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**Low vulnerability of the Mediterranean antipatharian *Antipathella subpinnata* (Ellis & Solander, 1786) to ocean warming**

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## Abstract

Antipatharians (black corals) are major components of mesophotic ecosystems in the Mediterranean Sea. The arborescent species *Antipathella subpinnata* has received particular attention as it is the most abundant and forms dense forests harbouring high levels of biodiversity. This species is currently categorized as “Near Threatened” in the IUCN Red List, due to increasing fishing pressure and bottom-trawling activities. Yet, the effects of ocean warming have never been investigated for this species, nor for any other antipatharians from temperate regions. Our study aimed at evaluating the effects of increasing seawater temperatures on *A. subpinnata*, by combining predictive distribution modelling with a physiological tolerance experiment. During the latter, we exposed *A. subpinnata* for 15 days to different temperature conditions spanning the current seasonal range to forecasted temperatures for 2100, while measuring biological endpoints such as oxygen consumption rates and different signs of stress (tissue necrosis, total antioxidant capacity). Unexpectedly, no stress was found at organism nor cellular level (wide thermal breadth) suggesting low susceptibility of this species to mid-term temperature increase. If the response to the 15-days heat stress is representative of the response to longer-term warming, ocean warming is unlikely to affect *A. subpinnata*. The species distribution model predicted the presence of *A. subpinnata* at depths that correspond to temperatures colder than its maximum thermal tolerance (as determined by the physiology experiment). This suggests that the presence of *A. subpinnata* at shallower depths is not limited by physiological constraints but by other ecological factors including interspecific competition.

**Keywords:** Antipatharia, thermotolerance, mesophotic, Mediterranean Sea, physiology, niche modelling

## 1. Introduction

Greenhouse gas emission since 1750 has committed the global ocean to future warming. While the amplitude of warming remains to be determined by our current actions, increase in global ocean temperature is already irreversible (IPCC, 2022). The Mediterranean Sea and associated ecosystems represent no exception. From 1982 to 2019, Mediterranean Sea surface temperatures (SST) have increased by 0.35°C per decade (Pastor et al., 2020) and, under business-as-usual emissions (RCP8.5), models forecast a rise of SST (0-150m) of +2.07-3.71°C by the end of the century (Soto-Navarro et al., 2020).

Increasing ocean temperature is inducing a wide range of effects on marine organisms, as temperature is one of the most important environmental factors for the majority of marine organisms (Yao & Somero, 2014). Among the observed effects, ocean warming has been showed to modify the distribution of certain species, which use this strategy to move towards areas matching their environmental preferenda (Jorda et al., 2020). Other strategies to cope with ocean warming may involve acclimatization to the new environmental conditions (i.e., phenotypic plasticity) or genetic adaptation. Thus, experimental studies addressing responses to environmental changes should be performed using organisms from different habitats as they can be adapted to local conditions and this may explain why some ecosystems are more sensitive to warming than others. For example, a small increase in temperature can be enough to drive significant consequences in ecosystems characterised by extremely stable temperature, such as in the Southern Ocean (Hogg et al., 2011). Benthic organisms, such as those forming Marine Animal Forests (MAFs; sensu Rossi et al., 2017), may also be particularly threatened by ocean warming due to their inability to move away from adverse environmental conditions.

The concept of MAF was recently introduced to describe benthic communities formed by sessile suspension feeders (i.e., ecosystem engineers such as corals, sponges or bryozoans) that form three-dimensional structures, resembling terrestrial forests. These communities increase habitat

heterogeneity, providing food, shelter and reproductive facilities for a plethora of associated fauna (Rossi et al., 2017). The development of underwater imagery (Remotely Operated Vehicles, submersibles) and deep diving techniques in recent years contributed to uncover that antipatharians can also form MAFs (i.e., black coral forests) throughout the world oceans (Terrana et al., 2020; Wagner et al., 2012).

In the Mediterranean Sea, the branched antipatharian *Antipathella subpinnata* (Ellis & Solander, 1786) was reported to be one of the most frequently observed species in the mesophotic zone (Bo et al., 2008, 2018, 2019; Ingrassia & Di Bella, 2021). Forests of *A. subpinnata* have been described in the Tyrrhenian Sea (Bo et al., 2009, 2014; Gravier, 1918), the Ligurian Sea (Bo et al., 2008), the Adriatic Sea (Chimienti et al., 2020), the Sardinian coast (Cau et al., 2015) and the Sicily Channel (Deidun et al., 2014). The role of *A. subpinnata* as habitat forming species was evidenced by the great diversity of associated fauna (Bo et al., 2012, 2015a), including multiple species of conservation and commercial interest (Bo et al., 2009; Chimienti et al., 2020). The main anthropogenic threats for antipatharians in the Mediterranean Sea are fishing and bottom trawling (Bo et al., 2009, 2019; Chimienti et al., 2020), which may have long-lasting effects considering the low growth rates of these species (Bo et al., 2015a). For these reasons, antipatharians have been mentioned in multiple international agreements such as in the Appendix II of the CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora), the Annex II of a Barcelona Convention Protocol for the Specially Protected Area of Mediterranean Interest and the Annex III of the Berna Convention. Since 2014, *A. subpinnata* is categorized as “Near Threatened” by the International Union for Conservation of Nature (IUCN) Red List of Mediterranean Anthozoa (Bo et al., 2015b, 2017).

It is today acknowledged that ectotherms may be particularly sensitive to ocean warming as temperature has direct effects on their biological processes across all levels of organization (Pörtner and Farrell, 2008). Moreover, previous studies on Mediterranean epibenthic suspension feeders showed that increasing temperature may have deleterious impacts, both in experimental conditions

and *in situ*, including mass-mortality events (Arizmendi-Mejía et al., 2015; Bramanti et al., 2005; Cerrano et al., 2000; Garrabou et al., 2009; Kružić et al., 2016; Kipson et al., 2012; Linares et al., 2013). To date, only one experiment addressed the effects of thermal stress in an antipatharian species (*Stichopathes* sp.; Godefroid et al., 2022). This mesophotic tropical species was experimentally exposed to medium-term (16 days) heat stress (up to 4.5°C), and results highlighted metabolic depression, impairment of healing capacities and activation of stress response mechanisms (i.e., tissue necrosis, mucus production and antioxidant responses). In the Mediterranean Sea, the effects of increasing temperature on antipatharian species have never been investigated, despite the fact that temperature has been shown to significantly influence their distribution (Etnoyer et al., 2018; Wagner, 2015; Yesson et al., 2017). Investigating the effects of ocean warming is particularly relevant for *A. subpinnata* forests, whose vulnerability is increased by the low genetic connectivity between offshore and coastal populations (Terzin et al., 2021). To date, we only know that the species is likely limited below an upper thermal threshold of 15°C, based on its depth distribution (mainly between 65 and 200m; Bo et al., 2008). However, physiological studies on the effects of ocean warming on this species are currently lacking.

In this study, we investigated the effects of increasing seawater temperature on the mesophotic antipatharian *A. subpinnata* from the Mediterranean Sea, by combining experimental and distribution modelling approaches. First, the experimental study aimed at establishing the thermal performance curve (TPC) for respiration of *A. subpinnata*, as well as the impact of temperature on stress response variables (tissue necrosis, antioxidant capacity, mortality). TPC allows describing thermal sensitivity of organisms by determining a thermal window of performance (i.e., thermal breadth,  $T_{br}$ ), characterized by the so-called optimal temperature ( $T_{opt}$ ) at which the performance is maximal ( $P_{max}$ ) and beyond which it starts to decrease (Angilletta, 2009; Schulte et al., 2011). Large  $T_{br}$  is often good indicator of low sensitivity to changes in temperature, while narrow  $T_{br}$  often indicates high susceptibility as only a small increase in temperature may result in suboptimal conditions (Jurriaans & Hoogenboom, 2020). Based on Godefroid et al. (2022), we hypothesized that *A. subpinnata* has a narrow thermal window

and might be severely impacted by increasing temperatures. Then, we developed a Species Distribution Model (SDM) to explore the role of temperature in the distribution of *A. subpinnata*. SDMs are based on a statistical relationship between occurrence records and environmental data (Elith et al., 2006; Elith & Leathwick, 2009), which are both available for *A. subpinnata* in the Mediterranean Sea. Here, we used environmental conditions at the location of available presence-only data to generate a matrix to build the SDM. The output represents the probability distribution of *A. subpinnata* occurrence projected on a map, allowing to identify regions in the Mediterranean Sea where the environment fulfils the required conditions. We also aimed at generating partial dependence plots for each environmental descriptors used in the model, to assess if temperature is one of the main environmental drivers for the distribution of *A. subpinnata* (as in Guillaumot et al., 2018). The combination of the two approaches used in this study (physiological experiment + SDM) allowed to improve predictions accuracy with respect to an approach based on the sole SDMs, as well as to facilitate interpretation and infer robust conclusions (Benito Garzón et al., 2019; Buckley et al., 2010, 2011; Dormann et al., 2018; Elith et al., 2010; López-Farrán et al., 2021; Singer et al., 2016).

## **2. Materials and Methods**

### **2.1 Thermotolerance experiment**

#### **2.1.1 Experimental design**

Portions of seven adult colonies of *A. subpinnata* were collected by SCUBA diving (Self-Contained Underwater Breathing Apparatus) with closed circuit rebreather at 70m depth in Bordighera (43°46.11' N, 7°40.82' E, Ligurian sea, Italy) on March 29<sup>th</sup> 2021 (Fig. 1A). Seawater temperature at the time and depth of collection was 14.5°C. During the collection, all the portions of the same colony were sealed in the same plastic bag with seawater from the collection site. Seven plastic bags, containing portions of seven coral colonies, were transported to Banyuls-sur-Mer aquarium facilities (*Biodiversarium*, France) and portions of colonies were suspended in an open-circuit 2000-L tank filled with 0.2mm-

149 filtered seawater pumped at 12m depth and maintained, for 49 days, at 14.5°C using a water chiller  
150 (AQUAVIE ICE-2000). After this acclimation period, six apical fragments (8-10 cm) were cut from each  
151 colony, fixed on a PVC base using epoxy resin (Aquarium Systems, Holdfast epoxy) and installed in six  
152 experimental aquaria (17 L) at 14.5°C (TECO; Fig. 1B). Each aquarium contained one fragment from  
153 each colony ( $n=7$ ). Fragments were left one week at 14.5°C and then temperature was progressively  
154 decreased/increased by 0.5°C/day until reaching the target temperature. Treatment temperatures  
155 were selected to span over the seasonal range of temperatures (13-16°C; Soto-Navarro et al., 2020) as  
156 well as to include temperatures expected by the end of the century under Representative  
157 Concentration Pathway (RCP) 8.5: 14, 15, 16, 17, 18 and 19°C. The six aquaria were placed in a  
158 circulating water bath at 13°C which temperature was controlled using a water chiller (Teco; Fig. 1B).  
159 In addition, temperature was controlled independently in each aquarium using temperature  
160 controllers (Hobby Biotherm Pro) connected to a titanium heating resistance. Temperature was  
161 manually checked at least twice per day with a thermometer (Ebro TFX-410-1). Filtered seawater (12m  
162 depth, 0.2 mm diameter) was continuously flowing in each aquarium at a rate of  $1.2 \pm 0.3$  L/hour. The  
163 room was equipped with blue lights to simulate the natural light regime ( $0.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ ; photoperiod:  
164 12h/day and 12h/night; based on Coppari et al., 2020). Colonies were fed once a day with live *Artemia*  
165 *salina* and Rotifera provided by the aquarium facilities of *Biodiversarium*.

166 Outflows of seawater from each aquarium was equipped with a propagule trap composed of a 0.2 mm  
167 net to catch bailed-out propagules. The formation of motile propagules from individual polyps was  
168 proposed as an ultimate escape strategy in response to stressful conditions. It was previously observed  
169 on *A. subpinnata* (Coppari et al., 2020) but never as a response to increasing temperatures. Every  
170 morning, traps were checked for the presence of propagules under a dissecting microscope. Nets were  
171 then cleaned before being placed back in the propagule traps.

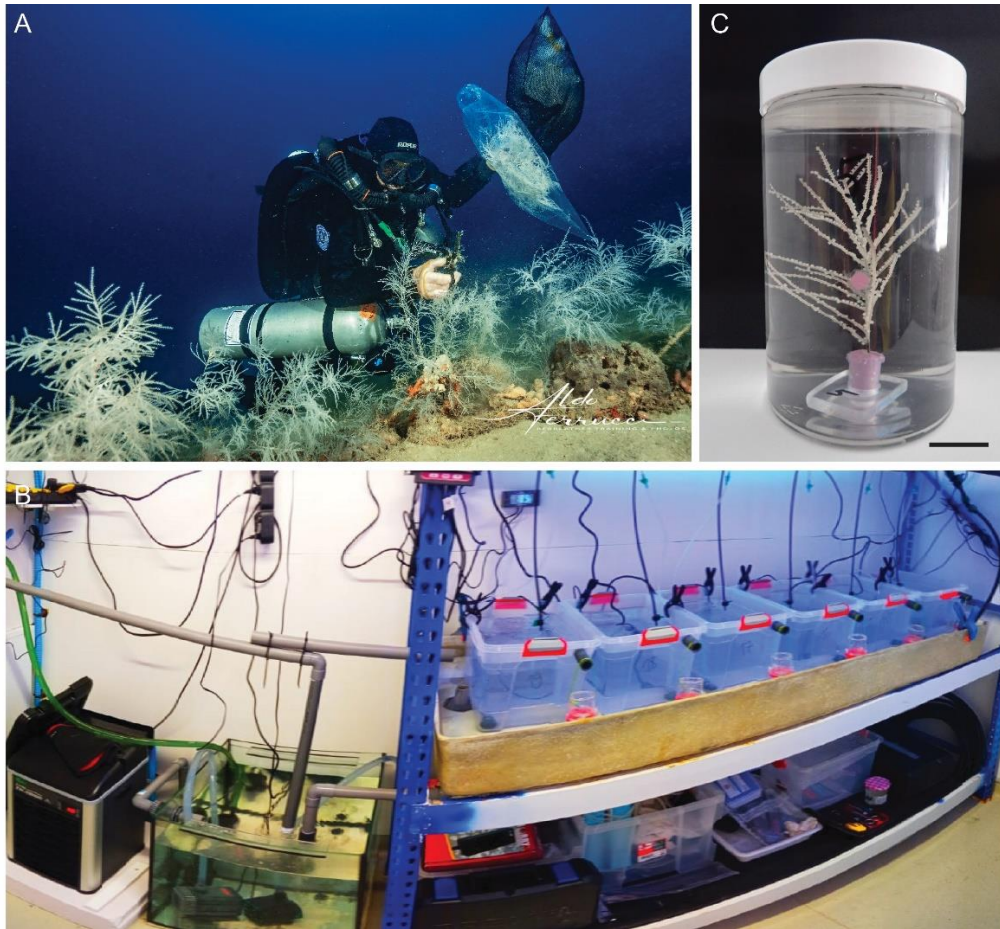


Tissue necrosis (i.e., the partial loss of live tissues around the skeleton) was recorded daily for all fragments, as an estimated surface proportion (0, 25, 50, 75, 100%). Mortality (i.e., 100% tissue loss) was also checked daily for all fragments and reported on a binary scale (dead/alive).

After 15 days of exposure, standard metabolic rate was inferred from oxygen consumption rates on every fragment. Fragments were placed in individual 400-mL respirometry chambers filled with seawater from the corresponding aquarium and provided with an oxygen sensor spot (PreSens SP-PSt3-NAU-D5-YOP-SA) and a magnetic stir bar allowing complete homogenization of the water during the measurement (Fig. 1C). Measurements of oxygen consumption were taken simultaneously on eight respirometry chambers, with two respirometers (PreSens OXY-4 SMA G2 and OXY-4 SMA G3). One chamber was only filled with seawater to measure the rate of background respiration (the respiration of the microorganisms naturally present in seawater). The chambers were placed in a 60-L tank which temperature was controlled with a heating resistance. First, chambers were left open for one hour in the dark to allow the fragments to acclimatize to these conditions. Then, chambers were closed and oxygen saturation (in %) was recorded every five seconds for three to four hours, using the Presens Measurement Studio 2 software. Oxygen saturation measurements were normalized based on the volume of seawater in the experimental chambers, calculated from the density of seawater (Millero & Huang, 2009; Millero & Poisson, 1981). Oxygen saturation was then converted to oxygen concentration (in  $\mu\text{mol L}^{-1}$ ) and the rate of oxygen consumption was calculated from the slope of its linear regression with time. Oxygen consumption rate of the fragments was corrected according to the consumption rate of the seawater-only chamber and normalized by the total length of the fragment (i.e., sum of length of all branches and branchlets) measured using ImageJ (Schneider et al., 2012). Oxygen consumption rates were expressed in  $\mu\text{mol O}_2 \text{ hr}^{-1} \text{ cm}^{-1}$  and in  $\mu\text{mol O}_2 \text{ hour}^{-1} \text{ g}^{-1}$  (Fig. S4).

At the end of the respirometry assay, a 2-3 cm piece was cut from each coral fragment and placed in a tube with phosphate buffer (50 mM), for biomarker analysis. Tissues were separated from the skeleton and homogenized using a micro pestle. Homogenates were centrifuged for 10 min at 4°C (10000g,

Eppendorf Centrifuge 5430R) and the supernatant was transferred into a new tube and stored at -80°C until analysis. The subsequent protocol was identical to that reported in Godefroid et al. (2022). Total protein content in the samples was determined using a commercial reagent kit based on the Bradford assay (Pierce™ BCA Protein Assay Kit, ThermoFisher Scientific Inc., USA) with bovine serum albumin (BSA) as standard (2 mg/mL). Protein contents were used for biomarker normalization. Measurement of total antioxidant capacity (TAC) was carried out using OxiSelect™ Total Antioxidant Capacity Assay Kit (Cell Biolabs Inc., USA), an electron-transfer based assay (Huang et al., 2005) that measures the capacity of an antioxidant solution to reduce an oxidant (Copper (II) reduced into Copper (I)). The chromatic change is proportional with the sample antioxidant concentration. Absorbance was measured at 490 nm in a microplate reader (Beckman Coulter Paradigm) and compared to uric acid standard curves. Results were normalized to the protein content and expressed as “mM Copper Reducing Equivalents per g of protein”.



**Figure 1.** (A) Collection of portions of colonies of *Antipathella subpinnata* at 70m in Bordighera (Italy). Photo credit: Aldo Ferrucci ; (B) Experimental set-up with the 6 aquaria, in the aquarium facilities of the *Biodiversarium*. Photo credit: Lorenzo Bramanti; (C) respirometry chamber containing a fragment of *Antipathella subpinnata*. Scale bar: 2cm. Photo credit: Tom Zeimes.

### 2.1.2 Data analysis

The relationship between respiration rate and temperature was analysed using a symmetrical Gaussian function (Rodolfo-Metalpa et al., 2014) fitted by non-linear regression with the R package *nlstools* (Baty et al., 2015):

$$P = P_{\max} e^{0.5 \left( \frac{T - T_{\text{opt}}}{c} \right)^2}$$

where  $P$  is the temperature dependent physiological response,  $T_{\text{opt}}$  is the optimal temperature at which this response is maximal ( $P_{\text{max}}$ ) and  $c$  indicates the breadth of the thermal response. The standard error of the parameters estimates was also obtained with the model. The effect of temperature on TAC was analysed using simple linear regression, with temperature as the independent variable.

## 2.2 Species distribution modelling

### 2.2.1 Occurrence dataset

Georeferenced presence-only data of *A. subpinnata* in the Mediterranean Sea were retrieved from the archives of the *Università di Genova* ( $n=85$ ) (Bo & Toma, unpublished data), the scientific literature ( $n=34$ ) (Bo et al., 2008, 2009, 2012, 2014; Canovas-Molinas et al., 2016; Cau et al., 2015, 2017; Chimienti et al., 2020; Coppari et al., 2019; Fabri et al., 2014, 2019, 2021; Gaino & Scoccia, 2010; Pierdomenico et al., 2016; Santin et al., 2021; van de Water et al., 2020), and the open-source GBIF (Global Biodiversity Information Facility,  $n=10$ ; Fautin, 2013; Orrell et al., 2022; iNaturalist, 2022; Inventaire National du Patrimoine Naturel, 2022a, 2022b) and OBIS (Ocean Biodiversity Information System,  $n=2$ ; Hellenic Centre for Marine Research, 2022) databases. Some historical records were not considered because they were lacking a systematic description (doubtful taxonomic determination) and/or because coordinates were not available for the collected specimen (Bo et al., 2008). The dataset was checked for redundant information (duplicates), georeferencing errors and inconsistencies. The final dataset used for the distribution model included 131 presence-only records (Fig. S1). Absence records were not taken into account.

### 2.2.2 Environmental data sets

The distribution of *A. subpinnata* was modelled using eight environmental descriptors (Table 1). Depth and slope were retrieved from the MARSPEC database (Sbrocco & Barber, 2013). The other six environmental descriptors were loaded from Bio-Oracle marine layers (Assis et al., 2018; Tyberghein et al., 2012).

All environmental layers were cropped to cover the same geographic area (Latitude: 28.60°N to 47.60°N, Longitude: 5.75°W to 38.25°E). In order to limit extrapolation of the model, projection area was limited to habitats presenting a maximum depth of 1500m (Guillaumot et al., 2020a, 2021).

In order to identify and remove collinearity (i.e., the non-independence of predictor variables that are linearly related in a statistical model; Dormann et al., 2013) between environmental descriptors, the Variance Inflation Factor (VIF) and the Spearman correlation index were used (Guillaumot et al., 2019).

The VIF was calculated based on the equation:

$$VIF_i = \frac{1}{R_i^2}$$

where  $R_i^2$  is the determination coefficient of the prediction of all other variables (Dormann et al., 2013).

**Table 1.** Environmental descriptors and associated sources used for the distribution model. The Bio-ORACLE (<https://www.bio-oracle.org/>) environmental layers provide average monthly values for the period 2000-2014 at a spatial resolution of 0.083° and MARSPEC (<https://www.marspec.org/>) provides data layers at a spatial resolution of 0.0083°. ORAP: Global Ocean Physics Reanalysis ECMWF; ARMOR: Global Observed Ocean Physics Reprocessing; PISCES: Global Ocean Biogeochemistry Non-assimilative Hindcast.

Descriptor	Unit	Spatial resolution	Source	Layers metadata
Depth	m	0.086°	MARSPEC	Extracted from SRTM30_PLUS V6.0 dataset (Becker et al., 2009; Sbrocco & Paul, 2013)
Slope	degrees (°)	0.086°	MARSPEC	Derived from bathymetry using ArcGIS 9.3.1; (Sbrocco & Paul, 2013)
Mean seafloor current	m.s <sup>-1</sup>	0.086°	Bio-ORACLE	ORAP (Assis et al., 2017)

Mean seafloor temperature	°C	0.086°	Bio-ORACLE	ARMOR (Assis et al., 2017)
Minimum seafloor temperature	°C	0.086°	Bio-ORACLE	ARMOR (Assis et al., 2017)
Maximal seafloor temperature	°C	0.086°	Bio-ORACLE	ARMOR (Assis et al., 2017)
Mean seafloor oxygen concentration	μmol.L <sup>-1</sup>	0.086°	Bio-ORACLE	PISCES (Assis et al., 2017)
Mean sea surface chlorophyll- <i>a</i> concentration	mg.m <sup>-3</sup>	0.086°	Bio-ORACLE	PISCES (Assis et al., 2017)

### 2.2.3 Spatial aggregation: evaluation and correction

The distribution map of *A. subpinnata* in the Mediterranean Sea shows spatial heterogeneity in the occurrence data, with more georeferenced data in the Tyrrhenian and Ligurian Seas (Fig. S1). Spatial aggregation may result in overestimating the contribution of environmental variables in the most densely sampled areas (Araújo & Guisan, 2006; Dormann, 2007). To correct the effect of spatial aggregation of the presence-only data on modelling performance, we used a targeted sampling of background data samples (Phillips et al., 2009). Background data are used in SDM having only presence-only records to characterize the environmental conditions reported in the area where the model will be projected (Barbet-Massin et al., 2012; Elith et al., 2006; Pearce & Boyce, 2006). Here, the background data were sampled following the scheme of a Kernel Density Estimation layer (KDE) that gives an estimate of the aggregation bias (Guillaumot et al., 2019). The KDE was calculated using the function *kde2d* of the R package *MASS* (Fig. S2; Ripley, 2015). The significance of spatial aggregation of presence data was quantified before and after the KDE correction, using the Moran's I index, that evaluates the correlation between presence data and the probability of predicted presence based on model residuals (Luoto et al., 2005). Moran's I values vary between -1 and 1, with positive values (0 to 1) reflecting that spatially close residuals will share similar presence probability and negative values (-1 to 0) indicating a maximal or random dispersion of residuals in space (Cliff & Ord, 1981). This was calculated using the R package *ape* (Paradis et al., 2019) for 15 model replicates.

284

#### 285 2.2.4 Model calibration

286 SDMs were built using the Boosted Regression Trees (BRTs) algorithm, which were calibrated based on  
287 the method provided in Elith et al. (2008). BRTs were selected as they were shown to be well-suited to  
288 accommodate presence-only data and to integrate complex interactions between environmental  
289 descriptors (Elith et al., 2008). Moreover, BRTs were shown to be suitable for oceanic datasets with  
290 spatially autocorrelated and broad-scale presence-only datasets (Guillaumot et al., 2019). BRTs were  
291 also shown to identify and delete redundant environmental information, therefore minimizing the  
292 effect of collinearity of environmental descriptors (Guillaumot et al., 2020b). To calibrate the models,  
293 the following settings were used: tree complexity 4; bag fraction 0.8; learning rate 0.011; and number  
294 of background data sampled 10000. These parameters were chosen to minimise the model predictive  
295 deviance to the test data (reduction of error) and to optimize the model with the minimum number of  
296 trees (reduction of complexity) (Fig. S3).

297

#### 298 2.2.5 Spatial cross-validation and model performances

299 Modelling performance was assessed using a spatial random cross-validation procedure, as in  
300 Guillaumot et al. (2019). Considering the spatial aggregation of occurrence records in the dataset, the  
301 occurrence dataset was randomly split into four spatial groups, using the function *get.block* from the  
302 R package *ENMeval* (Kass et al., 2021). Three out of four groups were used as a training subset and one  
303 group as a test subset. When the proportion of correct predictions in the test group was above 70%,  
304 the pixel was considered as favourable for *A. subpinnata*. Model performance was also assessed using  
305 the area under the curve (AUC; Fielding & Bell, 1997), the true skill statistics (TSS; Allouche et al., 2006)  
306 and the biserial correlation metrics (COR; Elith et al., 2006).

307

## 2.2.6 Spatial extrapolation

The Multivariate Environmental Similarity Surface (MESS) index (Elith et al., 2010) was used to remove extrapolation errors in the model, using the R function *mess* in the package *dismo* (Hijmans et al., 2017). It consists in extracting the environmental conditions where presence data were recorded and determining for each pixel of the model projection layer if environmental conditions are covered by presence record (Guillaumot et al., 2019). It allows to dismiss areas where environmental conditions are not met, when the value of at least one environmental descriptor is beyond the environmental range of presence records (model extrapolation; negative MESS values).

## 2.2.7 Model outputs

In total, 50 SDMs with distinct background samplings were generated with the R function *compute.brt* of the package *SDMPlay* (Guillaumot et al., 2021). The average of the 50 replicates was used to build the SDM projections of the presence probability. *SDMPlay* was also used to assess the contribution of each environmental descriptors to the model, i.e. the importance of each descriptor in the model calibration.

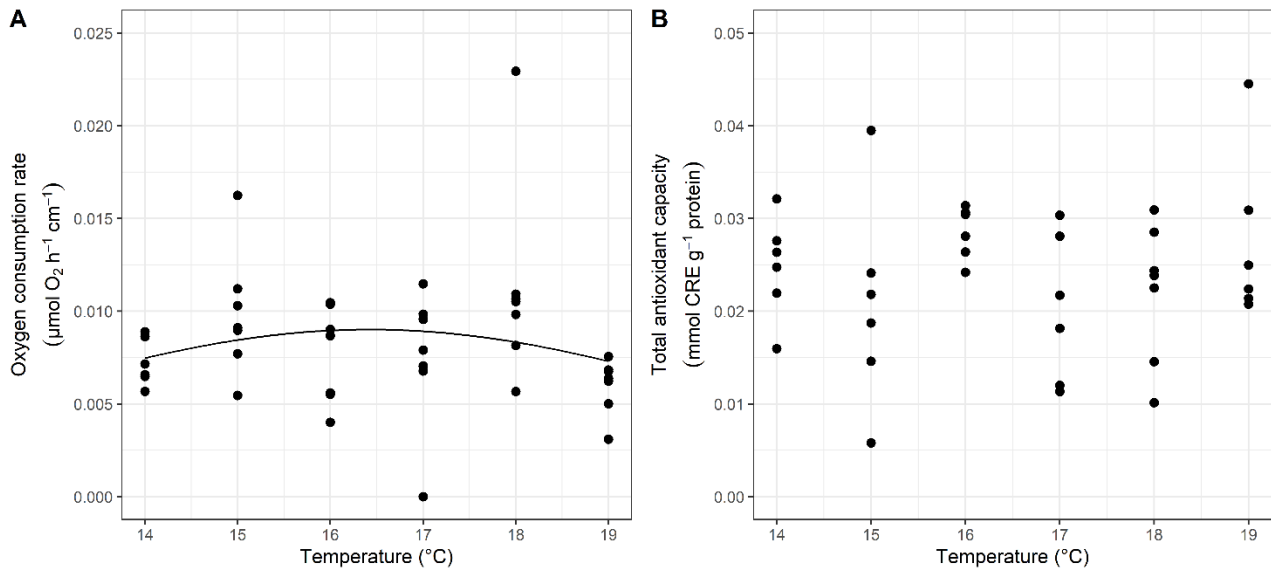
# 3. Results

## 3.1 Thermotolerance experiment

Neither tissue necrosis, mortality nor polyp bail-out were observed in any treatment over the course of the experiment. The relationship between oxygen consumption rate and temperature can be described by a Gaussian curve (Fig. 2A) with its maximum ( $0.009 \pm 0.001 \mu\text{mol O}_2 \text{ h}^{-1} \text{ cm}^{-2}$ ; mean  $\pm$  se;  $p < 0.001$ ;  $P_{\text{max}}$ ) at  $16.4 \pm 0.7^\circ\text{C}$  ( $p < 0.001$ ;  $T_{\text{opt}}$ ). The standard deviation of the curve ( $c$ ) was estimated in  $4.0 \pm 1.7^\circ\text{C}$  ( $p < 0.05$ ). Similar results were obtained when oxygen consumption was normalized using



the weight of the fragments (Fig. S4, Table S1). Finally, temperature had no significant effect on the antioxidant capacity of *A. subpinnata* (linear regression,  $p=0.76$ ; Fig. 2B).



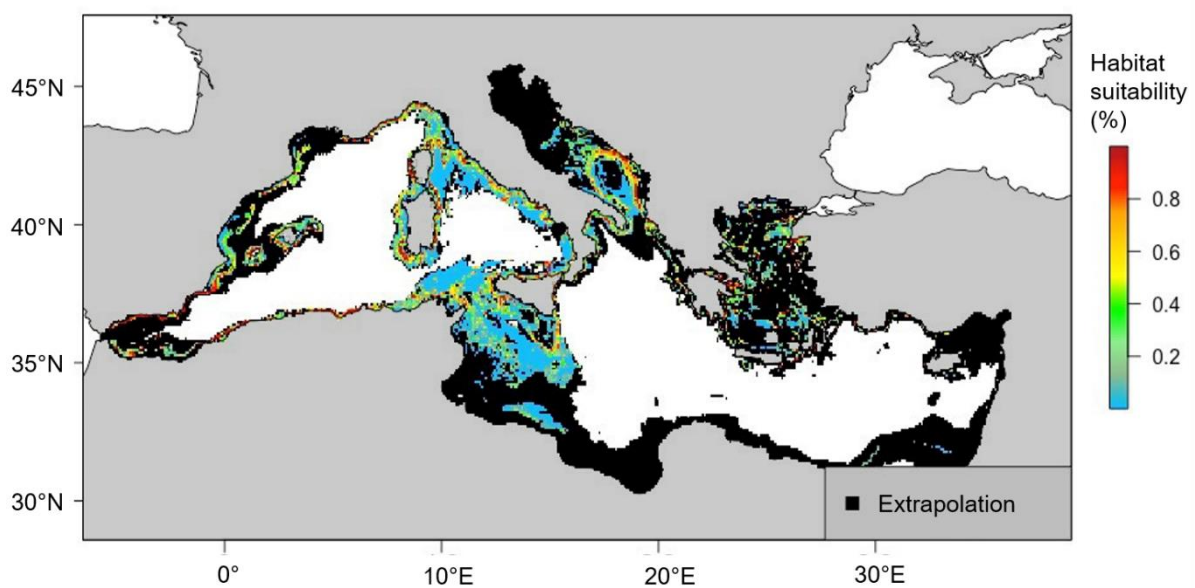
**Figure 2.** Effects of temperature on *Antipathella subpinnata* (A) Oxygen consumption rate (μmol O<sub>2</sub> h<sup>-1</sup> cm<sup>-1</sup>), (B) Total antioxidant capacity (mmol Copper Reducing Equivalents g<sup>-1</sup> protein).

### 3.2 SDM projections under current environmental conditions (2000-2014)

SDMs showed high performance scores, with AUC of  $0.999 \pm 0.001$ , TSS of  $0.738 \pm 0.017$  and COR of  $0.972 \pm 0.007$ . The proportion of correctly classified test data also showed high values for the four groups of occurrence data used for spatial cross-validation, with  $98.42 \pm 2.49\%$  (mean  $\pm$  se) for group 1,  $98.19 \pm 2.81\%$  for group 2,  $99.60 \pm 1.47\%$  for group 3 and  $96.69 \pm 4.04\%$  for group 4. The proportion of extrapolated area was 65.86% (Fig. 3), supporting the use of the MESS method (Guillaumot et al., 2019, 2020a).

In addition to the occurrence data of *A. subpinnata* in the Tyrrhenian, Ligurian, Adriatic, Ionian and Aegean Seas (Fig. S1), the model projected very high presence probabilities in the Alboran Sea (South coast of Spain and North coast of Morocco), along the Algerian coast, around the Balearic Islands, along

the East coast of the Adriatic Sea (Coasts of Croatia, Bosnia and Herzegovina, Montenegro, Albania) and in the South coast of Greece, near Athens (Fig. 3). Model projections also suggested an intermediate probability of presence in the Balearic and Adriatic Seas, around Corsica, Sardinia, Sicily and Malta, and in the waters between the coast of Tunisia and Sicily (Fig. 3).



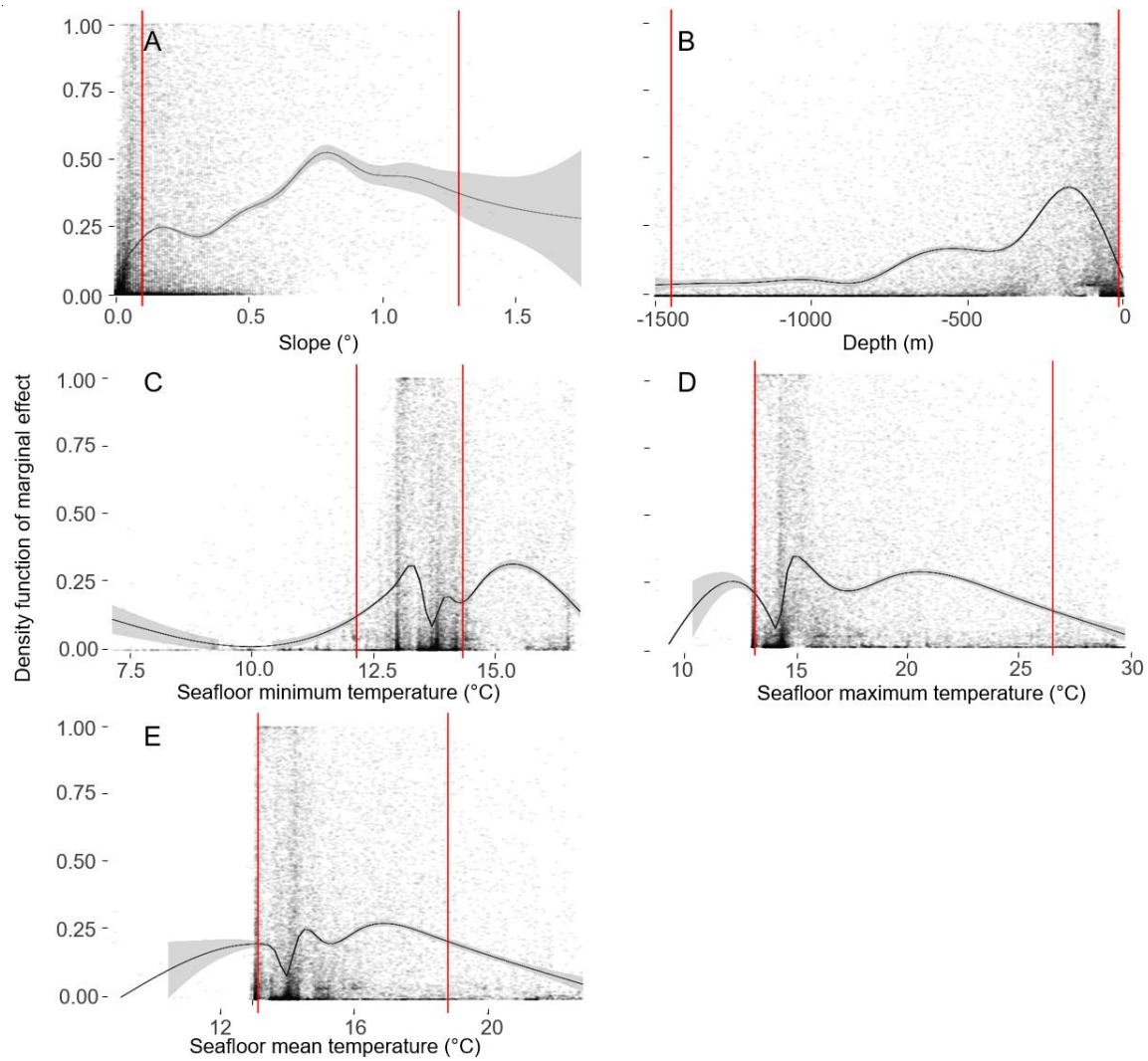
**Figure 3.** Distribution model predictions of the likelihood of presence of *Antipathella subpinnata* (between 0 and 1) under current environmental conditions (2000-2014) for the Mediterranean Sea. Model results are the average of 50 model replicates. Black pixels indicate areas of model extrapolation, where environmental conditions are outside the conditions used for their calibration (i.e., Multivariate Environmental Similarity Surface, MESS index evaluation). White pixels correspond to areas of the Mediterranean Sea that are deeper than 1,500m.

The two main descriptors contributing to the species distribution model are slope ( $45.9 \pm 13.2\%$ ) and depth ( $43.9 \pm 13.6\%$ ), which together contributed to 89.8% (Table 2). In contrast, environmental descriptors characterizing seafloor temperature only contributed for 5.4%, including  $2.4 \pm 0.8\%$  for minimum,  $1.7 \pm 0.8\%$  for maximum and  $1.3 \pm 0.6\%$  for mean seafloor temperatures. Suitable areas for

depth were found in the range of 60 to 325m, with a maximum occurrence probability at 240m. Occurrence probability as predicted by the model remained high between 325 and 600m depth but were unlikely below 600m (Fig. 4). Suitable habitats for temperature corresponded to mean temperatures between 14.3 and 15.9°C (with a predicted maximum at 14.9°C), maximum temperatures between 14.7 and 18°C (with a predicted maximum at 15.2°C) (Fig. 4). Despite its major contribution to the model, partial dependence plot for the slope did not allow identifying clear environmental preferences for this descriptor (Fig. 4).

**Table 2.** Environmental descriptors contributions (mean and standard deviation - SD) to model calibration

Environmental descriptor	Mean $\pm$ SD (%)
Slope	45.9 $\pm$ 13.2
Depth	43.9 $\pm$ 13.6
Minimum seafloor temperature	2.4 $\pm$ 0.8
Mean sea surface chlorophyll- <i>a</i> concentration	1.9 $\pm$ 0.7
Maximum seafloor temperature	1.7 $\pm$ 0.8
Mean seafloor current	1.6 $\pm$ 0.6
Mean seafloor oxygen	1.4 $\pm$ 0.4
Mean seafloor temperature	1.3 $\pm$ 0.6



**Figure 4.** Partial dependence plots for the two descriptors that contributed the most to the model: Slope (A) and Depth (B); and for the environmental descriptors associated to seafloor temperature: Minimum (C), Maximum (D) and Mean (E). Data points (black) were fitted with General Additive Model (GAM, black line). Vertical red lines indicate the range of values in which the model does not extrapolate.

#### 4. Discussion

Spatial ecology and experimental biology have long been considered as separate research disciplines. Yet, a number of studies have shown that combining both approaches can improve species distribution projections in the context of ongoing climate change (Kotta et al., 2019; Urban et al., 2016). In order to achieve more robust projections of biotic patterns, information gathered from physiological

tolerance experiments should also be incorporated (Buckley et al., 2010). For these reasons, we combined experimental and modelling approaches to investigate the effects of increasing temperatures on the branched antipatharian *A. subpinnata* from the Mediterranean Sea. Results from spatial predictive modelling indicated that the distribution of *A. subpinnata* is driven by a combination of interacting factors rather than by a single leading environmental descriptor. For depth, the upper and lower bathymetric limits estimated by the model at 60 and 600m respectively, match with observations from Bo et al. (2008). Ocean current is also important for antipatharians as it provides them with suspended food particles (Genin et al., 1986; Warner, 1981). However, hydrodynamic preferences vary between species. The unbranched species from Indonesia were shown to preferentially select sites with higher hydrodynamics than branched species (Tazioli et al., 2007), as further supported by higher bending resistance in unbranched species (Dugauquier et al., 2021). This may explain the preferences of *A. subpinnata* to relatively gentle slopes and moderate current speeds. For temperature, mean temperature correlating with its distribution ranged between 14.3 and 15.9°C (with a maximum at 14.9°C) and the upper limit of the range of maximum temperature was 18°C, suggesting that *A. subpinnata* can thrive at 18°C for several days. Such a narrow temperature interval may either indicate that the species is not physiologically able to survive at temperatures outside this range, or that other factors involved in the areas where temperatures are not in this range prevent the establishment of *A. subpinnata*. SDM projections also highlighted the areas with favourable environmental conditions for *A. subpinnata* but where no occurrences have been recorded to date in the Mediterranean Sea. These model outputs could help guide future exploration and sampling efforts as well as providing further validation of the model. In addition, some areas in the Mediterranean Sea where high probability of presence were identified by the model to coincide with areas of some of the historical taxonomic determinations that could not be used in the presence data to build the model as they were doubtful and/or lacked georeferencing data (Bo et al., 2008). Examples include specimens near Gibraltar (Alboran Sea; Ellis & Solander, 1786) and along the Algerian coast (Vafidis & Koukouras; 1998). This provides additional data supporting the model.

414 Results obtained from the thermotolerance experiment suggest that *A. subpinnata* will not be  
415 impacted by temperature expected by the end of the century (19°C, +4.5°C), at the studied time scale  
416 (15 days). No signs of stress were detected, without mortality, tissue necrosis nor effects on the  
417 antioxidant response at any temperature, while a previous experiment on the tropical antipatharian  
418 *Stichopathes* sp. recorded tissue necrosis under only +3°C for 16 days (Godefroid et al., 2022). High  
419 tissue necrosis was also noticed in the temperate coral *Cladocora caespitosa* subjected to +3°C for 3  
420 weeks, followed by subsequent mortality (Kersting et al., 2013; Rodolfo-Metalpa et al., 2005). In  
421 addition, bail-out propagules were never found in the traps, which may indicate that these  
422 temperature conditions were not stressful for *A. subpinnata* or that temperature do not trigger the  
423 formation of propagules. Indeed, the stress factor responsible for the release of free-living propagules  
424 in *A. subpinnata* has not yet been identified (Coppari et al., 2020). Despite this, active detachment of  
425 polyps from the colony under warmer conditions was previously observed for the tropical scleractinian  
426 *Pocillopora damicornis* (Fordyce et al., 2017), supporting the idea that temperature projected for 2100  
427 is not high enough to trigger this response in *A. subpinnata*. This is further supported by the absence  
428 of antioxidant response. If increasing temperature had created oxidative stress at cellular level, the  
429 organism would have used antioxidant defence mechanisms to counter these effects. Such response  
430 was previously observed in the antipatharian *Stichopathes* sp. (+4.5°C for 16 days; Godefroid et al.,  
431 2022) and in tropical corals (+4°C for 60 days; Dias et al., 2019).

432 The effects of temperature on oxygen consumption rates allowed to identify an optimal temperature  
433 ( $T_{opt}$ ) at 16.4°C, beyond which metabolic rate starts to decrease with temperature. This is likely related  
434 to the disruption of enzymatic activities with increasing temperature, rather than by a reduction of  
435 metabolic costs (Jurriaans & Hoogenboom, 2020). However, the width of the thermal window of  
436 performance ( $T_{br}$ ) was large (6°C) as compared to a similar thermotolerance experiment on the tropical  
437 antipatharian *Stichopathes* sp. (with  $T_{br}$  of 3.2°C; Godefroid et al., 2022), suggesting that increasing  
438 temperature is likely to have less impact on *A. subpinnata*. A wide  $T_{br}$  is often described as a good

strategy in front of ocean warming as it implies that an increase in temperature will have milder effects on performances as compared to species with narrow  $T_{br}$  (Jurriaans & Hoogenboom, 2020).

Overall, physiological results suggest that *A. subpinnata* is not strongly influenced by temperature and is likely a thermal generalist species with low thermal sensitivity. This strategy is characterized by the ability of the species to maintain the integrity of their physiological functions over a wide range of temperatures (Angiletta, 2009). However, SDMs showed that the distribution of *A. subpinnata* is more likely between mean temperatures of 14.3-15.9°C, which is below  $T_{opt}$  (16.4°C). Ideally, *A. subpinnata* should be present in habitats which temperature is close to  $T_{opt}$ , to optimize its metabolic activity. However, this inconsistency should be weighed by the wide thermal breadth ( $T_{br}$ ) of *A. subpinnata* (6°C) which covers the entire range of mean temperatures predicted by the model. That is, even if *A. subpinnata* lives in suboptimal conditions in terms of metabolic performances, the drop in performance remains low owing to its wide  $T_{br}$ .

A possible explanation for the mismatch between  $T_{opt}$  and suitable average temperatures for *A. subpinnata* calculated by the SDM may be biotic interactions such as interspecific competition. SDMs are built based on presence-only data and allow to represent the realized niche of a species (i.e., the area in which the species is found), constrained by biotic factors, abiotic conditions and the regions that are accessible to dispersal by the species (Soberon & Peterson, 2005). However, SDMs are limited by their incapacity to explicitly integrate biotic interactions in model construction (Saucède et al., 2019).

In tropical reef ecosystems, community structure is characterized by depth zonation caused by multiple factors such as competitive interactions or light. Shallow waters are dominated by obligatory photosynthetic organisms such as algae and corals, while deep waters are mainly composed of facultatively or non-photosynthetic organisms (Kahng & Kelley, 2007; Wagner et al., 2012). Temperature and light gradient are key intercorrelated factors in regulating the distribution of species across depths (Kahng & Kelley, 2007). Suitable habitats and bathymetric distribution of antipatharians

are thus the result of abiotic and biotic interactions (Tazioli et al., 2007; Wagner et al., 2012). In tropical shallow habitats, antipatharians compete for space with zooxanthellate scleractinians (Tazioli et al., 2007) and macrophytes (Kahng & Kelley, 2007). Larvae or bailed-out propagules' settlement could be inhibited by the mechanical action of the macrophytes sweeping the substrate. In case of successful settlement, they would probably be outcompeted by surrounding macrophytes and scleractinians which are characterized by faster growth rates. We suggest that the competition for space with crustose coralline algae and other habitat-forming species (sponges and Anthozoans) may also explain the distribution of *A. subpinnata* in the Mediterranean Sea. The actual distribution of *A. subpinnata* would therefore not be the consequence of physiological limitations, as suggested by Bo et al. (2008), but rather the result of interspecific competition and probably also larval dispersal (completely unknown for this species).

As a consequence of global warming, mean shallow-water temperature (0-150m) in the Mediterranean is expected to increase by 3.7°C under the most pessimistic scenario (RCP 8.5; Soto-Navarro et al., 2020). Even under this extreme scenario, seawater temperature will remain within the large thermal tolerance window of *A. subpinnata*, suggesting that it should not suffer from deleterious physiological impacts, if results obtained here over short-term (15 days) also apply to longer term. How thermal tolerance estimated under experimental conditions can be extrapolated to natural settings is an ongoing debate. It is noteworthy that the duration and intensity of the experimental assay influence the observed response (Sinclair et al., 2016). For example, the mechanisms influencing performance at acute and chronic time scales may be quite different, and TPC shape can change with acclimation (Schulte et al., 2011). Rezende et al (2014) demonstrated that the temperature range that an organism can tolerate is expected to narrow down with the duration of the thermal challenge. With this in mind, it could be that we did not observe any effects over 15d but would have if exposure had been longer (>15d). Despite this, none of the endpoints recorded during the experiment seem to indicate a sign of stress, neither at the physiological, nor at the subcellular level (antioxidant response). In addition, the capacity for plastic responses to changing temperatures can also depend on the rate of temperature



change, and generally, organisms that are shifted slowly to higher temperatures are expected to perform better than those that are exposed to fast warming rate (e.g. Sobek et al. 2011). Here, warming rate from the acclimatisation to the test temperature was faster than the warming rate expected under OW. The observed responses therefore potentially worsen the effects, compared to a more gradual (realistic) temperature increase. For all these reasons, we do not see any obvious reason to doubt the high tolerance of *A. subpinnata* under OW.

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513 **CRedit (Contribution Roles Taxonomy) author statement**

514 **Godefroid Mathilde:** Conceptualization, Methodology, Software, Formal analysis, Investigation,  
515 Writing – Original draft, Visualization, Funding acquisition; **Zeimes Tom:** Conceptualization,  
516 Methodology, Software, Formal analysis, Investigation, Writing – Review & Editing; **Bramanti Lorenzo:**  
517 Resources, Supervision, Writing – Review & Editing, Funding acquisition; **Romans Pascal:** Resources,  
518 Writing – Review & Editing; **Bo Marzia:** Resources, Writing – Review & Editing; **Toma Margherita:**  
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522 Editing.

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## References

- Allouche, O., Tsoar, A., & Kadmon, R. (2006). Assessing the accuracy of species distribution models: Prevalence, kappa and the true skill statistic (TSS): Assessing the accuracy of distribution models. *Journal of Applied Ecology*, 43(6), 1223–1232. <https://doi.org/10.1111/j.1365-2664.2006.01214.x>
- Angilletta, M. J. (2009). *Thermal adaptation: A theoretical and empirical synthesis*. Oxford University Press.
- Araújo, M. B., & Guisan, A. (2006). Five (or so) challenges for species distribution modelling. *Journal of Biogeography*, 33(10), 1677–1688. <https://doi.org/10.1111/j.1365-2699.2006.01584.x>
- Arizmendi-Mejía, R., Ledoux, J. B., Civit, S., Antunes, A., Thanopoulou, Z., Garrabou, J., & Linares, C. (2015). Demographic responses to warming: reproductive maturity and sex influence vulnerability in an octocoral. *Coral Reefs*, 34(4), 1207–1216.
- Assis, J., Tyberghein, L., Bosch, S., Verbruggen, H., Serrão, E. A., De Clerck, O., & Tittensor, D. (2018). Bio-ORACLE v2.0: Extending marine data layers for bioclimatic modelling. *Global Ecology and Biogeography*, 27(3), 277–284. <https://doi.org/10.1111/geb.12693>
- Barbet-Massin, M., Jiguet, F., Albert, C. H., & Thuiller, W. (2012). Selecting pseudo-absences for species distribution models: How, where and how many?: *How to use pseudo-absences in niche modelling? Methods in Ecology and Evolution*, 3(2), 327–338. <https://doi.org/10.1111/j.2041-210X.2011.00172.x>
- Baty F, Ritz C, Charles S, Brutsche M, Flandrois J-P, Delignette-Muller M-L (2015). A Toolbox for Nonlinear Regression in R: The Package nlstools. *Journal of Statistical Software*, 66(5), 1–21. <https://doi.org/10.18637/jss.v066.i05>
- Becker, J. J., D. T. Sandwell, W. H. F. Smith, J. Braud, B. Binder, J. Depner, D. Fabre, J. Factor, S. Ingalls, S-H. Kim, R. Ladner, K. Marks, S. Nelson, A. Pharaoh, R. Trimmer, J. Von Rosenberg, G. Wallace, and P. Weatherall. 2009. Global Bathymetry and Elevation Data at 30 Arc Seconds Resolution: SRTM30\_PLUS. *Marine Geodesy* 32:355–371. <https://doi.org/10.1080/01490410903297766>
- Benito Garzón, M., Robson, T. M., & Hampe, A. (2019). ΔTrait SDMs: Species distribution models that account for local adaptation and phenotypic plasticity. *New Phytologist*, 222(4), 1757–1765. <https://doi.org/10.1111/nph.15716>
- Bo, M., Barucca, M., Biscotti, M. A., Brugler, M. R., Canapa, A., Canese, S., Lo Iacono, C., & Bavestrello, G. (2018). Phylogenetic relationships of Mediterranean black corals (Cnidaria:

557 Anthozoa : Hexacorallia) and implications for classification within the order Antipatharia.  
 558 *Invertebrate Systematics*, 32(5), 1102. <https://doi.org/10.1071/IS17043>  
 559 Bo, M., Bavestrello, G., Angiolillo, M., Calcagnile, L., Canese, S., Cannas, R., Cau, A., D'Elia, M.,  
 560 D'Oriano, F., Follesa, M. C., Quarta, G., & Cau, A. (2015a). Persistence of Pristine Deep-Sea  
 561 Coral Gardens in the Mediterranean Sea (SW Sardinia). *PLOS ONE*, 10(3), e0119393.  
 562 <https://doi.org/10.1371/journal.pone.0119393>  
 563 Bo, M., Orejas, C., Garcia, S., Antoniadou, C. & Cerrano, C. (2015b). *Antipathella subpinnata*. *The*  
 564 *IUCN Red List of Threatened Species* 2015: e.T50902681A50902879. Accessed on 10 February  
 565 2022.  
 566 Bo, M., Bavestrello, G., Canese, S., Giusti, M., Salvati, E., Angiolillo, M., & Greco, S. (2009).  
 567 Characteristics of a black coral meadow in the twilight zone of the central Mediterranean  
 568 Sea. *Marine Ecology Progress Series*, 397, 53–61. <https://doi.org/10.3354/meps08185>  
 569 Bo, M., Canese, S., & Bavestrello, G. (2014). Discovering Mediterranean black coral forests:  
 570 *Parantipathes larix* (Anthozoa: Hexacorallia) in the Tuscan Archipelago, Italy. *Italian Journal of*  
 571 *Zoology*, 81(1), 112–125. <https://doi.org/10.1080/11250003.2013.859750>  
 572 Bo, M., Canese, S., Spaggiari, C., Pusceddu, A., Bertolino, M., Angiolillo, M., Giusti, M., Loreto, M. F.,  
 573 Salvati, E., Greco, S., & Bavestrello, G. (2012). Deep Coral Oases in the South Tyrrhenian Sea.  
 574 *PLoS ONE*, 7(11), e49870. <https://doi.org/10.1371/journal.pone.0049870>  
 575 Bo, M., Montgomery, A. D., Opresko, D. M., Wagner, D., & Bavestrello, G. (2019). Antipatharians of  
 576 the Mesophotic Zone: Four Case Studies. In Y. Loya, K. A. Puglise, & T. C. L. Bridge (Eds.),  
 577 *Mesophotic Coral Ecosystems* (Vol. 12, pp. 683–708). Springer International Publishing.  
 578 [https://doi.org/10.1007/978-3-319-92735-0\\_37](https://doi.org/10.1007/978-3-319-92735-0_37)  
 579 Bo, M., Numa, C., del Mar Otero, M., Orejas, C., Garrabou, J., Cerrano, C., Kružić, P., Antoniadou, C.,  
 580 Aguilar, R., Kipson, S., Linares, C., Terrón-Sigler, A., Brossard, J., Kersting, D., Casado-Amezúa,  
 581 P., García, S., Goffredo, S., Ocaña, O., Caroselli, E., ... Özalp, B. (2017). *Overview of the*  
 582 *conservation status of Mediterranean anthozoa*. IUCN International Union for Conservation  
 583 of Nature. <https://doi.org/10.2305/IUCN.CH.2017.RA.2.en>  
 584 Bo, M., Tazioli, S., Spanò, N., & Bavestrello, G. (2008). *Antipathella subpinnata* (Antipatharia,  
 585 Myriopathidae) in Italian seas. *Italian Journal of Zoology*, 75(2), 185–195.  
 586 <https://doi.org/10.1080/11250000701882908>  
 587 Buckley, L. B., Urban, M. C., Angilletta, M. J., Crozier, L. G., Rissler, L. J., & Sears, M. W. (2010). Can  
 588 mechanism inform species' distribution models?: Correlative and mechanistic range models.  
 589 *Ecology Letters*, no-no. <https://doi.org/10.1111/j.1461-0248.2010.01479.x>

590 Buckley, L. B., Waaser, S. A., MacLean, H. J., & Fox, R. (2011). Does including physiology improve  
 591 species distribution model predictions of responses to recent climate change? *Ecology*,  
 592 92(12), 2214–2221. <https://doi.org/10.1890/11-0066.1>  
 593 Cánovas-Molina, A., Montefalcone, M., Bavestrello, G., Cau, A., Bianchi, C. N., Morri, C., ... & Bo, M.  
 594 (2016). A new ecological index for the status of mesophotic megabenthic assemblages in the  
 595 Mediterranean based on ROV photography and video footage. *Continental Shelf*  
 596 *Research*, 121, 13-20. <https://doi.org/10.1016/j.csr.2016.01.008>  
 597 Cau, A., Follesa, M. C., Moccia, D., Alvito, A., Bo, M., Angiolillo, M., Canese, S., Paliaga, E. M., Orrù, P.  
 598 E., Sacco, F., & Cannas, R. (2015). Deepwater corals biodiversity along roche du large  
 599 ecosystems with different habitat complexity along the south Sardinia continental margin  
 600 (CW Mediterranean Sea). *Marine Biology*, 162(9), 1865–1878.  
 601 <https://doi.org/10.1007/s00227-015-2718-5>  
 602 Cau, A., Moccia, D., Follesa, M. C., Alvito, A., Canese, S., Angiolillo, M., Cuccu, D., Bo, M., & Cannas, R.  
 603 (2017). Coral forests diversity in the outer shelf of the south Sardinian continental margin.  
 604 *Deep Sea Research Part I: Oceanographic Research Papers*, 122, 60–70.  
 605 <https://doi.org/10.1016/j.dsr.2017.01.016>  
 606 Cerrano, C., Bavestrello, G., Bianchi, C. N., Cattaneo-vietti, R., Bava, S., Morganti, C., Morri, C., Picco,  
 607 P., Sara, G., Schiaparelli, S., Siccardi, A., & Sponga, F. (2000). A catastrophic mass-mortality  
 608 episode of gorgonians and other organisms in the Ligurian Sea (North-western  
 609 Mediterranean), summer 1999. *Ecology Letters*, 3(4), 284–293.  
 610 <https://doi.org/10.1046/j.1461-0248.2000.00152.x>  
 611 Chimienti, G., De Padova, D., Mossa, M., & Mastrototaro, F. (2020). A mesophotic black coral forest  
 612 in the Adriatic Sea. *Scientific Reports*, 10(1). <https://doi.org/10.1038/s41598-020-65266-9>  
 613 Cliff, A. & Ord, J.K. (1981). Spatial Processes Models and Applications. Pion Ltd.  
 614 Coppari, M., Fumarola, L., Bramanti, L., Romans, P., Pillot, R., Bavestrello, G., & Bo, M. (2020).  
 615 Unveiling asexual reproductive traits in black corals: Polyp bail-out in Antipathella  
 616 subpinnata. *Coral Reefs*. <https://doi.org/10.1007/s00338-020-02018-1>  
 617 Coppari, M., Mestice, F., Betti, F., Bavestrello, G., Castellano, L., & Bo, M. (2019). Fragmentation, re-  
 618 attachment ability and growth rate of the Mediterranean black coral Antipathella  
 619 subpinnata. *Coral Reefs*, 38(1), 1–14. <https://doi.org/10.1007/s00338-018-01764-7>  
 620 Deidun, A., Andaloro, F., Bavestrello, G., Canese, S., Consoli, P., Micallef, A., Romeo, T., & Bo, M.  
 621 (2014). First characterisation of a *Leiopathes glaberrima* (Cnidaria: Anthozoa: Antipatharia)  
 622 forest in Maltese exploited fishing grounds. *Italian Journal of Zoology*, 1–10.  
 623 <https://doi.org/10.1080/11250003.2014.986544>

624 Dias, M., Madeira, C., Jogee, N., Ferreira, A., Gouveia, R., Cabral, H., Diniz, M., & Vinagre, C. (2019).  
625 Oxidative stress on scleractinian coral fragments following exposure to high temperature and  
626 low salinity. *Ecological Indicators*, 107, 105586.  
627 <https://doi.org/10.1016/j.ecolind.2019.105586>

628 Dormann, C. F. (2007). Effects of incorporating spatial autocorrelation into the analysis of species  
629 distribution data. *Global Ecology and Biogeography*, 16(2), 129–138.  
630 <https://doi.org/10.1111/j.1466-8238.2006.00279.x>

631 Dormann, C. F., Bobrowski, M., Dehling, D. M., Harris, D. J., Hartig, F., Lischke, H., Moretti, M. D.,  
632 Pagel, J., Pinkert, S., Schleuning, M., Schmidt, S. I., Sheppard, C. S., Steinbauer, M. J., Zeuss,  
633 D., & Kraan, C. (2018). Biotic interactions in species distribution modelling: 10 questions to  
634 guide interpretation and avoid false conclusions. *Global Ecology and Biogeography*, 27(9),  
635 1004–1016. <https://doi.org/10.1111/geb.12759>

636 Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B.,  
637 Lafourcade, B., Leitão, P. J., Münkemüller, T., McClean, C., Osborne, P. E., Reineking, B.,  
638 Schröder, B., Skidmore, A. K., Zurell, D., & Lautenbach, S. (2013). Collinearity: A review of  
639 methods to deal with it and a simulation study evaluating their performance. *Ecography*,  
640 36(1), 27–46. <https://doi.org/10.1111/j.1600-0587.2012.07348.x>

641 Dugauquier, J., Godefroid, M., M'Zoudi, S., Terrana, L., Todinanahary, G., Eeckhaut, I., & Dubois, P.  
642 (2021). Ecomechanics of black corals (Cnidaria: Anthozoa: Hexacorallia: Antipatharia): A  
643 comparative approach. *Invertebrate Biology*. <https://doi.org/10.1111/ivb.12347>

644 Elith, J., H. Graham, C., P. Anderson, R., Dudík, M., Ferrier, S., Guisan, A., J. Hijmans, R., Huettmann,  
645 F., R. Leathwick, J., Lehmann, A., Li, J., G. Lohmann, L., A. Loiselle, B., Manion, G., Moritz, C.,  
646 Nakamura, M., Nakazawa, Y., McC. M. Overton, J., Townsend Peterson, A., ... E.  
647 Zimmermann, N. (2006). Novel methods improve prediction of species' distributions from  
648 occurrence data. *Ecography*, 29(2), 129–151. [https://doi.org/10.1111/j.2006.0906-](https://doi.org/10.1111/j.2006.0906-7590.04596.x)  
649 [7590.04596.x](https://doi.org/10.1111/j.2006.0906-7590.04596.x)

650 Elith, J., Kearney, M., & Phillips, S. (2010). The art of modelling range-shifting species: *The art of*  
651 *modelling range-shifting species*. *Methods in Ecology and Evolution*, 1(4), 330–342.  
652 <https://doi.org/10.1111/j.2041-210X.2010.00036.x>

653 Elith, J., & Leathwick, J. R. (2009). Species Distribution Models: Ecological Explanation and Prediction  
654 Across Space and Time. *Annual Review of Ecology, Evolution, and Systematics*, 40(1), 677–  
655 697. <https://doi.org/10.1146/annurev.ecolsys.110308.120159>

656 Elith, J., Leathwick, J. R., & Hastie, T. (2008). A working guide to boosted regression trees. *Journal of*  
657 *Animal Ecology*, 77(4), 802–813. <https://doi.org/10.1111/j.1365-2656.2008.01390.x>

658 Ellis, J.& Solander, D. (1786). The Natural History of many curious and uncommon Zoophytes,  
 659 collected from various parts of the Globe. Systematically arranged and described by the late  
 660 Daniel Solander. 4.(Benjamin White & Son: London): 1-206, pls 1-63., *available online*  
 661 at <https://www.biodiversitylibrary.org/page/41943909>

662 Etnoyer, P. J., Wagner, D., Fowle, H. A., Poti, M., Kinlan, B., Georgian, S. E., & Cordes, E. E. (2018).  
 663 Models of habitat suitability, size, and age-class structure for the deep-sea black coral  
 664 *Leiopathes glaberrima* in the Gulf of Mexico. *Deep Sea Research Part II: Topical Studies in*  
 665 *Oceanography*, 150, 218–228. <https://doi.org/10.1016/j.dsr2.2017.10.008>

666 Fabri, M.-C., Pedel, L., Beuck, L., Galgani, F., Hebbeln, D., & Freiwald, A. (2014). Megafauna of  
 667 vulnerable marine ecosystems in French mediterranean submarine canyons: Spatial  
 668 distribution and anthropogenic impacts. *Deep Sea Research Part II: Topical Studies in*  
 669 *Oceanography*, 104, 184–207. <https://doi.org/10.1016/j.dsr2.2013.06.016>

670 Fabri Marie-Claire (2021). Antipatharians (Hexacorallia) presence and absence data reported from  
 671 canyons along the french mediterranean coast (2009-2010).  
 672 Ifremer. <https://doi.org/10.12770/1d1e0bdd-f72e-461b-8294-5f0c0c17239c>

673 Fabri, M.-C., Vinha, B., Allais, A.-G., Bouhier, M.-E., Dugornay, O., Gaillot, A., & Arnaubec, A. (2019).  
 674 Evaluating the ecological status of cold-water coral habitats using non-invasive methods: An  
 675 example from Cassidaigne canyon, northwestern Mediterranean Sea. *Progress in*  
 676 *Oceanography*, 178, 102172. <https://doi.org/10.1016/j.pocean.2019.102172>

677 Fautin, Daphne G. (2013). Hexacorallians of the World. <https://doi.org/10.15468/90drpi> accessed via  
 678 GBIF.org on 2022-06-09. <https://www.gbif.org/occurrence/2520740051>

679 Fielding, A. H., & Bell, J. F. (1997). A review of methods for the assessment of prediction errors in  
 680 conservation presence/absence models. *Environmental Conservation*, 24(1), 38–49.  
 681 <https://doi.org/10.1017/S0376892997000088>

682 Fordyce, A. J., Camp, E. F., & Ainsworth, T. D. (2017). *Table of qualitative observations of polyp*  
 683 *bailout in control and heat-treated mesocosms*. [Data set]. F1000Research.  
 684 <https://doi.org/10.5256/F1000RESEARCH.11522.D161213>

685 Gaino, E., & Scoccia, F. (2010). Gamete spawning in *Antipathella subpinnata* (Anthozoa,  
 686 Antipatharia): A structural and ultrastructural investigation. *Zoomorphology*, 129(4), 213–  
 687 219. <https://doi.org/10.1007/s00435-010-0112-x>

688 Garrabou, J., Coma, R., Bensoussan, N., Bally, M., Chevaldonné, P., Cigliano, M., ... & Cerrano, C.  
 689 (2009). Mass mortality in Northwestern Mediterranean rocky benthic communities: effects of  
 690 the 2003 heat wave. *Global change biology*, 15(5), 1090-1103. [https://doi-](https://doi-org.ezproxy.ulb.ac.be/10.1111/j.1365-2486.2008.01823.x)  
 691 [org.ezproxy.ulb.ac.be/10.1111/j.1365-2486.2008.01823.x](https://doi-org.ezproxy.ulb.ac.be/10.1111/j.1365-2486.2008.01823.x)

692

693 Genin, A., Dayton, P. K., Lonsdale, P. F., & Spiess, F. N. (1986). Corals on seamount peaks provide  
694 evidence of current acceleration over deep-sea topography. *Nature*, 322(6074), 59–61.  
695 <https://doi.org/10.1038/322059a0>

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

700 Gravier, C. Notes on the Antipatharians of the Gulf of Naples. (1918). *Pubblicazioni della Stazione*  
701 *Zoologica di Napoli* 2, 223–240.

702 Guillaumot, C., Artois, J., Saucède, T., Demoustier, L., Moreau, C., Eléaume, M., Agüera, A., & Danis,  
703 B. (2019). Broad-scale species distribution models applied to data-poor areas. *Progress in*  
704 *Oceanography*, 175, 198–207. <https://doi.org/10.1016/j.pocean.2019.04.007>

705 Guillaumot, C., Fabri-Ruiz, S., Martin, A., Eléaume, M., Danis, B., Féral, J.-P., & Saucède, T. (2018).  
706 Benthic species of the Kerguelen Plateau show contrasting distribution shifts in response to  
707 environmental changes. *Ecology and Evolution*, 8(12), 6210–6225.  
708 <https://doi.org/10.1002/ece3.4091>

709 Guillaumot, C., Moreau, C., Danis, B., & Saucède, T. (2020a). Extrapolation in species distribution  
710 modelling. Application to Southern Ocean marine species. *Progress in Oceanography*, 188,  
711 102438. <https://doi.org/10.1016/j.pocean.2020.102438>

712 Guillaumot, C., Danis, B. & Saucède, T. (2020b). Selecting environmental descriptors is critical for  
713 modelling the distribution of Antarctic benthic species. *Polar Biology*, 43(9), 1363–1381.  
714 <https://doi.org/10.1007/s00300-020-02714-2>

715 Guillaumot, C., Martin, A., Eleaume, M., & Saucède, T. (2021). SDMPlay : Species Distribution  
716 Modelling Playground. <https://CRAN.R-project.org/package=SDMPlay>

717 Hellenic Centre for Marine Research, MedOBIS - Mediterranean Ocean Biodiversity Information  
718 System. (2022). Hellenic Centre for Marine Research; Institute of Marine Biology and Genetics;  
719 Biodiversity and Ecosystem Management Department, Heraklion, Greece.  
720 <http://ipt.vliz.be/eurobis/>

721 Hijmans, R.J., Phillips, S., Leathwick, J. & Elith, J. (2017). R package “dismo”.  
722 <https://CRAN.Rproject.org/package=dismo>



723 Hogg, O. T., Barnes, D. K. A., & Griffiths, H. J. (2011). Highly Diverse, Poorly Studied and Uniquely  
 724 Threatened by Climate Change: An Assessment of Marine Biodiversity on South Georgia's  
 725 Continental Shelf. *PLoS ONE*, 6(5), e19795. <https://doi.org/10.1371/journal.pone.0019795>  
 726 iNaturalist contributors, iNaturalist (2022). iNaturalist Research-grade Observations. iNaturalist.org.  
 727 Occurrence dataset <https://doi.org/10.15468/ab3s5x> accessed via GBIF.org on 2022-06-09.  
 728 Ingrassia, M., & Di Bella, L. (2021). Black Coral Distribution in the Italian Seas: A Review. *Diversity*, 13(7),  
 729 334. <https://doi.org/10.3390/d13070334>  
 730 Inventaire National du Patrimoine Naturel N (2022a). Programme d'acquisition et de valorisation de  
 731 données naturalistes BioObs - Observations naturalistes des Amis de BioObs.. Version 1.1. UMS  
 732 PatriNat (OFB-CNRS-MNHN), Paris. Occurrence dataset <https://doi.org/10.15468/ldch7a>  
 733 accessed via GBIF.org on 2022-06-09. <https://www.gbif.org/occurrence/3472852485>  
 734 Inventaire National du Patrimoine Naturel N (2022b). Programme CARTHAM: Inventaire biologique  
 735 dans le cadre de Natura 2000 en Mer. Version 1.1. UMS PatriNat (OFB-CNRS-MNHN), Paris.  
 736 Occurrence dataset <https://doi.org/10.15468/3isrct> accessed via GBIF.org on 2022-06-09.  
 737 <https://www.gbif.org/occurrence/2488021119>  
 738 IPCC. (2022). Summary for Policymakers [H.-O. Pörtner, D.C. Roberts, E.S. Poloczanska, K.  
 739 Mintenbeck, M. Tignor, A. Alegría, M. Craig, S. Langsdorf, S. Löschke, V. Möller, A. Okem  
 740 (eds.)]. In: Climate Change 2022: Impacts, Adaptation, and Vulnerability. Contribution of  
 741 Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate  
 742 Change [H.-O. Pörtner, D.C. Roberts, M. Tignor, E.S. Poloczanska, K. Mintenbeck, A. Alegría,  
 743 M. Craig, S. Langsdorf, S. Löschke, V. Möller, A. Okem, B. Rama (eds.)]. Cambridge University  
 744 Press. In Press.  
 745 Jorda, G., Marbà, N., Bennett, S., Santana-Garcon, J., Agusti, S., & Duarte, C. M. (2020). Ocean  
 746 warming compresses the three-dimensional habitat of marine life. *Nature Ecology &*  
 747 *Evolution*, 4(1), 109–114. <https://doi.org/10.1038/s41559-019-1058-0>  
 748 Jurriaans, S., & Hoogenboom, M. (2020). Seasonal acclimation of thermal performance in two species  
 749 of reef-building corals. *Marine Ecology Progress Series*, 635, 55–70.  
 750 <https://doi.org/10.3354/meps13203>  
 751 Kahng, S. E., & Kelley, C. D. (2007). Vertical zonation of megabenthic taxa on a deep photosynthetic  
 752 reef (50–140 m) in the Au'au Channel, Hawaii. *Coral Reefs*, 26(3), 679–687.  
 753 <https://doi.org/10.1007/s00338-007-0253-7>  
 754 Kass, J. M., Muscarella, R., Galante, P. J., Bohl, C. L., Pinilla-Buitrago, G. E., Boria, R. A., Soley-Guardia,  
 755 M., & Anderson, R. P. (2021). ENMeval 2.0: Redesigned for customizable and reproducible

756 modeling of species' niches and distributions. *Methods in Ecology and Evolution*, 12(9),  
757 1602–1608. <https://doi.org/10.1111/2041-210X.13628>

758 Kersting, D. K., Bensoussan, N., & Linares, C. (2013). Long-Term Responses of the Endemic Reef-  
759 Builder *Cladocora caespitosa* to Mediterranean Warming. *PLoS ONE*, 8(8), e70820.  
760 <https://doi.org/10.1371/journal.pone.0070820>

761 Kipson, S., Linares, C., Teixidó, N., Bakran-Petricioli, T., & Garrabou, J. (2012). Effects of thermal stress  
762 on early developmental stages of a gorgonian coral. *Marine Ecology Progress Series*, 470, 69-  
763 78. <https://doi.org/10.3354/meps09982>

764 Kotta, J., Vanhatalo, J., Jänes, H., Orav-Kotta, H., Rugiu, L., Jormalainen, V., Bobsien, I., Viitasalo, M.,  
765 Virtanen, E., Sandman, A. N., Isaeus, M., Leidenberger, S., Jonsson, P. R., & Johannesson, K.  
766 (2019). Integrating experimental and distribution data to predict future species patterns.  
767 *Scientific Reports*, 9(1). <https://doi.org/10.1038/s41598-018-38416-3>

768 Kružić, P., Rodić, P., Popijač, A., & Sertić, M. (2016). Impacts of temperature anomalies on mortality  
769 of benthic organisms in the Adriatic Sea. *Marine ecology*, 37(6), 1190-  
770 1209. <https://doi.org/10.1111/maec.12293>

771 Linares, C., Cebrian, E., Kipson, S., & Garrabou, J. (2013). Does thermal history influence the tolerance  
772 of temperate gorgonians to future warming?. *Marine environmental research*, 89, 45-52.  
773 <https://doi.org/10.1016/j.marenvres.2013.04.009>

774 López-Farrán, Z., Guillaumot, C., Vargas-Chacoff, L., Paschke, K., Dulière, V., Danis, B., Poulin, E.,  
775 Saucède, T., Waters, J., & Gérard, K. (2021). Is the southern crab *Halicarcinus planatus*  
776 (Fabricius, 1775) the next invader of Antarctica? *Global Change Biology*, 27(15), 3487–3504.  
777 <https://doi.org/10.1111/gcb.15674>

778 Luoto, M., Pöyry, J., Heikkinen, R. K., & Saarinen, K. (2005). Uncertainty of bioclimate envelope  
779 models based on the geographical distribution of species: Uncertainty of bioclimate envelope  
780 models. *Global Ecology and Biogeography*, 14(6), 575–584. [https://doi.org/10.1111/j.1466-](https://doi.org/10.1111/j.1466-822X.2005.00186.x)  
781 [822X.2005.00186.x](https://doi.org/10.1111/j.1466-822X.2005.00186.x)

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

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

788 Orrell T, Informatics Office (2022). NMNH Material Samples (USNM). Version 1.41. National Museum  
789 of Natural History, Smithsonian Institution. Occurrence dataset

790 <https://doi.org/10.15468/jb9tdf> accessed via GBIF.org on 2022-06-09.  
 791 <https://www.gbif.org/occurrence/3027965257>

792 Paradis, B. T., Henry, R. P., & Chadwick, N. E. (2019). Compound effects of thermal stress and tissue  
 793 abrasion on photosynthesis and respiration in the reef-building coral *Acropora cervicornis*  
 794 (Lamarck, 1816). *Journal of Experimental Marine Biology and Ecology*, 521, 151222.  
 795 <https://doi.org/10.1016/j.jembe.2019.151222>

796 Pastor, F., Valiente, J. A., & Khodayar, S. (2020). A Warming Mediterranean: 38 Years of Increasing  
 797 Sea Surface Temperature. *Remote Sensing*, 12(17), 2687.  
 798 <https://doi.org/10.3390/rs12172687>

799 Pearce, J. L., & Boyce, M. S. (2006). Modelling distribution and abundance with presence-only data.  
 800 *Journal of Applied Ecology*, 43(3), 405–412. [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-2664.2005.01112.x)  
 801 [2664.2005.01112.x](https://doi.org/10.1111/j.1365-2664.2005.01112.x)

802 Phillips, S. J., Dudík, M., Elith, J., Graham, C. H., Lehmann, A., Leathwick, J., & Ferrier, S. (2009).  
 803 Sample selection bias and presence-only distribution models: Implications for background  
 804 and pseudo-absence data. *Ecological Applications*, 19(1), 181–197.  
 805 <https://doi.org/10.1890/07-2153.1>

806 Pierdomenico, M., Martorelli, E., Dominguez-Carrió, C., Gili, J. M., & Chiocci, F. L. (2016). Seafloor  
 807 characterization and benthic megafaunal distribution of an active submarine canyon and  
 808 surrounding sectors: The case of Gioia Canyon (Southern Tyrrhenian Sea). *Journal of Marine*  
 809 *Systems*, 157, 101-117. <https://doi.org/10.1016/j.jmarsys.2016.01.005>

810 Pörtner, H. O., & Farrell, A. P. (2008). Physiology and climate change. *Science*, 690-692.

811 Ripley, B. (2015). MASS: Support Functions and Datasets for Venables and Ripley's MASS. 2015.  
 812 <https://CRAN.R-project.org/package=MASS>. R package version, pp. 7–3.

813 Rodolfo-Metalpa, R., Bianchi, C. N., Peirano, A., & Morri, C. (2005). Tissue necrosis and mortality of  
 814 the temperate coral *Cladocora Caespitosa*. *Italian Journal of Zoology*, 72(4), 271–276.  
 815 <https://doi.org/10.1080/11250000509356685>

816 Rodolfo-Metalpa, R., Hoogenboom, M. O., Rottier, C., Ramos-Esplá, A., Baker, A. C., Fine, M., &  
 817 Ferrier-Pagès, C. (2014). Thermally tolerant corals have limited capacity to acclimatize to  
 818 future warming. *Global Change Biology*, 20(10), 3036–3049.  
 819 <https://doi.org/10.1111/gcb.12571>

820 Rossi, S., Bramanti, L., Gori, A., Orejas, C. (2017). An Overview of the Animal Forests of the World. *In*  
 821 *book: Marine Animal Forests, pp.1-26. SPRINGER.[DOI: 10.1007/978-3-319-17001-5\_1-1]*

822 Santin, A., Aguilar, R., Akyol, O., Begburs, C., Benoit, L., Chimienti, G., ... & Andreu, S. (2021). New  
823 records of rare species in the Mediterranean Sea (March 2021). *Mediterranean Marine*  
824 *Science*, 22(1), 199-217.

825 Saucède, T., Guillaumot, C., Michel, L. N., Fabri-Ruiz, S., Bazin, A., Cabessut, M., García-Berro, A.,  
826 Mateos, A., Ridder, C. D., Dubois, P., Danis, B., David, B., Lepoint, G., Motreuil, S., Poulin, E.,  
827 & Féral, J.-P. (2019). *Modelling species response to climate change in sub-Antarctic islands:*  
828 *Echinoids as a case study for the Kerguelen Plateau*. 22.

829 Sbrocco, E., & Barber, P. (2013). MARSPEC: ocean climate layers for marine spatial ecology: Ecological  
830 Archives E094-086. *Ecology*, 94(4), 979.

831 Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of image  
832 analysis. *Nature Methods*, 9(7), 671–675. [doi:10.1038/nmeth.2089](https://doi.org/10.1038/nmeth.2089)

833 Schulte, P. M., Healy, T. M., & Fangue, N. A. (2011). Thermal Performance Curves, Phenotypic  
834 Plasticity, and the Time Scales of Temperature Exposure. *Integrative and Comparative*  
835 *Biology*, 51(5), 691–702. <https://doi.org/10.1093/icb/ucr097>

836 Singer, A., Johst, K., Banitz, T., Fowler, M. S., Groeneveld, J., Gutiérrez, A. G., Hartig, F., Krug, R. M.,  
837 Liess, M., Matlack, G., Meyer, K. M., Pe'er, G., Radchuk, V., Voinopol-Sassu, A.-J., & Travis, J.  
838 M. J. (2016). Community dynamics under environmental change: How can next generation  
839 mechanistic models improve projections of species distributions? *Ecological Modelling*, 326,  
840 63–74. <https://doi.org/10.1016/j.ecolmodel.2015.11.007>

841 Soberon, J., & Peterson, A. T. (2005). Interpretation of Models of Fundamental Ecological Niches and  
842 Species' Distributional Areas. *Biodiversity Informatics*, 2(0).  
843 <https://doi.org/10.17161/bi.v2i0.4>

844 Soto-Navarro, J., Jordá, G., Amores, A., Cabos, W., Somot, S., Sevault, F., Macías, D., Djurdjevic, V.,  
845 Sannino, G., Li, L., & Sein, D. (2020). Evolution of Mediterranean Sea water properties under  
846 climate change scenarios in the Med-CORDEX ensemble. *Climate Dynamics*, 54(3–4), 2135–  
847 2165. <https://doi.org/10.1007/s00382-019-05105-4>

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

851 Terrana, L., Bo, M., Opresko, D. M., & Eeckhaut, I. (2020). Shallow-water black corals (Cnidaria:  
852 Anthozoa: Hexacorallia: Antipatharia) from SW Madagascar. *Zootaxa*, 4826(1), 1–62.  
853 <https://doi.org/10.11646/zootaxa.4826.1.1>

854 Terzin, M., Paletta, M. G., Matterson, K., Coppari, M., Bavestrello, G., Abbiati, M., Bo, M., &  
855 Costantini, F. (2021). Population genomic structure of the black coral *Antipathella subpinnata*

- in Mediterranean Vulnerable Marine Ecosystems. *Coral Reefs*, 40(3), 751–766.  
<https://doi.org/10.1007/s00338-021-02078-x>
- Tyberghein, L., Verbruggen, H., Pauly, K., Troupin, C., Mineur, F., & De Clerck, O. (2012). Bio-ORACLE: A global environmental dataset for marine species distribution modelling: Bio-ORACLE marine environmental data rasters. *Global Ecology and Biogeography*, 21(2), 272–281.  
<https://doi.org/10.1111/j.1466-8238.2011.00656.x>
- Urban, M. C., Bocedi, G., Hendry, A. P., Mihoub, J.-B., Pe’er, G., Singer, A., Bridle, J. R., Crozier, L. G., De Meester, L., Godsoe, W., Gonzalez, A., Hellmann, J. J., Holt, R. D., Huth, A., Johst, K., Krug, C. B., Leadley, P. W., Palmer, S. C. F., Pantel, J. H., ... Travis, J. M. J. (2016). Improving the forecast for biodiversity under climate change. *Science*, 353(6304).  
<https://doi.org/10.1126/science.aad8466>
- Vafidis D, Koukouras A. (1998). Antipatharia, Ceriantharia and Zoantharia (Hexacorallia, Anthozoa) of the Aegean Sea with a check list of the Mediterranean and Black Sea Species. *Annales de l’Institut océanographique*, Paris 74:115–126.
- van de Water, J. A. J. M., Coppari, M., Enrichetti, F., Ferrier-Pagès, C., & Bo, M. (2020). Local Conditions Influence the Prokaryotic Communities Associated With the Mesophotic Black Coral *Antipathella subpinnata*. *Frontiers in Microbiology*, 11.  
<https://doi.org/10.3389/fmicb.2020.537813>
- Wagner, D. (2015). The spatial distribution of shallow-water (<150 m) black corals (Cnidaria: Antipatharia) in the Hawaiian Archipelago. *Marine Biodiversity Records*, 8.  
<https://doi.org/10.1017/S1755267215000202>
- Wagner, D., Luck, D. G., & Toonen, R. J. (2012). The Biology and Ecology of Black Corals (Cnidaria: Anthozoa: Hexacorallia: Antipatharia). In *Advances in Marine Biology* (Vol. 63, pp. 67–132). Elsevier. <https://doi.org/10.1016/B978-0-12-394282-1.00002-8>
- Warner, G. F. (1981). *Species Descriptions and Ecological Observations of Black Corals (Antipatharia) from Trinidad*. 17.
- Yao, C.-L., & Somero, G. N. (2014). The impact of ocean warming on marine organisms. *Chinese Science Bulletin*, 59(5–6), 468–479. <https://doi.org/10.1007/s11434-014-0113-0>
- Yesson, C., Bedford, F., Rogers, A. D., & Taylor, M. L. (2017). The global distribution of deep-water Antipatharia habitat. *Deep Sea Research Part II: Topical Studies in Oceanography*, 145, 79–86.  
<https://doi.org/10.1016/j.dsr2.2015.12.004>