal analysis, investigation, methodology, visualization, and writing (original draft preparation). Allisan Aquilina-Beck was responsible for investigation, methodology, and writing (review and editing). Mark McCauley was responsible for investigation, methodology, and writing (review and editing). Julia Johnstone was responsible for investigation and writing (review and editing). Amanda Demopoulos was responsible for resources, supervision, and writing (review and editing). Thomas Greig was responsible for resources, supervision, and writing (review and editing). Jody M. Beers was responsible for conceptualization, resources, methodology, investigation, supervision, and writing (review and editing). Heather L. Spalding was responsible for conceptualization, resources, methodology, investigation, supervision, and writing (review and editing). Peter J. Etnoyer was responsible for conceptualization, resources, funding acquisition, supervision, and writing (review and editing).

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Conflicts of Interest

None declared.

Data Availability Statement

The datasets generated and/or analyzed during the current study and code are publicly available on GitHub at https://github.com/kassidylange/Ecophysiology-of-two-mesophotic-octocorals-code-and-data/tree/main.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

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