

1 **Higher daily temperature range at depth is linked with higher thermotolerance in Antipatharians**  
2 **from the Canary Islands**

3 Mathilde Godefroid<sup>1</sup>, Adriana Gouveia<sup>2,3</sup>, Francisco Otero-Ferrer<sup>2</sup>, Fernando Espino<sup>2</sup>, Fernando Tuya<sup>2</sup>,  
4 Philippe Dubois<sup>1</sup>

5

6 <sup>1</sup>Marine Biology Laboratory, Université Libre de Bruxelles, Av. F.D. Roosevelt, CP 160/15, 1050  
7 Bruxelles, Belgium

8 <sup>2</sup>BIOCON, IU-ECOQUA, Parque Científico Tecnológico Marino de Taliarte, Universidad de las Palmas  
9 de Gran Canaria, 35214, Gran Canaria, Spain

10 <sup>3</sup>Department of Biology, University of Aveiro, 3810-193, Aveiro, Portugal

11

12 **Corresponding author:** Mathilde Godefroid

13 godefroid.mathilde1@gmail.com

14 Av. F.D. Roosevelt, 50 CP160/15, 1050 Brussels, Belgium

15

16

17 **Abstract**

18 Sensitivity to ocean warming is generally expected to be lower in populations from more  
19 heterogeneous thermal environments, owing to greater phenotypic plasticity and/or genotype  
20 selection. While resilience of benthic populations from thermally fluctuating environments has been  
21 investigated at a variety of spatial scales, this has received limited attention across depths and has  
22 remained unresolved for Antipatharian corals, key habitat-forming species across a wide bathymetric  
23 range in all of the world oceans. In this study, we aimed at addressing the thermal sensitivity of  
24 Antipatharian corals across depths characterized by different levels of temperature fluctuations. We  
25 used an acute ramping experimental approach to compare the thermal sensitivity of colonies of (1)  
26 the branched Antipatharian *Antipathella wollastoni* (Gray, 1857) from two distinct depths (25 and 40  
27 m) in Gran Canaria (Canary Islands, Spain); and of (2) unbranched mesophotic (80 m) *Stichopathes*  
28 species, from Lanzarote (Canary Islands, Spain; *S. gracilis* (Gray, 1857)), and *Stichopathes* sp. clade C  
29 from Mo'orea, French Polynesia. Results showed that the daily temperature range in Gran Canaria was  
30 larger at mesophotic depths (3.9°C vs. 2.8°C at 40 and 25 m, respectively) and this coincided with lower  
31 thermal sensitivity in mesophotic colonies of *A. wollastoni*. Second, *S. gracilis* from Lanzarote showed  
32 a lower thermal sensitivity than the previously studied *Stichopathes* sp. clade C from Mo'orea (French  
33 Polynesia) inhabiting a less variable habitat. These results are in line with the climate variability  
34 hypothesis, which states that populations under more variable thermal conditions have a lower  
35 sensitivity to warming than those from more stable environments, as they have adapted/acclimated  
36 to these higher levels of temperature fluctuations.

37

38 **Keywords**

39 Black corals, Thermotolerance, Marine Animal Forests, Acute ramping, *Stichopathes gracilis*,  
40 *Antipathella wollastoni*

41

## 42        **1. Introduction**

43        In the last IPCC report, scientists stated that increases in greenhouse gas concentrations from 1750  
44        have been unequivocally caused by human activities (Cooley et al., 2022). The increase and  
45        accumulation of greenhouse gases in the atmosphere have led to increasing global temperatures,  
46        including in the ocean. Since the 1980s, the surface of the ocean has, on average, increased by 0.6°C  
47        (95% CI [0.44-0.74°C]) and marine heatwaves (i.e., prolonged anomalously warm water events; Hobday  
48        et al., 2016) have approximately doubled in frequency (Cooley et al., 2022). Marine heatwaves are  
49        predicted to increase in intensity, frequency and duration under all Shared Socioeconomic Pathways  
50        (SSPs; Cooley et al., 2022). Under the five SSPs that cover a wide range of plausible scenarios, sea  
51        surface temperatures (SST), from 1995-2014 to 2081-2100, are projected to increase by +0.86°C (95%  
52        CI [0.43-1.47°C], SSP1-2.6; best-case scenario) up to +2.89°C (95% CI [2.01-4.07°C], SSP5-8.5; worst-  
53        case scenario).

54        Ongoing ocean warming (OW) is predicted to affect marine ecosystems at all levels of biological  
55        organization, from physiological effects on species to effects on the functioning of communities (Yao  
56        & Somero, 2014). Temperature effects on marine organisms differ among species and life-stages  
57        (Byrne et al., 2020; Putnam, 2021; Putnam et al., 2013). Furthermore, thermal sensitivity (the level of  
58        response to increased temperature) may differ between populations of a species when  
59        adaptation/genetic selection or acclimatization (phenotypic plasticity) to local thermal environments  
60        occurred (Johnson et al., 2021; Oliver & Palumbi, 2011; Putnam, 2021). Populations whose individuals  
61        are more responsive (sensitive) are expected to suffer more from heat stress than those that show a  
62        lower response. Depending on this sensitivity, responses of populations to OW may result in shifts in  
63        the biogeographic ranges, leading to global tropicalization and meridionalization of marine faunas  
64        (Perry et al., 2005; Sunday et al., 2012; Vergés et al., 2014; Yapici, 2016). Vertical redistribution of  
65        marine organisms to reach colder mean temperatures can occur, with limits imposed by factors such  
66        as seafloor depth and type of substrate, food availability, connectivity across depths and photic layer

67 depth that constraints photosynthetic organisms within the photic zone (Garcia-Molinos et al., 2016;  
68 Jorda et al., 2020; Pinsky et al., 2020).

69 Local adaptation or acclimatization, which contributes to different physiological sensitivities (i.e. levels  
70 of response of a physiological variable) to thermal stress across populations, could be modulated by  
71 thermal history, in particular by temperature variability. Studies showed that thermal performances of  
72 scleractinians can vary across latitudes (*Astrangia poculata*, Aichelman et al., 2019; *Orbicella franksi*,  
73 Silbiger et al., 2019; *Stylophora pistillata*, *Acropora muricata*, *Porites lobata*, *Seriatopora hystrix*, and  
74 *Pocillopora verrucosa*; Banc-Prandi et al., 2022) and seasons (*Porites cylindrical* and *Acropora*  
75 *valenciennesi*; Jurriaans et al., 2019), due to thermal adaptation/acclimatization. Studies that have  
76 compared thermal sensitivities of scleractinians across depths either found no differences in thermal  
77 sensitivity (instantaneous acute heat stress, 5-10 vs. 30-35m; Gould et al., 2021), higher sensitivity  
78 (ramping of 1°C/day; 20 vs. 43m; Frates et al., 2021) or lower sensitivity (ramping of 1°C/hour; 25 vs.  
79 85m; Godefroid et al., 2023) in mesophotic colonies. Lower sensitivity is linked to a large thermal  
80 window for the considered variable, characteristic of so-called thermal generalists.

81 Mesophotic depths (ca. 30 to 150m; Lesser et al., 2018) may be protected from, or less impacted by,  
82 major disturbances such as temperature anomalies and storm events (reviewed in Bongaerts et al.,  
83 2010). However, evidence revealed that they may show large variations in temperatures, even more  
84 than shallow waters, due to physical processes such as internal waves and tides (Leichter et al., 2012;  
85 Wall et al., 2015). Internal waves are waves generated between different water masses within the  
86 ocean, either by wind-driven disturbance of the surface layer, or by the interaction of internal currents  
87 on seafloor topography (Wall et al., 2015). These generate high-frequency temperature fluctuations  
88 (several degrees) between water masses, which were showed to reduce the risk of scleractinian  
89 bleaching (in particular, large daily temperature range; Safaie et al., 2018; Nash et al., 2012). In the  
90 Andaman Sea, internal waves create sudden (within minutes), large (up to 10°C), short (15-30 min  
91 duration) and intermittent (several per cycle) temperature drops, which rarely extend to the sea  
92 surface. These were showed to mitigate heat accumulation, coral bleaching and mortality, in contrast

93 with waters sheltered from these internal waves (Reid et al., 2019; Wall et al., 2015; Wyatt et al., 2020).  
94 Yet, this concept is now disputed as internal waves proved, in some instances, to be insufficient to  
95 prevent bleaching at mesophotic depths (Frade et al., 2018; Smith et al., 2016). By providing cold  
96 nutrient-rich waters, they also reduce coral growth rate and increase turbidity (Wall et al., 2015). So,  
97 the benefit of internal wave exposure likely depends on a combination of factors, such as their  
98 duration, intensity and the taxa investigated.

99 Ectotherms may be particularly sensitive to OW, as temperature is likely the most important  
100 environmental variable affecting their performances (Angilletta et al., 2002). Their sensitivity to OW  
101 will thus depend, in the first instance, on their physiological ability to tolerate warmer temperatures.  
102 Physiological plasticity is essential when the rates of environmental change (here, warming) exceed  
103 the pace of natural adaptation (Logan et al., 2014). It is particularly important for sessile ectotherms  
104 that are unable to move into colder waters when facing heat stress events (Solan & Whiteley, 2016).  
105 This is the case of epi-zoobenthic taxa that make 'Marine Animal Forests' (MAFs *sensu* Rossi et al.,  
106 2017), such as Antipatharian corals. Antipatharians, also known as black corals, are colonial  
107 Hexacorallia, which are widely distributed across oceans and depths (Wagner et al., 2012). Their  
108 skeleton differs from the calcareous scleractinian corals by being made of chitin and proteins.  
109 Moreover, they exclusively feed heterotrophically and do not rely on *Symbiodiniaceae* for energy  
110 acquisition (Gress et al., 2021; Wagner et al., 2011, 2012). Under favourable conditions, antipatharians  
111 form dense and extensive MAFs that create a diversity of microhabitats and favour a high biodiversity  
112 of associated fauna. They are therefore considered as 'engineer' species (Bo et al., 2014, 2019; De  
113 Clippele et al., 2019; Tazioli et al., 2007; Terrana et al., 2019).

114 The effects of temperature increase on Antipatharian corals are known through only three studies.  
115 Godefroid et al. (2022a, 2023) showed that the mesophotic *Stichopathes* sp. clade C in the tropics (80  
116 m, Mo'orea, French Polynesia, 16-days experiment and ramping 1°C/hour) had a narrow thermal  
117 window of performance (4.4°C [2.0-6.5] 95% CI) and lived close to its tipping point temperature  
118 ("thermal optima", in thermal biology, 28.8°C, [27.6-31.5] 95% CI). The experiment was performed at

119 the end of the cold season, yet *Stichopathes* sp. lived at performances below the tipping point  
120 (“suboptimal”), suggesting that this species has a low acclimatization capacity. An increase in seawater  
121 temperature of 1°C exceeded its tipping point temperature with significant resulting effects (tissue  
122 necrosis, impairment of healing capacities, mucus and antioxidant production; Godefroid et al., 2022a).  
123 Another 15-days experiment performed on the Mediterranean Antipatharian *Antipathella subpinnata*  
124 (70 m, Bordighera, Italy) revealed a wide thermal performance window (6.1°C) and no significant  
125 effects at any temperature, up to +4.5°C above the annual mean thermal conditions, suggesting very  
126 low sensitivity of this species (Godefroid et al., 2022b). So far, the paucity of studies on Antipatharians  
127 prevents drawing a global picture of the sensitivity of antipatharians to increased temperatures.

128 In subtropical regions such as the Canary Islands (Eastern Atlantic), mesophotic rocky communities  
129 harbour antipatharians, among which the arborescent *Antipathella wollastoni* occurs from 25 m to  
130 more than 1000 m, creating extensive MAFs throughout the Macaronesia (Bianchi et al., 2000; Ocaña  
131 & Brito, 2004; Molodtsova, 2006; Czechowska et al., 2020). The whip shaped *Stichopathes gracilis* also  
132 occurs in this archipelago at depths from 30 to 150 m, creating dense populations around the island of  
133 Lanzarote (Ocaña & Brito, 2004). Ocean temperatures are increasing rapidly in the Canary Islands, so  
134 it is of particular interest to study the resilience of black coral communities in this region. Indeed, it  
135 was shown that SSTs in the Canary upwelling system have the highest warming rate of all four Eastern  
136 Boundary Upwelling systems (Aristegui et al., 2009). SST trends vary from +0.16°C (Siemer et al., 2021)  
137 to +0.5°C per decade (Demarcq, 2009), according to the period and data source (Table 1). Increasing  
138 temperatures across the archipelago has already resulted in biogeographical shifts, with the arrival of  
139 tropical species and the expansion of thermophilic endemic species around several islands (BrITO et al.,  
140 2014, 2017; Espino et al., 2019).

141 If considering that current SST increase trends will continue in the upcoming decades, an overall  
142 maximum warming of ca. +4°C can be expected by the end of the century (0.5 °C dec<sup>-1</sup> over 80 years;  
143 Demarcq, 2009). On top of that overall temperature increase, internal waves were reported in the  
144 southwest shelf-break of Gran Canaria Island (Sangrà et al., 2001). These uplifted waters induce

145 upward transport of cold and nutrient-rich waters, which enhance biological production locally and  
 146 may benefit heterotrophic feeders, such as Antipatharians. They are responsible for vertical  
 147 oscillations of temperatures around the pycnocline that is centred around 80 m in Gran Canaria.  
 148 Isotherms show vertical oscillations with about 10 m amplitude in the thermocline and 50 m in the  
 149 mixed layer (Sangrà et al., 2001).

150

151 **Table 1.** Sea surface temperature (SST) trends for the Canary Islands related to the period and data sources.

Study	T° increase	Period	Data source
Espino et al., 2019	0.21°C dec <sup>-1</sup>	33 years, 1985-2018	Marine Copernicus European system
Vélez-Belchi et al., 2015	0.28°C dec <sup>-1</sup>	31 years, 1982-2013	AVHRR, ICOADS
Belkin, 2009	0.22 dec <sup>-1</sup>	24 years, 1892-2006	UK Meteorological Office Hadley, Centre SST climatology
Siemer et al., 2021	0.16°C dec <sup>-1</sup>	37 years, 1982-2019	AVHRR, ICOADS
Demarcq, 2009	0.35-0.44°C dec <sup>-1</sup>	9 years, 1998-2007	ICOADS, AVHRR Pathfinder v. 5.1
Demarcq, 2009	0.5°C dec <sup>-1</sup>	22 years, 1985-2007	ICOADS, AVHRR Pathfinder v. 5.1
Carson & Harrison, 2008	warming (0-300m)	48 years, 1955-2003	WOD05
Pardo et al., 2011	0.21°C dec <sup>-1</sup>	39 years, 1970-2009	NCEP/NCAR

152 Modified from Siemer et al. (2021). Dec refers to decades.

153

154 In light of the rapid warming expected in the Canary Islands upwelling system (Aristegui et al., 2009),  
 155 it appears particularly relevant to assess thermal sensitivities of 'engineer' species of this region,  
 156 including Antipatharians, which are particularly understudied from this point of view. This is also a  
 157 good case study to provide more insight into the effects of temperature variability on the thermal  
 158 sensitivity of Antipatharians from mesophotic depths and to test if higher temperature variability leads  
 159 to lower thermal sensitivity. Therefore, the aims of this study were (1) to assess the thermal  
 160 sensitivities of the Antipatharians *A. wollastoni* and *S. gracilis* and (2) to determine if high temperature  
 161 fluctuations at mesophotic depths increase thermal tolerance. For this purpose, we compared the  
 162 physiological tolerance of two populations of *A. wollastoni* from distinct depths (25 m vs. 40 m), under  
 163 different thermal regimes in Gran Canaria, using a short-term ramping method. Because internal wave

164 activity is higher at 40 m, we expected these colonies to be more tolerant to increasing temperatures  
165 than those from 25 m. Then, we assessed the thermal response of the lower mesophotic (80 m)  
166 Antipatharian *Stichopathes gracilis* from Lanzarote in order to compare its thermal sensitivity with a  
167 previously studied *Stichopathes* species from Mo'orea (French Polynesia) that inhabits a less variable  
168 habitat (Godefroid et al., 2023).

169

## 170 **2. Material and methods**

### 171 2.1 *In situ* thermal environment

172 Temperature data loggers were attached to 50 cm-long metal stakes partially buried into the seabed  
173 (Hobo data-logger Pendant Temp-Light, Onset Computer Corporation, USA), at 25 m ~~and 40 m~~ in  
174 Gando Bay (27°55'56.1"N 15°21'11.0"W; Fig. 2a), located on the Eastern coast of Gran Canaria (Canary  
175 Islands, Spain) in sites where *A. wollastoni* fragments were collected. At 25 m, loggers were set up to  
176 record measurements every 2 hours, from October 9<sup>th</sup>, 2019, to June 3<sup>rd</sup>, 2020 (one logger), and then  
177 every 15 minutes from June 3<sup>rd</sup>, 2020, to October 7<sup>th</sup>, 2021 (one logger). Loggers were also installed in  
178 sites where *S. gracilllis* fragments were collected at 80 m depth in Playa Chica (Lanzarote; 28°55'04.7"N  
179 13°40'11.8"W; Fig. 2a), located on the Southeastern coast of Lanzarote (Canary Islands, Spain). These  
180 recorded temperature data every 4 hours, from January 10<sup>th</sup> to February 17<sup>th</sup>, 2021 (one logger), and  
181 every 15 minutes from February 17<sup>th</sup> to October 19<sup>th</sup>, 2021 (one logger). The whole temperature  
182 dataset was deposited in open-access in Zenodo (DOI: 10.5281/zenodo.7180090). Temperature time  
183 series data in Gando Bay was also retrieved from Otero-Ferrer et al. (2020). Temperature data at both  
184 depths was available for two periods: (1) from July 12<sup>th</sup> to August 25<sup>th</sup>, 2017 (45 days, 1 measure every  
185 5 minutes) and (2) from September 20<sup>th</sup> to October 10<sup>th</sup>, 2018 (21 days, 1 measure per minute).

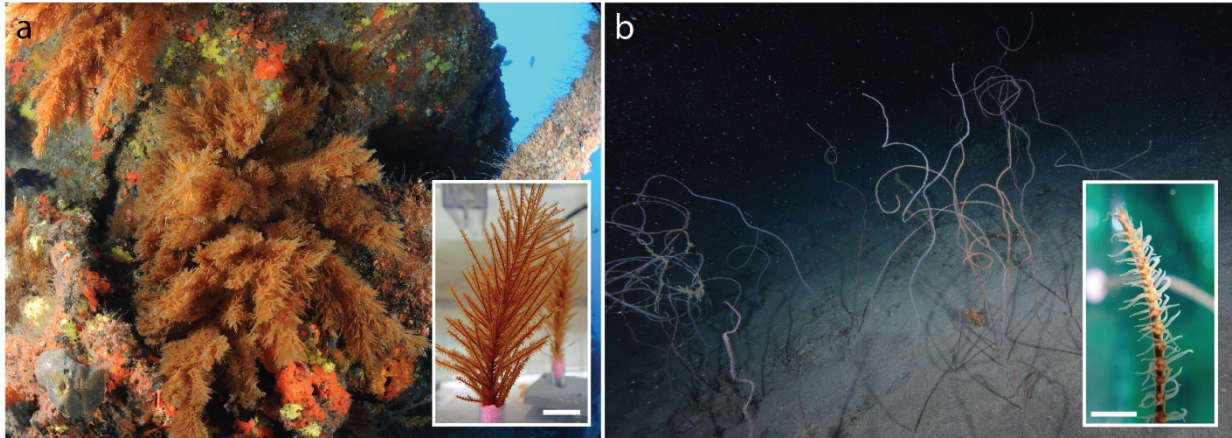
186

### 187 2.2 Antipatharian collection



188 All coral fragments were collected between October 7<sup>th</sup> and November 11<sup>th</sup>, 2021. Sites were selected  
189 on the basis of previous records of black coral species in the Canary Islands (Czechowska et al., 2020;  
190 Ocaña & Brito, 2004). Two fragments, approximately 10 cm long, were cut from seven colonies.  
191 Fragments of *A. wollastoni* (Fig. 1a) were collected at 25 and 40 m depth in Gando Bay. Seawater  
192 temperature recorded at the time of collection was 23°C and 21°C, respectively. Fragments from 25 m  
193 are, thereafter, referred as “the mid-depth fragments” and those from 40 m as “the mesophotic  
194 fragments”. Fragments of *S. gracilis* (Fig. 1b) were collected at 80 m depth in Playa Chica where  
195 recorded seawater temperature at the time of collection was 19°C. After collection, all fragments were  
196 transported in cool boxes with seawater from the collection sites to the Parque Científico Tecnológico  
197 Marino de Taliarte (Telde, Gran Canaria). In the laboratory, fragments were attached to a support using  
198 EPOXY resin (Holdfast, Aquarium Systems, France) and placed in an open-circuit system composed of  
199 ten aquariums (30 L, salinity 36.8 ‰) under identical temperature relative to the sites of collection (19,  
200 21 and 23°C). The open-circuit renewal rate was adjusted to be constant and to be able to maintain a  
201 stable seawater temperature in the system. Total seawater volume was renewed every two days.  
202 Seawater delivered to all aquariums was cooled at 19°C using a chiller (Johnson control A350; ± 0.5°C)  
203 and was heated in individual aquariums (for 21 and 23°C) using two 100 W heating resistances  
204 connected to a temperature controller (Inkbird ITC-308; ± 0.3°C). Fragments were left to recover  
205 between six and ten days before starting the experiment. After this recovery period, no signs of stress  
206 were visible (no mucus production, polyps open and feeding at night). Fragments were fed daily (at  
207 dawn) with a mix composed of freshly hatched *Artemia*, copepods and phytoplankton. Seawater  
208 parameters were checked daily using a handheld meter (WTW Multi 350i for temperature, pH and  
209 conductivity) and colorimetric tests (for nitrates and nitrites), to ensure good seawater quality.

210



211

212 **Figure 1.** *In situ* photographs of (a) *Antipathella wollastoni* from 25 m in Gran Canaria (Gando Bay) and (b) *Stichopathes*  
213 *gracilis* from 80 m in Lanzarote (Playa Chica). Insets: fragments of the two species. Scale bars: 2 cm.

214

### 215 2.3 Heat stress experiment

216 Thermal sensitivity was quantified by measuring the oxygen consumption rate of the fragments over  
217 a range of temperatures. Based on the oxygen and capacity-limited thermal tolerance hypothesis,  
218 oxygen represents the energy available for an organism to perform essential functions (Pörtner, 2010;  
219 Schulte, 2015). An increase in oxygen consumption is therefore indicative of an increase in energy cost  
220 and hence, in the thermal sensitivity of the fragments. Oxygen consumption rate of the fragments was  
221 measured using a ramping methodology that was proven efficient with antipatharian corals (Godefroid  
222 et al., 2023). The ramping method represents a trade-off between the range of possible methodologies  
223 (chronic exposure, acute thermal stress), as it gives some time for acclimation at each temperature  
224 steps (much less than under chronic exposure but more than under acute thermal stress). The ramping  
225 method has proved to be useful when the practical extent of a study cannot match the process of  
226 interest, such as climate change (Blois et al., 2013; Pickett, 1989; Silbiger et al., 2019), and allows  
227 comparing the relative sensitivities of populations or species.

228

229 The ramping system was made of an open-circuit buffer tank (300 L) connected to a chiller (Johnson  
230 control A350) and, through a pump, to an experimental tank (80 L) where the respirometry chambers  
231 were installed. The experimental tank was overflowing into the buffer tank and excess seawater in the  
232 buffer tank was removed from the system by overflow. The experimental tank was equipped with a  
233 circulation pump and a bubbling system to ensure complete temperature homogenisation and  
234 aeration of the seawater. Two 100 W heating resistance, connected to a temperature controller  
235 (Inkbird ITC-308;  $\pm 0.3^{\circ}\text{C}$ ), were also installed to allow increasing the temperature quickly between  
236 experimental stages.

237 Ramp experiments were performed with coral fragments from the three populations (*A. wollastoni*  
238 from 25 m and 40 m and *S. gracilis* from 80 m). Each ramp was divided in two legs, respectively called  
239 'hot ramp' and 'cold ramp', both starting at the acclimation temperature. Here, we define 'ramp  
240 experiment', as the progressive increase/decrease (hot/cold ramp) by gradual steps of temperature.  
241 The minimum temperature tested corresponded to the lower seasonal temperature experienced by  
242 the organism in its environment. The maximum temperature tested was the highest seasonal  
243 temperature experienced by the organism in its environment +3°C. Therefore, temperatures tested at  
244 each step differed among populations, but the number of steps in the hot ramp was identical for the  
245 three populations (Table 2). This avoids potential bias from different times of exposure among  
246 populations. Each time, one fragment of a colony was used for the hot ramp and the second fragment,  
247 from the same colony, was used for the cold ramp. This allowed every fragment to be used only in a  
248 single ramp (and not reused), as well as to have paired replicates (fragments from the same colony)  
249 between hot and cold ramps.

250 Each ramp proceeded identically for specimens from the three populations. Seven fragments from  
251 different colonies were moved from their acclimation tank to one of the eight respirometry chambers  
252 held in the experimental tank. They were first left to acclimate for 1 hour in darkness and then the  
253 chambers were closed, and oxygen consumption was measured for 40 min in darkness, starting at the

254 acclimation temperature. After this period of stable temperature, the chambers were opened in the  
 255 experimental tank (allowing water exchange between the water in the chambers and in the  
 256 experimental tank) and temperature was increased/decreased for 30 min to the next step of  
 257 temperature. Once reached, the fragments were left 30 more min in their open chambers to acclimate  
 258 to the new temperature, before starting a new 40 min measurement period (with closed chambers).  
 259 Oxygen saturation in the chambers was always above 80%. This procedure was repeated for each step  
 260 of temperature. At the end of the last respiration rate measurement, chambers were opened,  
 261 temperature was decreased back to the acclimation temperature and new measurements of  
 262 respiration rate were taken after 2.5 hours and 12 hours, to evaluate whether the fragments were able  
 263 to recover from the heat stress (recovery capacity; Table 2). The recovery capacity was only assessed  
 264 at the end of the hot ramp (not at the end of the cold ramp). During all ramps, one chamber was left  
 265 free from any fragment (blank/control chamber) to account for background respiration (i.e., part of  
 266 the respiration attributed to seawater microbes and/or instrument drift).

267

268 **Table 2.** Temperature steps tested during the hot and cold ramps, for *Antipathella wollastoni* fragments from 25 and 40 m  
 269 depth and *Stichopathes gracilis* fragments from 80 m depth. Colour code: Gray, temperatures of acclimation, which are the  
 270 same temperatures than for the recovery; blue gradient, temperatures colder than the acclimation temperatures (cold ramp);  
 271 yellow-orange-red colours, temperatures warmer than the acclimation temperatures (hot ramp). Orange-red colours are  
 272 temperatures above the highest temperature experienced by the organism in the environment, including short-term  
 273 temperature variability related to internal waves. Red colour are temperatures 3°C higher than the maximum temperature  
 274 recorded at the corresponding site.

Species Depth (m)	Cold ramp (°C)					Hot ramp (°C)					Recovery 2.5 h	Recovery 12 h	
<i>A. wollastoni</i> 25 m	19	20	21	22	23	23	24	25	26	27	28	23	23
<i>A. wollastoni</i> 40 m		18	19	20	21	21	22	23.5	25	26.5	28	21	21
<i>S. gracilis</i> 80 m			17	18	19	19	20.5	22	23.5	25	26.5	19	19

275

276 Oxygen consumption of the fragments, expressed in oxygen saturation, was measured for the eight  
277 respirometry chambers simultaneously, through time. One measure was recorded every 5 s on each  
278 chamber using fibre-optic oxygen sensors connected to two 4-channel Fibre Optic Oxygen Transmitter  
279 (OXY-4 SMA G2 and OXY-4 SMA G3, Pre-Sens Precision Sensing GmbH, Germany). The volume and  
280 shape of the chambers changed based on the morphology of the species: fragments of *A. wollastoni*  
281 (bushy) were placed in 400 mL cylindrical plastic chambers and fragments of *S. gracilis* (unbranched,  
282 long and thin corallum) in 50 mL Falcon tubes. A new oxygen sensor spot (PreSens SP-PSt3-NAU-D5-  
283 YOP-SA) was glued in every chamber and calibrated according to the supplier's manual. A magnetic stir  
284 bar, separated from the fragment by a mesh, allowed to maintain constant homogenization of the  
285 dissolved gas in the chambers. Respiration rate of the control chamber was subtracted from respiration  
286 rate of the chambers containing a coral fragment. After the ramp and recovery period, each fragment  
287 was weighed (wet weight) and measured (length and diameter) to allow normalizing the respiration  
288 rate measurements. Length and diameter measurements were used to calculate the surface area of  
289 the *S. gracilis* fragments using the formula of a cylinder. Due to the complex morphology of *A.*  
290 *wollastoni*, surface area could not be calculated for this species. Instead, the total length of all  
291 ramifications was measured by taking a photo with a scale (resolution 1 mm) of all cut branches laid  
292 out in two dimensions. Subsequent photographs were analysed using the software ImageJ (Schneider  
293 et al., 2012). These normalization methods allowed comparison with previous results (*A. subpinnata*  
294 in Godefroid et al., 2022b; *Stichopathes* sp. in Godefroid et al., 2022a). Respiration rate was calculated  
295 using the slope of the linear regression of seawater oxygen concentration against time, after  
296 accounting for the seawater volume (based on the seawater density calculations from Millero & Huang,  
297 2009; Millero & Poisson, 1981) and normalized by the surface area/length and by the wet weight of  
298 the fragment. Rates of respiration were expressed in  $\mu\text{mol of O}_2 \text{ h}^{-1}$  and  $\text{cm}^{-2}$  for *S. gracilis*, in  $\mu\text{mol of}$   
299  $\text{O}_2 \text{ h}^{-1}$  and cm for *A. wollastoni* and in  $\mu\text{mol of O}_2 \text{ h}^{-1} \text{ g}^{-1}$  when normalized by the wet weight. Row data  
300 for respiration were deposited in open-access in Zenodo (DOI: 10.5281/zenodo.7684112).

301

## 302 2.4 Data analysis

303 To compare daily temperature fluctuations at 25 and 40 m depths in Gando Bay (Gran Canaria), data  
304 from Otero-Ferrer et al. (2020) were used. First, daily temperature ranges were calculated (daily  
305 maximum temperature – daily minimum temperature). Then, daily temperature ranges across depths  
306 were compared using one-factor repeated measures model, with depth as a fixed factor, time as a  
307 repeated measure (random factor) and daily temperature range as a dependant variable.

308 Total annual temperature ranges across depths were not compared statistically because temperature  
309 time series were not of equal length (sometimes being less than one year) and did not cover the same  
310 period.

311 Respiration rates were analysed using linear least square regression models with temperature as a  
312 predictor variable, for the three populations and the two normalization methods (by length or surface  
313 and by wet weight). Linearity assumptions were checked by analysis of residuals. Comparison of slopes  
314 between regressions for *A. wollastoni* from 25 and 40 m depth were performed using the R package  
315 *lsmeans* that performs two-way ANOVA (Russel, 2016). Non-linear models were also tested but did not  
316 converge.

317 Differences in respiration rates were tested for each population between the start of the ramping (i.e.,  
318 at acclimation temperatures), the end of the ramping and after 2.5 and 12 h of post ramping recovery  
319 via a linear mixed-effect model and *a posteriori* pairwise comparison (Tukey's HSD). In the linear mixed-  
320 effect model, time was a fixed repeated effect (4 levels), colony was a random factor (7 levels) and the  
321 respiration rate was the dependent variable. Linearity assumptions were checked by analysis of  
322 residuals.

323 All analyses were performed using the software R, version R 4.2.1 (R Core Team, 2022).

324

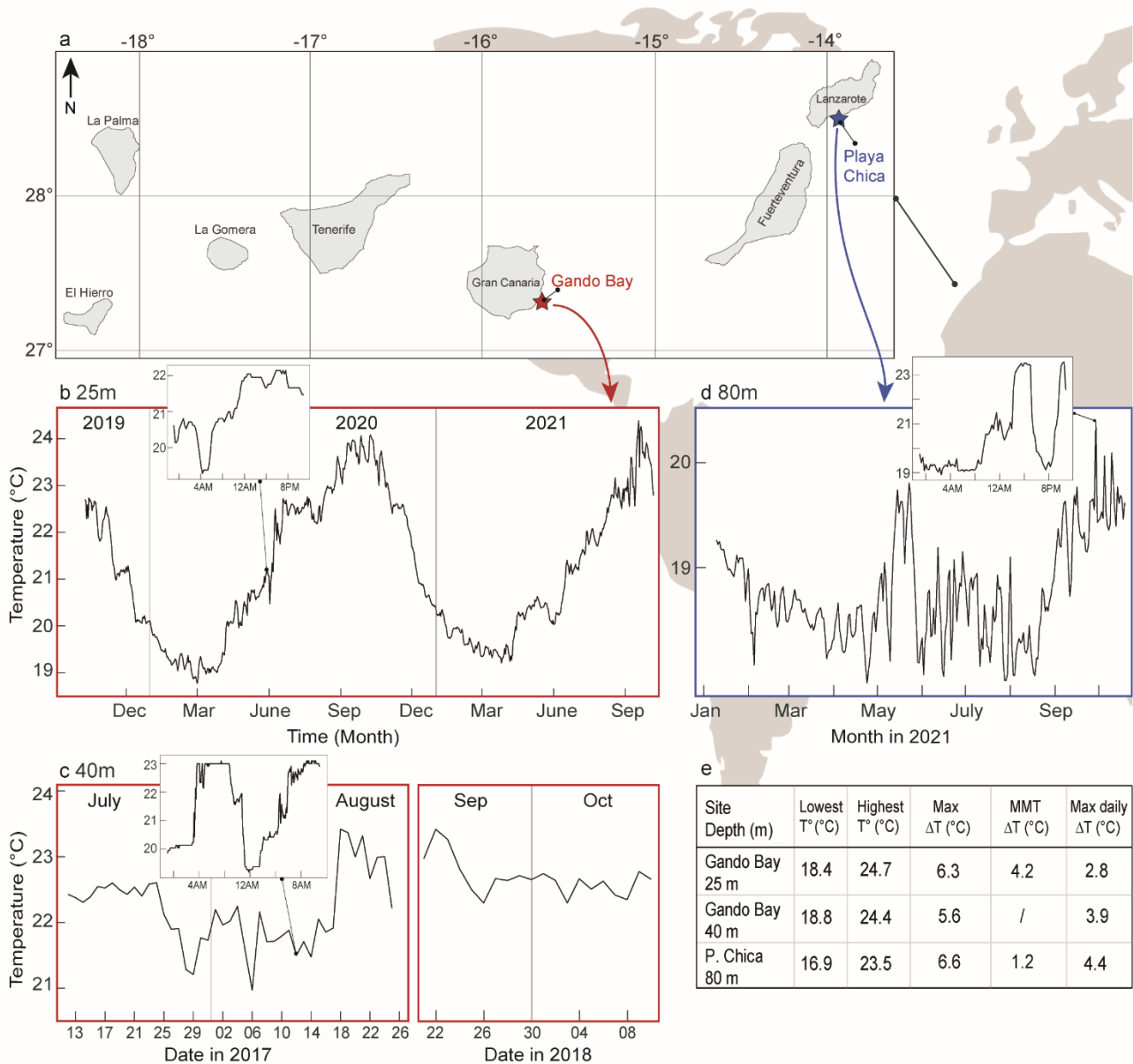
## 325 3. Results

326 3.1 *In situ* thermal environments

327 Absolute annual temperature range at 25 m in Gando Bay (Gran Canaria Island) was 6.3°C, based on  
328 the two years of available temperature data (October 9<sup>th</sup>, 2019, to October 7<sup>th</sup>, 2021; Fig. 2b,e).  
329 Average annual temperature range between the warmest (September, 23.6 ± 0.6°C, mean ± sd,  
330 n=5,765) and coldest (March, 19.4 ± 0.2°C, mean ± sd, n=3,348) months of the dataset was 4.2°C (Fig.  
331 2e; Table S1). Absolute temperatures range from available data at 40 m was 5.6°C, with 18.8°C being  
332 the minimum recorded temperature and 24.4°C being the maximum recorded temperature (Fig. 2c,e;  
333 Table S1). Absolute temperature range from data recorded at 80 m in Playa Chica (Lanzarote Island)  
334 was 6.6°C (January 10<sup>th</sup> to October 19<sup>th</sup>, 2021; Fig. 2d,e) and average temperature range was 1.2°C  
335 between the warmest (October, 19.6 ± 0.7°C, mean ± sd, n=1,769) and coldest months (April, 18.4 ±  
336 0.4, mean ± sd, n=2,880) (Fig. 2e; Table S1).

337 Short-term temperature fluctuations were evidenced, which amplitude increased with depth.  
338 Comparison of daily temperature ranges at 25 and 40 m based on temperature time series from Otero-  
339 Ferrer et al. (2020), showed that daily temperature ranges at 40 m (means: 2.24°C and 2.88°C for data  
340 in 2017 and 2018, respectively) were significantly higher than at 25 m (means: 1.06°C and 1.89°C for  
341 data in 2017 and 2018, respectively) ( $p < 0.001$  for both time series; Tables S2).

342 Based on available temperature time series (Figure 2), maximum daily temperature ranges were 2.8°C  
343 at 25 m (June 6<sup>th</sup> 2020), 3.9°C at 40 m (August 12<sup>th</sup> 2017) and 4.4°C at 80 m (August 8<sup>th</sup> 2021) (Fig. 2e).  
344 Temperature fluctuations over the year showed a seasonal pattern. At 25 m, the lowest monthly  
345 temperature range (1.4°C) was observed from January to March (cold season) and the highest (3.0-  
346 4.1°C) from June to October (warm season) (Fig. 2b; Table S1). A similar pattern was observed at 80 m,  
347 with the lowest monthly temperature ranges (1.1-1.6°C) from January to March and the highest (4.8-  
348 5.7°C) from July to October (Fig. 2d; Table S1).



349  
 350 **Figure 2.** Thermal regimes at the three study sites. (a) Map of the study sites. (b) Temperature at 25 m in Gando Bay (Gran  
 351 Canaria) from October 9<sup>th</sup>, 2019, to June 3<sup>rd</sup>, 2020 (n=2,855; 2 h interval; mean per day) and from June 3<sup>rd</sup>, 2020, to October  
 352 7<sup>th</sup>, 2021 (n=47,131; 15 min interval; mean per day). (c) Temperature at 40 m in Gando Bay (Gran Canaria) from July 12<sup>th</sup>  
 353 August 25<sup>th</sup>, 2017 (n=12,711; 5 min interval; mean per day) and from September 21<sup>st</sup> to October 10<sup>th</sup>, 2018 (n=28,130; 4h  
 354 interval; mean per day). (d) Temperature at 80 m in Playa Chica (Lanzarote) from January 10<sup>th</sup> to February 17<sup>th</sup>, 2021 (n=227;  
 355 4 h interval; mean per day) and from February 17<sup>th</sup> to October 19<sup>th</sup>, 2021 (n=23,421; 15 min interval; mean per day). (e)  
 356 Metrics of temperature in the three study sites. Lowest and highest temperatures (°C) are the lowest and highest  
 357 temperatures recorded in each study site during the considered periods; Max ΔT is the difference between the highest and  
 358 lowest temperatures ever recorded in each study site; Mean monthly temperature (MMT) ΔT is the annual temperature  
 359 range based on mean monthly temperatures (mean of the warmest month – mean of the coldest month); Max daily ΔT is



360 the highest difference between the maximum and minimum temperature recorded on a single day. Full details of the metrics  
361 are available in Table S1. Insets: zooms on a day with high thermal variability.

362

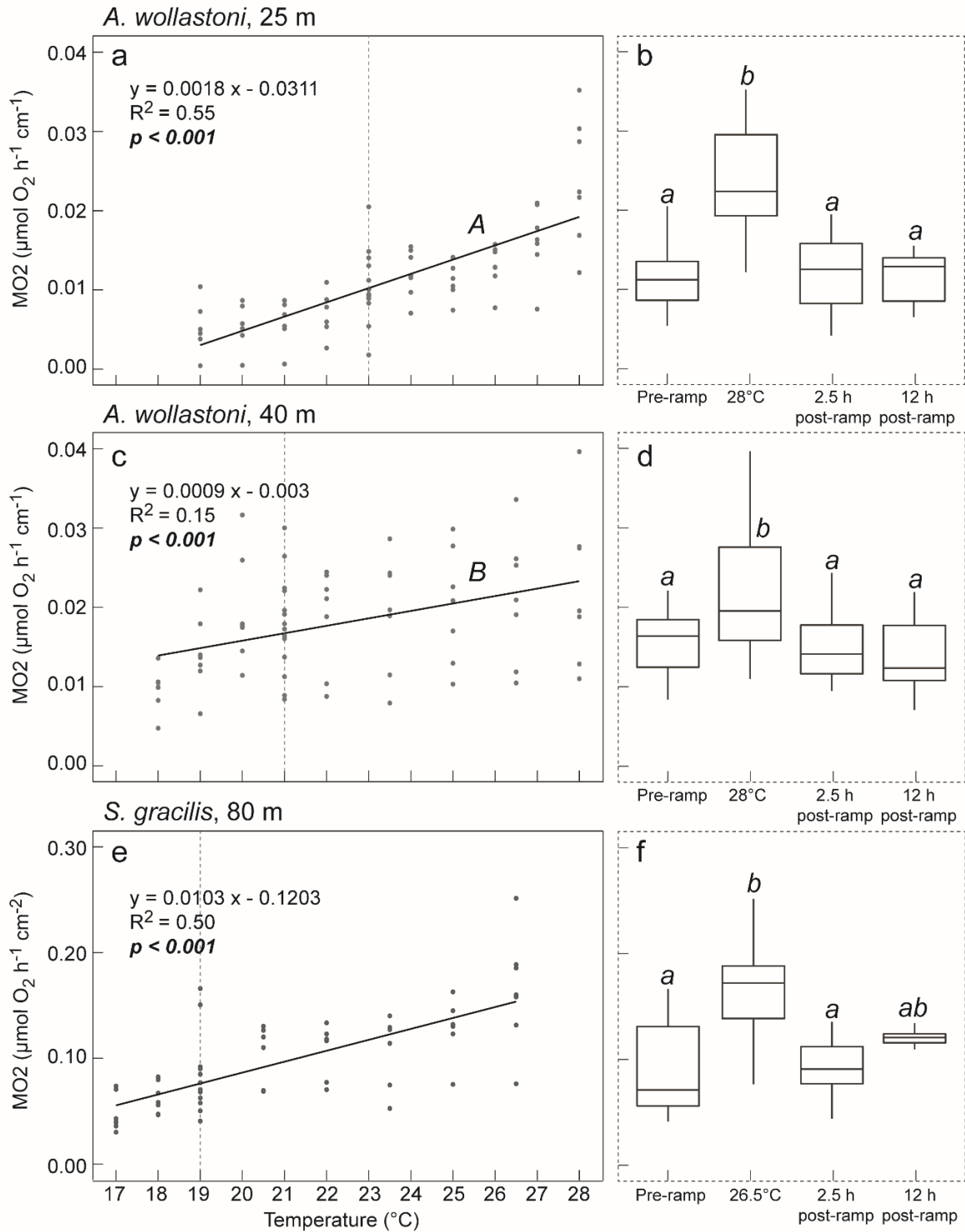
### 363 3.2 Metabolic responses with temperature

364 Respiration rates (normalized by length) increased linearly with temperature for *A. wollastoni* from 25  
365 and 40 m, with respective slopes being 0.0018 and 0.0009 (Fig. 3a, c;  $p < 0.001$  for both populations,  
366 Table S3). Respiration rates increased significantly faster (i.e., steeper slope) with temperature in the  
367 mid-depth than in the mesophotic colonies (Comparison of slopes,  $p = 0.01$ , Table S4). For *S. gracilis*,  
368 respiration rates (normalized by surface area) also increased linearly with temperature (Fig. 3e,  
369  $p < 0.001$ , Table S3).

370 When respiration rates of the three populations were normalized by the weight of the fragments,  
371 linear regressions were also significant for all populations, although temperature only accounted for  
372 4% of the variation in *A. wollastoni* from 40m (Figure 4, Table S6;  $p < 0.001$  for *A. wollastoni* from 25 m  
373 and *S. gracilis* and  $p < 0.05$  for *A. wollastoni* from 40 m). Mid-depth colonies of *A. wollastoni* were  
374 significantly more responsive to increasing seawater temperature than deeper colonies of *A.*  
375 *wollastoni* (Figure 4, Table S7; Comparison of slopes and Tukey's test).

376 For all populations, respiration rates were significantly lower at the start of the ramping (i.e., at  
377 acclimation pre-ramp temperatures) than at the highest tested temperature (Fig. 3b, d, f; Table S5;  
378 Linear Mixed Model and Tukey's tests). However, respiration rates did not differ significantly between  
379 the start of the ramping and after 2.5 and 12 h of post ramping recovery, for all populations (Fig. 3b,  
380 d, f; Table S5; Linear Mixed Model and Tukey's tests).

381

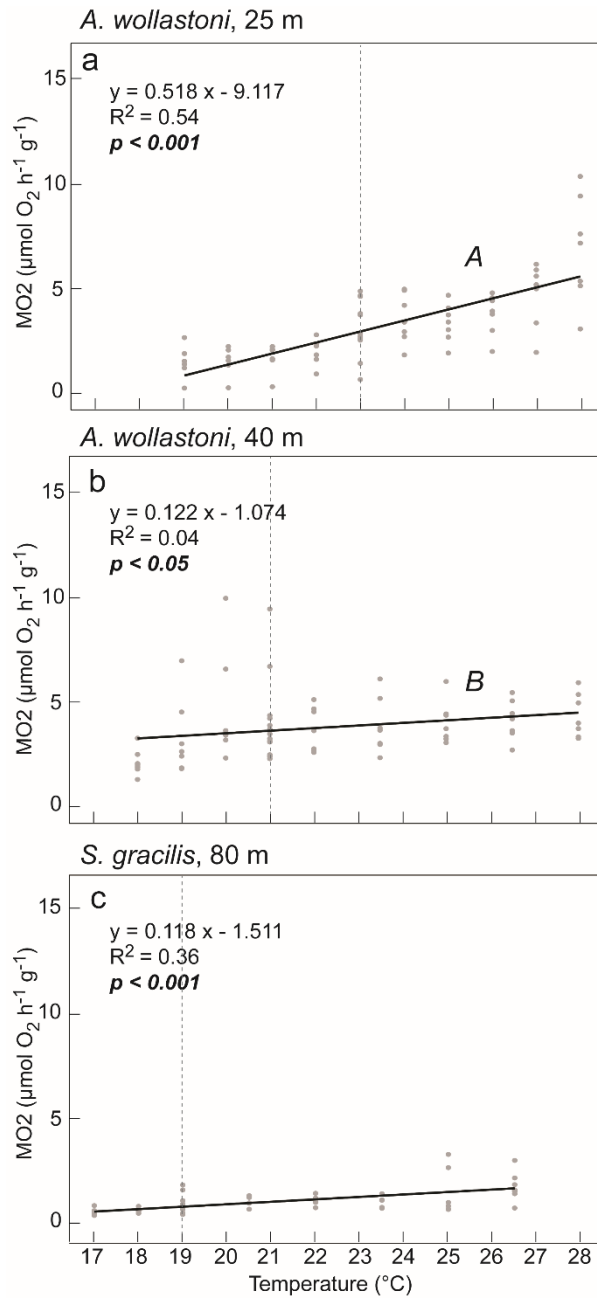


383

384 **Figure 3.** Respiration rate (MO2) normalized by the length/surface of the fragments according to temperature, for (a, c)  
 385 *Antipathella wollastoni* from 25 and 40 m (Gran Canaria) and (e) *Stichopathes gracilis* from 80 m (Lanzarote). Modelling using  
 386 Linear Least Square Regression (black line). Vertical dotted lines are the acclimation temperatures. Different uppercase letters  
 387 indicate slopes that differ significantly, for the two populations of *A. wollastoni*. (b, d, f) Comparison of the recovery capacity  
 388 of the fragments before the ramp experiment (Pre-ramp), at the end of the ramp experiment (highest temperature) and 2.5  
 389 h and 12 h post-ramp, back to acclimation temperature, for the three studied populations. Boxes for the same population

390 sharing the same lowercase letters do not have significantly different means (Tukey's test). Boxplot median (horizontal line);  
391 box 25 to 75 percentiles ;upper and lower whiskers r maximum and minimum values, respectively.

392



393

394 **Figure 4.** Respiration rate normalized by the wet weight of the fragments according to temperature, for (a) *A. wollastoni* from  
395 25 m; (b) *A. wollastoni* from 40 m and (c) *S. gracilis* from 80 m. Different uppercase letters indicate slopes that differ  
396 significantly, for the two populations of *A. wollastoni*. These were not compared with the slope for *S.gracilis* because the  
397 species differs by many biological features.

398

## 399 4. Discussion

### 400 4.1 *In situ* thermal environment

401 Temperatures at the three collection sites differed depending on the time scale considered. Total  
402 annual temperature ranges across depths could not be compared statistically, due to lack of  
403 comparable temperature time series. Indeed, duration of recorded temperature also varied across  
404 sites, with up to 3 years of temperature data at 25 m in Gando Bay, a few months at the same site at  
405 40 m, and almost a year at 80 m in Playa Chica. These differences in temperature data sampling  
406 between sites are due to the difficulty of accessing deeper sites, which requires more logistics than for  
407 shallower sites and to the unavailability of remote sensing of bottom temperatures at depth.  
408 Nevertheless, based on data available simultaneously at both depths from Otero-Ferrer et al. (2020),  
409 it was possible to show that daily temperature ranges differed significantly between 25 and 40m  
410 depths. In this dataset, temperature daily ranges were larger at 40 m than at 25 m (Fig. 2e; Table S1).

411

### 412 4.2 Thermal tolerance according to depth

413 The acute ramping experiments showed a steady increase in oxygen consumption rate with  
414 temperature for populations of *A. wollastoni* from both depths. Both populations were also able to  
415 recover a normal metabolic rate after the ramping, suggesting that the gradual, but fast, increase in  
416 temperatures did not lead to severe consequences. Only one experiment has previously assessed the  
417 effects of increasing temperatures on an Antipatharian within the same genus (*Antipathella*  
418 *subpinnata*; Godefroid et al., 2022b). In this experiment, fragments were exposed to a range of  
419 temperatures (14 to 19°C) over 15 days and results showed very low thermal sensitivity for this species,  
420 with no significant effects even at +4.5°C above the mean annual temperature. Ramping experiments  
421 may be less efficient in revealing thermal limitations for this specific species. However, in both species,  
422 very low (*A. subpinnata*) or no limitation (*A. wollastoni*) in metabolism was induced by temperature in  
423 the considered temperature ranges, suggesting that this genus is rather resistant to thermal stress.

424 The differences in thermal responses between depths for *A. wollastoni* (i.e. significant differences  
425 between regression slopes) coincide with differences in daily temperature ranges, which were  
426 significantly larger at 40 than at 25 m. Phenotypic plasticity, or genotype selection, was suggested as a  
427 mechanism enhancing tolerance for populations under variable environmental stress (Rivest et al.,  
428 2017). In the present study, these processes could have driven a fast acclimation capacity, which  
429 allowed mesophotic *A. wollastoni* to adjust their physiological performances faster (i.e., moderate  
430 slope) than the mid-depth colonies (i.e., steeper slope) during the ramping. Such fast acclimation  
431 capacity has been reported in scleractinians (e.g. Jurriaans and Hoogenboom, 2020).

432 Our results are in line with the hypothesis that environmental variability could modify the responses  
433 of organisms to ocean warming. Limited evidence from studies on scleractinian corals suggests that  
434 environmental history (temperature variability) can influence their response to changes in  
435 temperature. These studies compared the tolerance of corals from high- and low-variability sites, such  
436 as lagoon vs. back-reef pools (Oliver & Palumbi, 2011; Palumbi et al., 2014), or intertidal vs. subtidal  
437 sites (Schoepf et al., 2015). In contrast, information on the influence of temperature variability across  
438 depths on the thermal tolerance of scleractinian corals is poor, or derives from *in situ* observational  
439 studies (Pérez-Rosales et al., 2021; Wall et al., 2015; Wyatt et al., 2020). The present results suggest  
440 that short-term environmental temperature fluctuations, differing according to depth, may induce a  
441 reduced response to thermal stress in the antipatharian *A. wollastoni*, as observed in corals from highly  
442 variable sites.

443 Protection against disturbances at depth can occur in different shapes and forms (Smith et al., 2017a).  
444 It can relate to extrinsic protection, by avoiding disturbance, or to intrinsic protection, through high  
445 level of resistance or resilience (through rapid recovery) to disturbances (Bongaerts & Smith, 2019).  
446 Here, mesophotic depths will not escape current OW, nor the predicted increase in the frequency and  
447 intensity of marine heatwaves (Aristegui et al., 2009; Cooley et al., 2022). Hence, they should not be  
448 categorized as depth refuge/refugium. However, the lower response to thermal stress of the

449 mesophotic populations of Antipatharians suggests that these populations are more resistant due to  
450 selection/adaptation to the higher levels of temperature fluctuations at these depths, compared to  
451 shallower ones. We thus suggest that mesophotic depths in this region can be categorized as depth  
452 resilience area, as proposed by Bongaerts et al. (2019). This is not because they are protected from  
453 temperature anomalies affecting shallow waters, but due to the high-amplitude and short-term  
454 temperature fluctuations at these depths that likely contributed to increasing the phenotypic plasticity  
455 or genotype selection (i.e. decreasing the thermal sensitivity) of antipatharians from these depths,  
456 compared to those exposed to lower levels of temperature fluctuations. Antipatharians, which are not  
457 dependent on light, may also escape climate change effects by migrating vertically towards deeper  
458 waters, providing they are able to acclimatize to these new environmental conditions (in terms of  
459 current, temperature, food and substrate availability). This seems plausible regarding the wide  
460 bathymetric range of *A. wollastoni*, spanning depths from 20 to 1425 m (Molodtsova, 2006).

461

#### 462 4.3 Thermal tolerance across sites subjected to internal waves

463 Respiration rates of mesophotic (80 m) colonies of *S. gracilis* from Lanzarote increased linearly with  
464 temperature (for both normalization methods used). No tipping point beyond which respiration rate  
465 starts to decrease was reached (the so-called "thermal optimum" of thermal biology; Pörtner, 2010;  
466 Angilletta, 2009), despite the ramping up to 7.5°C above the acclimation temperature (19°C) and 3°C  
467 above the maximum annual temperature (23.5°C). This indicates that the organisms increased their  
468 metabolism (and energy expenditures) but did not reach their physiological limits beyond which they  
469 are unable to supply enough oxygen to the tissues (Pörtner, 2010). A similar experiment (acute  
470 temperature increase by ramping; temperature range of 9°C; ~4-4.5°C above the maximum annual  
471 temperature) was performed on another *Stichopathes* species belonging to clade C from 85 m in the  
472 tropics (Mo'orea Island, French Polynesia) and a tipping point ("thermal optimum") for respiration  
473 was reached after an increase by 2.6°C above the acclimation temperature (Fig. S1, Godefroid et al.,

2023). Another experiment on the latter species showed that metabolic depression with temperature was associated with other signs of stress/declines in performances, such as reduced healing capacity, increased mucus production, tissue necrosis and increased antioxidant response (Godefroid et al., 2022a). These results therefore suggested that the tropical *Stichopathes* would quickly become impacted beyond thermal optimum. This comparison between two congeners *Stichopathes* from different ocean basins (Atlantic vs. Pacific), but at similar depths (80 - 85 m), suggests that *S. gracilis* from Lanzarote (subtropical) are less sensitive to thermal stress than *Stichopathes* sp. from Mo'orea (tropical latitudes). The difference in trends between the two populations (linear vs. Gaussian; Fig. S1) precludes statistical comparison, but the exceedance of thermal optimum in one case, and not in the other, supports a difference in thermal sensitivity. This difference could be linked to inherent species differences and/or to the thermal environment to which the two populations are exposed. Corals at 80 m in Lanzarote are probably exposed to a wider range of annual (6.6°C) and daily (maximum 4.4°C) temperatures than those at a similar depth in Mo'orea. Temperature data in the latter site is only available over a 40 days period but during the high internal wave activity season, i.e. when short term variability is maximum (Leichter, 2012; Godefroid et al., 2022a). In this record, the maximum daily range was 3.4°C. This is consistent with the view that exposure to more variable temperatures provides better tolerance to heat stress and that low latitude species have a narrower thermal tolerance breadth (Sunday et al., 2010).

From an ecological perspective, the lack of a tipping point ("thermal optimum") for *S. gracilis* from Lanzarote, even when subjected to +3°C above the highest temperature recorded in the field, is encouraging for the future of this habitat-forming species, which is present throughout the Canary Islands and in high density all around the island of Lanzarote. Future investigations should consider evaluating the thermal performance of this species over longer-term, with other endpoints (growth rate, reproductive capacity, healing capacity, etc.), to better understand the effects of ongoing warming on the MAFs elaborated by this species. Finally, as *S. gracilis* is found deeper than 80 m, the

499 comparison of the present results with other colonies from another depth would also complete our  
500 current understanding.

501

502 **Credit author statement**

503 Mathilde Godefroid: Conceptualization, Formal analysis, Investigation, Resources, Visualization,  
504 Writing – Original Draft, Review and Editing; Adriana Gouveia: Investigation, Writing: Review and  
505 Editing ; Francisco Otero-Ferrer: Conceptualization, Investigation, Resources, Supervision, Writing:  
506 Review and Editing; Fernando Espino: Resources, Writing: Review and Editing; Fernando Tuya:  
507 Resources, Writing: Review and Editing; Philippe Dubois: Conceptualization, Formal analysis,  
508 Supervision, Writing: Review and Editing.

509



510 **Funding sources**

511 M. Godefroid is holder of a Belgian FRIA grant (number 1.E.066.19F). Ph. Dubois is a Research Director  
512 of the National Fund for Scientific Research (FRS-FNRS; Belgium). The study was supported by the FNRS  
513 project [COBICO PDR/OL T.0084.18] and by the Royal Belgian Zoological Society (RBZS). Financial  
514 support was also provided by the LIFE Programme of the European Union, the French Office for  
515 Biodiversity (OFB) and the French Development Agency (AFD) through the LIFE4BEST Program through  
516 the B-CHARMED (The Black Coral forests as unexplored Biodiversity Hotspots in the  
517 Macaronesian Region: ecosystem functions and services analysed) project. The contents of this  
518 document are the sole responsibility of B-CHARMED and can under no circumstances be regarded as  
519 reflecting the position of the European Union nor of the OFB and AFD.

520

521 **Acknowledgments**

522 We would like to thank technical divers involved in the collection of the mesophotic coral fragments  
523 in Lanzarote: Dr L. Terrana, Dr L. Bramanti. We also thank Dr. Rafael Gines for the disposal of IU  
524 ECOAQUA biosecurity facilities to run the experiments.

525

526 **References**

527 Angilletta, M. J., Niewiarowski, P. H., & Navas, C. A. (2002). The evolution of thermal physiology in  
528 ectotherms. *Journal of Thermal Biology*, 27(4), 249–268. [https://doi.org/10.1016/S0306-](https://doi.org/10.1016/S0306-4565(01)00094-8)  
529 4565(01)00094-8

530 Angilletta Jr, M. J. (2009). Thermal adaptation: a theoretical and empirical synthesis.

531 Arístegui, J., Barton, E. D., Álvarez-Salgado, X. A., Santos, A. M. P., Figueiras, F. G., Kifani, S., Hernández-  
532 León, S., Mason, E., Machú, E., & Demarcq, H. (2009). Sub-regional ecosystem variability in the

533 Canary Current upwelling. *Progress in Oceanography*, 83(1–4), 33–48.  
534 <https://doi.org/10.1016/j.pocean.2009.07.031>

535 Banc-Prandi, G., Evensen, N. R., Barshis, D. J., Perna, G., Moussa Omar, Y., & Fine, M. (2022).  
536 Assessment of temperature optimum signatures of corals at both latitudinal extremes of the  
537 Red Sea. *Conservation Physiology*, 10(1), coac002.

538 Belkin, I. M. (2009). Rapid warming of Large Marine Ecosystems. *Progress in Oceanography*, 81(1–4),  
539 207–213. <https://doi.org/10.1016/j.pocean.2009.04.011>

540 Bianchi, C. N., Morri, R. H. C., & Wirtz, P. (2000). The subtidal epibenthic communities off Puerto del  
541 Carmen (Lanzarote, Canary Islands). *Arquipelago: Life and Marine Science*.

542 Blois, J. L., Williams, J. W., Fitzpatrick, M. C., Jackson, S. T., & Ferrier, S. (2013). Space can substitute for  
543 time in predicting climate-change effects on biodiversity. *Proceedings of the National Academy*  
544 *of Sciences*, 110(23), 9374–9379. <https://doi.org/10.1073/pnas.1220228110>

545 Bo, M., Bavestrello, G., Di Muzio, G., Canese, S., & Betti, F. (2019). First record of a symbiotic  
546 relationship between a polyclad and a black coral with description of *Anthoplana antipathellae*  
547 gen. Et sp. Nov. (Acotylea, Notoplanidae). *Marine Biodiversity*.  
548 <https://doi.org/10.1007/s12526-019-00982-8>

549 Bo, M., Rouse, G. W., Martin, D., & Bavestrello, G. (2014). A myzostomid endoparasitic in black corals.  
550 *Coral Reefs*, 33(1), 273–273. <https://doi.org/10.1007/s00338-013-1095-0>

551 Bongaerts, P., Ridgway, T., Sampayo, E. M., & Hoegh-Guldberg, O. (2010). Assessing the ‘deep reef  
552 refugia’ hypothesis: Focus on Caribbean reefs. *Coral Reefs*, 29(2), 309–327.  
553 <https://doi.org/10.1007/s00338-009-0581-x>

554 Brito, A., C. Dorta, and J. M. Falcón. (2014). First valid record of *Gymnothorax vicinus* (Pisces:  
555 Muraenidae) for Macaronesian ecoregion (Canary Islands): A process of tropicalization. *Rev.*  
556 *Acad. Canaria Cienc*, 26: 71-78.

557 Brito, A., Moreno-Borges, S., Escáñez, A., Falcón, J. M., & Herrera, R. (2017). New records of  
558 Actinopterygian fishes from the Canary Islands: tropicalization as the most important driving  
559 force increasing fish diversity. *Revista de la Academia Canaria de Ciencias*, 29(1), 31-44.

560 Byrne, M., Foo, S. A., Ross, P. M., & Putnam, H. M. (2020). Limitations of cross- and multigenerational  
561 plasticity for marine invertebrates faced with global climate change. *Global Change Biology*,  
562 26(1), 80–102. <https://doi.org/10.1111/gcb.14882>

563 Carson, M., & Harrison, D. E. (2008). Is the Upper Ocean Warming? Comparisons of 50-Year Trends  
564 from Different Analyses. *Journal of Climate*, 21(10), 2259–2268.  
565 <https://doi.org/10.1175/2007JCLI2002.1>

566 Chown, S. L., Jumbam, K. R., Sørensen, J. G., & Terblanche, J. S. (2009). Phenotypic variance, plasticity  
567 and heritability estimates of critical thermal limits depend on methodological  
568 context. *Functional Ecology*, 23(1), 133-140.

569 Cooley, S., Schoeman, D., Bopp, L., Boyd, P., Donner, S., Ito, S. I., ... & Yool, A. (2022). Oceans and  
570 coastal ecosystems and their services. In *IPCC AR6 WGII*. Cambridge University Press.

571 Czechowska, K., Feldens, P., Tuya, F., Cosme de Esteban, M., Espino, F., Haroun, R., Schönke, M., &  
572 Otero-Ferrer, F. (2020). Testing Side-Scan Sonar and Multibeam Echosounder to Study Black  
573 Coral Gardens: A Case Study from Macaronesia. *Remote Sensing*, 12(19), 3244.  
574 <https://doi.org/10.3390/rs12193244>

575 De Clippele, L. H., Huvenne, V. A. I., Molodtsova, T. N., & Roberts, J. M. (2019). The Diversity and  
576 Ecological Role of Non-scleractinian Corals (Antipatharia and Alcyonacea) on Scleractinian  
577 Cold-Water Coral Mounds. *Frontiers in Marine Science*, 6.  
578 <https://doi.org/10.3389/fmars.2019.00184>

579 Demarcq, H. (2009). Trends in primary production, sea surface temperature and wind in upwelling  
580 systems (1998–2007). *Progress in Oceanography*, 83(1–4), 376–385.  
581 <https://doi.org/10.1016/j.pocean.2009.07.022>

582 Espino, F., Tuya, F., del Rosario, A., Bosch, N. E., Coca, J., González-Ramos, A. J., del Rosario, F., Otero-  
583 Ferrer, F. J., Moreno, Á. C., & Haroun, R. (2019). Geographical Range Extension of the Spotfin  
584 burrfish, *Chilomycterus reticulatus* (L. 1758), in the Canary Islands: A Response to Ocean  
585 Warming? *Diversity*, *11*(12), 230. <https://doi.org/10.3390/d11120230>

586 Frade, P. R., Bongaerts, P., Englebert, N., Rogers, A., Gonzalez-Rivero, M., & Hoegh-Guldberg, O. (2018).  
587 Deep reefs of the Great Barrier Reef offer limited thermal refuge during mass coral bleaching.  
588 *Nature Communications*, *9*(1). <https://doi.org/10.1038/s41467-018-05741-0>

589 Frates, E., Hughes, A., & Randall, A. (2021). *Orbicella faveolata*: Shallow Versus Mesophotic Coral  
590 Responses to Temperature Change.

591 García Molinos, J., Halpern, B. S., Schoeman, D. S., Brown, C. J., Kiessling, W., Moore, P. J., ... & Burrows,  
592 M. T. (2016). Climate velocity and the future global redistribution of marine  
593 biodiversity. *Nature Climate Change*, *6*(1), 83-88.

594 Godefroid, M., Hédouin, L., Mercière, A., & Dubois, P. (2022a). Thermal stress responses of the  
595 antipatharian *Stichopathes* sp. from the mesophotic reef of Mo'orea, French Polynesia. *Science*  
596 *of The Total Environment*, *820*, 153094. <https://doi.org/10.1016/j.scitotenv.2022.153094>

597 Godefroid, M., Zeimes, T., Bramanti, L., Romans, P., Bo, M., Toma, M., Danis, B., Dubois, P., &  
598 Guillaumot, C. (2022b). Low vulnerability of the Mediterranean antipatharian *Antipathella*  
599 *subpinnata* (Ellis & Solander, 1786) to ocean warming. *Ecological Modelling*, *475*, 110209.

600 Godefroid, M., Dubois, P., Hédouin, L., & Under The Pole Consortium. (2023). Thermal performance  
601 with depth: Comparison of a mesophotic scleractinian and an antipatharian species subjected  
602 to internal waves in Mo'orea, French Polynesia. *Marine Environmental Research*, *184*, 105851.

603 Gould, K., Bruno, J. F., Ju, R., & Goodbody-Gringley, G. (2021). Upper-mesophotic and shallow reef  
604 corals exhibit similar thermal tolerance, sensitivity and optima. *Coral Reefs*, *40*, 907-920.

605 Gress, E., Eeckhaut, I., Godefroid, M., Dubois, P., Richir, J., & Terrana, L. (2021). Investigating densities  
606 of Symbiodiniaceae in two species of Antipatharians (black corals) from Madagascar.  
607 Molecular Biology. <https://doi.org/10.1101/2021.01.22.427691>

608 Hobday, A. J., Alexander, L. V., Perkins, S. E., Smale, D. A., Straub, S. C., Oliver, E. C., ... & Wernberg, T.  
609 (2016). A hierarchical approach to defining marine heatwaves. *Progress in Oceanography*, *141*,  
610 227-238.

611 Huey, R., & Stevenson, R. (1979). Integrating thermal physiology and ecology of ectotherms: A  
612 discussion of approaches. *Am Zool*, *19*, 357–366.

613 Johnson, M. D., Bravo, L. M. R., Lucey, N., & Altieri, A. H. (2021). Environmental legacy effects and  
614 acclimatization of a crustose coralline alga to ocean acidification. *Climate Change Ecology*, *2*,  
615 100016. <https://doi.org/10.1016/j.ecochg.2021.100016>

616 Jorda, G., Marbà, N., Bennett, S., Santana-Garcon, J., Agusti, S., & Duarte, C. M. (2020). Ocean warming  
617 compresses the three-dimensional habitat of marine life. *Nature Ecology & Evolution*, *4*(1),  
618 109–114. <https://doi.org/10.1038/s41559-019-1058-0>

619 Jurriaans, S., & Hoogenboom, M. (2020). Seasonal acclimation of thermal performance in two species  
620 of reef-building corals. *Marine Ecology Progress Series*, *635*, 55–70.

621 Leichter, J. J., Wing, S. R., Miller, S. L., & Denny, M. W. (1996). Pulsed delivery of subthermocline water  
622 to Conch Reef (Florida Keys) by internal tidal bores. *Limnology and Oceanography*, *41*(7),  
623 1490–1501. <https://doi.org/10.4319/lo.1996.41.7.1490>

624 Leichter, J. J., Stokes, M. D., Hench, J. L., Witting, J., & Washburn, L. (2012). The island-scale internal  
625 wave climate of Moorea, French Polynesia: internal waves on Mo'orea. *Journal of Geophysical*  
626 *Research: Oceans*, *117*(C6)

627 Lesser, M. P., Slattery, M., & Leichter, J. J. (2009). Ecology of mesophotic coral reefs. *Journal of*  
628 *Experimental Marine Biology and Ecology*, *375*(1–2), 1–8.  
629 <https://doi.org/10.1016/j.jembe.2009.05.009>

630 Lesser, M. P., Slattery, M., & Mobley, C. D. (2018). Biodiversity and Functional Ecology of Mesophotic  
631 Coral Reefs. *Annual Review of Ecology, Evolution, and Systematics*, 49(1), 49–71.  
632 <https://doi.org/10.1146/annurev-ecolsys-110617-062423>

633 Logan, C.A., Dunne, J.P., Eakin, C.M., & Donner, S.D. (2014). Incorporating adaptive responses into  
634 future projections of coral bleaching. *Global Change Biology*, 20(1), 125–139.

635 McClanahan, T., Maina, J., Moothien-Pillay, R., & Baker, A. (2005). Effects of geography, taxa, water  
636 flow, and temperature variation on coral bleaching intensity in Mauritius. *Marine Ecology  
637 Progress Series*, 298, 131–142. <https://doi.org/10.3354/meps298131>

638 Millero, F. J., & Huang, F. (2009). The density of seawater as a function of salinity (5 to 70 g kg<sup>-1</sup>) and  
639 temperature (273.15 to 363.15 K). *Ocean Science*, 5(2), 91–100. [https://doi.org/10.5194/os-5-  
640 91-2009](https://doi.org/10.5194/os-5-91-2009)

641 Millero, F. J., & Poisson, A. (1981). International one-atmosphere equation of state of seawater. *Deep  
642 Sea Research Part A. Oceanographic Research Papers*, 28(6), 625–629.  
643 [https://doi.org/10.1016/0198-0149\(81\)90122-9](https://doi.org/10.1016/0198-0149(81)90122-9)

644 Mitchell, K. A., & Hoffmann, A. A. (2010). Thermal ramping rate influences evolutionary potential and  
645 species differences for upper thermal limits in *Drosophila*. *Functional Ecology*, 24(3), 694–700.  
646 <https://doi.org/10.1111/j.1365-2435.2009.01666.x>

647 Molodtsova, T. N. (2006). Black corals (Anthipatharia: Anthozoa: Cnidaria) of the north-eastern  
648 Atlantic. *Biogeography of the North Atlantic Seamounts*, 141-151.

649 Mora, C., & Maya, M. F. (2006). Effect of the rate of temperature increase of the dynamic method on  
650 the heat tolerance of fishes. *Journal of Thermal Biology*, 31(4), 337-341.

651 Nash, J. D., Kelly, S. M., Shroyer, E. L., Moum, J. N., & Duda, T. F. (2012). The Unpredictable Nature of  
652 Internal Tides on Continental Shelves. *Journal of Physical Oceanography*, 42(11), 1981–2000.  
653 <https://doi.org/10.1175/JPO-D-12-028.1>

654 Ocaña, O., Opresko, D. M., & Brito, A. (2006). First record of the black coral *Antipathella wollastoni*  
655 (Anthozoa: Antipatharia) outside of Macaronesian waters. *Revista de la Academia Canaria de*  
656 *Ciencias*, 18(4), 125-138.

657 Ocaña, B., & Brito, A. (2004). *Corales de las Islas Canarias: antozoos con esqueleto de los fondos*  
658 *litorales y profundos*. Francisco Lemus, Editor.

659 Oliver, T. A., & Palumbi, S. R. (2011). Do fluctuating temperature environments elevate coral thermal  
660 tolerance? *Coral Reefs*, 30(2), 429–440. <https://doi.org/10.1007/s00338-011-0721-y>

661 Otero-Ferrer, F., Cosme, M., Tuya, F., Espino, F., & Haroun, R. (2020). Effect of depth and seasonality  
662 on the functioning of rhodolith seabeds. *Estuarine, Coastal and Shelf Science*, 235, 106579.

663 Palumbi, S. R., Barshis, D. J., Traylor-Knowles, N., & Bay, R. A. (2014). Mechanisms of reef coral  
664 resistance to future climate change. *Science*, 344(6186), 895-898.

665 Pardo, P., Padín, X., Gilcoto, M., Farina-Busto, L., & Pérez, F. (2011). Evolution of upwelling systems  
666 coupled to the long-term variability in sea surface temperature and Ekman transport. *Climate*  
667 *Research*, 48(2), 231–246. <https://doi.org/10.3354/cr00989>

668 Pérez-Rosales, G., Rouzé, H., Torda, G., Bongaerts, P., Pichon, M., Under The Pole Consortium,  
669 Parravicini, V., & Hédouin, L. (2021). Mesophotic coral communities escape thermal coral  
670 bleaching in French Polynesia. *Royal Society Open Science*, 8(11).  
671 <https://doi.org/10.1098/rsos.210139>

672 Perry, A. L., Low, P. J., Ellis, J. R., & Reynolds, J. D. (2005). Climate Change and Distribution Shifts in  
673 Marine Fishes. *Science*, 308(5730), 1912–1915. <https://doi.org/10.1126/science.1111322>

674 Pickett, S. T. A. (1989). Space-for-Time Substitution as an Alternative to Long-Term Studies. In G. E.  
675 Likens (Ed.), *Long-Term Studies in Ecology* (pp. 110–135). Springer New York.  
676 [https://doi.org/10.1007/978-1-4615-7358-6\\_5](https://doi.org/10.1007/978-1-4615-7358-6_5)

677 Pinsky, M. L., Selden, R. L., & Kitchel, Z. J. (2020). Climate-Driven Shifts in Marine Species Ranges:  
678       Scaling from Organisms to Communities. *Annual Review of Marine Science*, 12(1), 153–179.  
679       <https://doi.org/10.1146/annurev-marine-010419-010916>

680 Pörtner, H.-O. (2010). Oxygen- and capacity-limitation of thermal tolerance: A matrix for integrating  
681       climate-related stressor effects in marine ecosystems. *Journal of Experimental Biology*, 213(6),  
682       881–893. <https://doi.org/10.1242/jeb.037523>

683 Pörtner, H.-O., Bock, C., & Mark, F. C. (2017). Oxygen- and capacity-limited thermal tolerance: Bridging  
684       ecology and physiology. *Journal of Experimental Biology*, 220(15), 2685–2696.  
685       <https://doi.org/10.1242/jeb.134585>

686 Putnam, H. M. (2021). Avenues of reef-building coral acclimatization in response to rapid  
687       environmental change. *Journal of Experimental Biology*, 224.  
688       <https://doi.org/10.1242/jeb.239319>

689 Putnam, H. M., Mayfield, A. B., Fan, T. Y., Chen, C. S., & Gates, R. D. (2013). The physiological and  
690       molecular responses of larvae from the reef-building coral *Pocillopora damicornis* exposed to  
691       near-future increases in temperature and pCO<sub>2</sub>. *Marine Biology*, 160(8), 2157–2173.  
692       <https://doi.org/10.1007/s00227-012-2129-9>

693 R Core Team (2022). R: A language and environment for statistical computing. R Foundation for  
694       Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.

695 Reid, E. C., DeCarlo, T. M., Cohen, A. L., Wong, G. T. F., Lentz, S. J., Safaie, A., Hall, A., & Davis, K. A.  
696       (2019). Internal waves influence the thermal and nutrient environment on a shallow coral reef.  
697       *Limnology and Oceanography*, 64(5), 1949–1965. <https://doi.org/10.1002/lno.11162>

698 Rezende, E. L., Tejedó, M., & Santos, M. (2011). Estimating the adaptive potential of critical thermal  
699       limits: methodological problems and evolutionary implications. *Functional Ecology*, 25(1), 111-  
700       121.



701 Rivest, E. B., Comeau, S., & Cornwall, C. E. (2017). The Role of Natural Variability in Shaping the  
702 Response of Coral Reef Organisms to Climate Change. *Current Climate Change Reports*, 3(4),  
703 271–281. <https://doi.org/10.1007/s40641-017-0082-x>

704 Rossi, S., Bramanti, L., Gori, A., & Orejas, C. (Eds.). (2017). *Marine Animal Forests: The Ecology of*  
705 *Benthic Biodiversity Hotspots*. Springer International Publishing. [https://doi.org/10.1007/978-](https://doi.org/10.1007/978-3-319-17001-5)  
706 3-319-17001-5

707 Russel, L. V. (2016). Least-squares means: the R package lsmeans. *Journal of statistical software*, 69, 1-  
708 33.

709 Safaie, A., Silbiger, N. J., McClanahan, T. R., Pawlak, G., Barshis, D. J., Hench, J. L., Rogers, J. S., Williams,  
710 G. J., & Davis, K. A. (2018). High frequency temperature variability reduces the risk of coral  
711 bleaching. *Nature Communications*, 9(1). <https://doi.org/10.1038/s41467-018-04074-2>

712 Sangrá Inciarte, P., Basterretxea Oyarzabal, G., Pelegrí Llopart, J. L., & Arístegui, J. (2001). Chlorophyll  
713 increase due to internal waves on the shelf break of Gran Canaria (Canary Islands). *Scientia*  
714 *Marina*.

715 Schneider, C.A., Rasband, W.S., Eliceiri, K.W. (2012). NIH Image to ImageJ: 25 years of image analysis.  
716 *Nature Methods* 9, 671-675.

717 Schoepf, V., Stat, M., Falter, J. L., & McCulloch, M. T. (2015). Limits to the thermal tolerance of corals  
718 adapted to a highly fluctuating, naturally extreme temperature environment. *Scientific*  
719 *Reports*, 5(1). <https://doi.org/10.1038/srep17639>

720 Schulte, P. M., Healy, T. M., & Fanguie, N. A. (2011). Thermal Performance Curves, Phenotypic Plasticity,  
721 and the Time Scales of Temperature Exposure. *Integrative and Comparative Biology*, 51(5),  
722 691–702. <https://doi.org/10.1093/icb/icr097>

723 Siemer, J. P., Machín, F., González-Vega, A., Arrieta, J. M., Gutiérrez-Guerra, M. A., Pérez-Hernández,  
724 M. D., Vélez-Belchí, P., Hernández-Guerra, A., & Fraile-Nuez, E. (2021). Recent Trends in SST,  
725 Chl-  $\alpha$  , Productivity and Wind Stress in Upwelling and Open Ocean Areas in the Upper Eastern

726 North Atlantic Subtropical Gyre. *Journal of Geophysical Research: Oceans*, 126(8).  
727 <https://doi.org/10.1029/2021JC017268>

728 Silbiger, N. J., Goodbody-Gringley, G., Bruno, J. F., & Putnam, H. M. (2019). Comparative thermal  
729 performance of the reef-building coral *Orbicella franksi* at its latitudinal range limits. *Marine*  
730 *Biology*, 166(10). <https://doi.org/10.1007/s00227-019-3573-6>

731 Smith, T. B., Gyory, J., Brandt, M. E., Miller, W. J., Jossart, J., & Nemeth, R. S. (2016). Caribbean  
732 mesophotic coral ecosystems are unlikely climate change refugia. *Global Change Biology*,  
733 22(8), 2756–2765. <https://doi.org/10.1111/gcb.13175>

734 Solan, M., & Whiteley, N. M. (Eds.). (2016). *Stressors in the marine environment: Physiological and*  
735 *ecological responses; societal implications* (First edition). Oxford University Press.

736 Somero, G. N. (2010). The physiology of climate change: How potentials for acclimatization and genetic  
737 adaptation will determine ‘winners’ and ‘losers’. *Journal of Experimental Biology*, 213(6), 912–  
738 920. <https://doi.org/10.1242/jeb.037473>

739 Sunday, J. M., Bates, A. E., & Dulvy, N. K. (2010). Global analysis of thermal tolerance and latitude in  
740 ectotherms. *Proceedings of the Royal Society B: Biological Sciences*, 278, 1823-1830.  
741 <https://doi.org/10.1098/rspb.2010.1295>

742 Sunday, J. M., Bates, A. E., & Dulvy, N. K. (2012). Thermal tolerance and the global redistribution of  
743 animals. *Nature Climate Change*, 2(9), 686–690. <https://doi.org/10.1038/nclimate1539>

744 Tazioli, S., Bo, M., Boyer, M., Rotinsulu, H., & Bavestrello, G. (2007). Ecological Observations of Some  
745 Common Antipatharian Corals in the Marine Park of Bunaken (North Sulawesi, Indonesia).  
746 *Zoological Studies*, 15.

747 Terblanche, J. S., Deere, J. A., Clusella-Trullas, S., Janion, C., & Chown, S. L. (2007). Critical thermal limits  
748 depend on methodological context. *Proceedings of the Royal Society B: Biological*  
749 *Sciences*, 274(1628), 2935-2943.

750 Terrana, L., Lepoint, G., & Eeckhaut, I. (2019). Assessing trophic relationships between shallow-water  
751 black corals (Antipatharia) and their symbionts using stable isotopes. *Belgian Journal of*  
752 *Zoology*, 149(1). <https://doi.org/10.26496/bjz.2019.33>

753 Vélez-Belchí, P., González-Carballo, M., Pérez-Hernández, M. D. and Hernández-Guerra, A. (2015).  
754 Open ocean temperature and salinity trends in the Canary Current  
755 Large Marine Ecosystem. In: *Oceanographic and biological features in the Canary Current Large*  
756 *Marine Ecosystem*. Valdés, L. and Déniz-González, I. (eds). IOC-UNESCO, Paris. IOC Technical  
757 Series, No. 115, pp. 299-308.

758 Vergés, A., Steinberg, P. D., Hay, M. E., Poore, A. G. B., Campbell, A. H., Ballesteros, E., Heck, K. L.,  
759 Booth, D. J., Coleman, M. A., Feary, D. A., Figueira, W., Langlois, T., Marzinelli, E. M., Mizerek,  
760 T., Mumby, P. J., Nakamura, Y., Roughan, M., van Sebille, E., Gupta, A. S., ... Wilson, S. K. (2014).  
761 The tropicalization of temperate marine ecosystems: Climate-mediated changes in herbivory  
762 and community phase shifts. *Proceedings of the Royal Society B: Biological Sciences*,  
763 281(1789), 20140846. <https://doi.org/10.1098/rspb.2014.0846>

764 Wagner, D., Luck, D. G., & Toonen, R. J. (2012). The Biology and Ecology of Black Corals (Cnidaria:  
765 Anthozoa: Hexacorallia: Antipatharia). In *Advances in Marine Biology* (Vol. 63, pp. 67–132).  
766 Elsevier. <https://doi.org/10.1016/B978-0-12-394282-1.00002-8>

767 Wagner, D., Pochon, X., Irwin, L., Toonen, R. J., & Gates, R. D. (2011). Azooxanthellate? Most Hawaiian  
768 black corals contain Symbiodinium. *Proceedings of the Royal Society B: Biological Sciences*,  
769 278(1710), 1323–1328. <https://doi.org/10.1098/rspb.2010.1681>

770 Wall, M., Putschim, L., Schmidt, G. M., Jantzen, C., Khokiattiwong, S., & Richter, C. (2015). Large-  
771 amplitude internal waves benefit corals during thermal stress. *Proceedings of the Royal Society*  
772 *B: Biological Sciences*, 282(1799), 20140650. <https://doi.org/10.1098/rspb.2014.0650>

773 Wyatt, A. S. J., Leichter, J. J., Toth, L. T., Miyajima, T., Aronson, R. B., & Nagata, T. (2020). Heat  
774 accumulation on coral reefs mitigated by internal waves. *Nature Geoscience*, 13(1), 28–34.  
775 <https://doi.org/10.1038/s41561-019-0486-4>

776 Yao, C.-L., & Somero, G. N. (2014). The impact of ocean warming on marine organisms. *Chinese Science*  
777 *Bulletin*, 59(5–6), 468–479. <https://doi.org/10.1007/s11434-014-0113-0>

778 Yapıcı, S., Filiz, H., & Bilge, G. (2016). Northwards range expansion of *Sparisoma cretense* (Linnaeus,  
779 1758) in the Turkish Aegean Sea. *Journal of Aquaculture Engineering and Fisheries*  
780 *Research*, 2(4), 201-207.

781