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

98 and *in situ*, including mass-mortality events (Arizmendi-Mejía et al., 2015; Bramanti et al., 2005;
99 Cerrano et al., 2000; Garrabou et al., 2009; Kružić et al., 2016; Kipson et al., 2012; Linares et al., 2013).
100 To date, only one experiment addressed the effects of thermal stress in an antipatharian species
101 (*Stichopathes sp.*; Godefroid et al., 2022). This mesophotic tropical species was experimentally exposed
102 to medium-term (16 days) heat stress (up to 4.5°C), and results highlighted metabolic depression,
103 impairment of healing capacities and activation of stress response mechanisms (i.e., tissue necrosis,
104 mucus production and antioxidant responses). In the Mediterranean Sea, the effects of increasing
105 temperature on antipatharian species have never been investigated, despite the fact that temperature
106 has been shown to significantly influence their distribution (Etnoyer et al., 2018; Wagner, 2015; Yesson
107 et al., 2017). Investigating the effects of ocean warming is particularly relevant for *A. subpinnata*
108 forests, whose vulnerability is increased by the low genetic connectivity between offshore and coastal
109 populations (Terzin et al., 2021). To date, we only know that the species is likely limited below an upper
110 thermal threshold of 15°C, based on its depth distribution (mainly between 65 and 200m; Bo et al.,
111 2008). However, physiological studies on the effects of ocean warming on this species are currently
112 lacking.

113 In this study, we investigated the effects of increasing seawater temperature on the mesophotic
114 antipatharian *A. subpinnata* from the Mediterranean Sea, by combining experimental and distribution
115 modelling approaches. First, the experimental study aimed at establishing the thermal performance
116 curve (TPC) for respiration of *A. subpinnata*, as well as the impact of temperature on stress response
117 variables (tissue necrosis, antioxidant capacity, mortality). TPC allows describing thermal sensitivity of
118 organisms by determining a thermal window of performance (i.e., thermal breadth, T_{br}), characterized
119 by the so-called optimal temperature (T_{opt}) at which the performance is maximal (P_{max}) and beyond
120 which it starts to decrease (Angilletta, 2009; Schulte et al., 2011). Large T_{br} is often good indicator of
121 low sensitivity to changes in temperature, while narrow T_{br} often indicates high susceptibility as only a
122 small increase in temperature may result in suboptimal conditions (Jurriaans & Hoogenboom, 2020).
123 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 29th 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 ± 0.3 L/hour. The
163 room was equipped with blue lights to simulate the natural light regime (0.5 µmol $m^{-2} s^{-1}$; 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 µmol 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 µmol O_2 hr^{-1} cm^{-1} and in µmol O_2 $hour^{-1}$ 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,

197 Eppendorf Centrifuge 5430R) and the supernatant was transferred into a new tube and stored at -80°C
198 until analysis. The subsequent protocol was identical to that reported in Godefroid et al. (2022). Total
199 protein content in the samples was determined using a commercial reagent kit based on the Bradford
200 assay (Pierce™ BCA Protein Assay Kit, ThermoFisher Scientific Inc., USA) with bovine serum albumin
201 (BSA) as standard (2 mg/mL). Protein contents were used for biomarker normalization. Measurement
202 of total antioxidant capacity (TAC) was carried out using OxiSelect™ Total Antioxidant Capacity Assay
203 Kit (Cell Biolabs Inc., USA), an electron-transfer based assay (Huang et al., 2005) that measures the
204 capacity of an antioxidant solution to reduce an oxidant (Copper (II) reduced into Copper (I)). The
205 chromatic change is proportional with the sample antioxidant concentration. Absorbance was
206 measured at 490 nm in a microplate reader (Beckman Coulter Paradigm) and compared to uric acid
207 standard curves. Results were normalized to the protein content and expressed as “mM Copper
208 Reducing Equivalents per g of protein”.
209

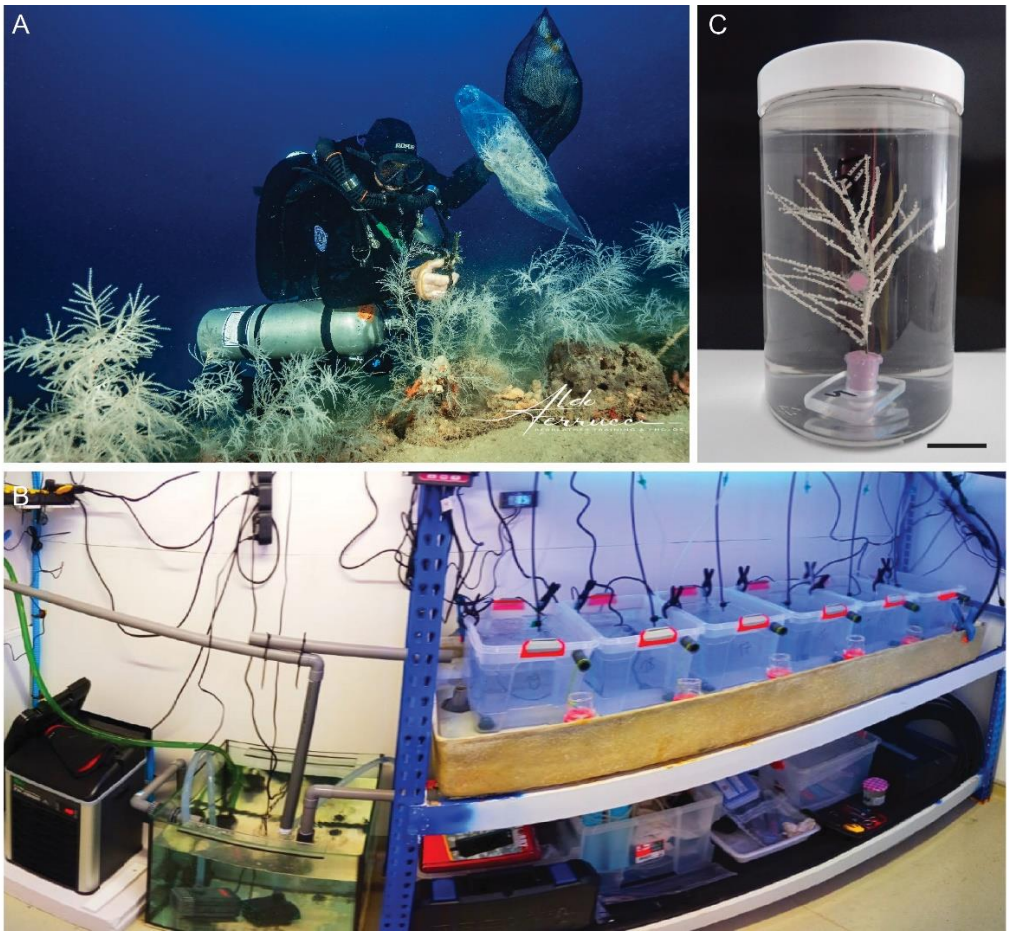

Figure 1. (A) Collection of portions of colonies of *Antipathella subpinnata* at 70m in Bordighera (Italy). Photo credit: Aldo Ferrucci ; (B) Experimental set-up with the 6 aquaria, in the aquarium facilities of the *Biodiversarium.* Photo credit: Lorenzo Bramanti; (C) respirometry chamber containing 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_{opt} is the optimal temperature at which this response is maximal (P_{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 Natural, 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	$m.s^{-1}$	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	$\mu mol.L^{-1}$	0.086°	Bio-ORACLE	PISCES (Assis et al., 2017)
Mean sea surface chlorophyll-*a* concentration	$mg.m^{-3}$	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.

2.2.4 Model calibration

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

2.2.5 Spatial cross-validation and model performances

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

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 ± 0.001 µmol O_2 h^{-1} cm^{-2}; mean ± se; $p<0.001$; P_{max}) at 16.4 ± 0.7°C ($p<0.001$; T_{opt}). The standard deviation of the curve (c) was estimated in 4.0 ± 1.7°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).

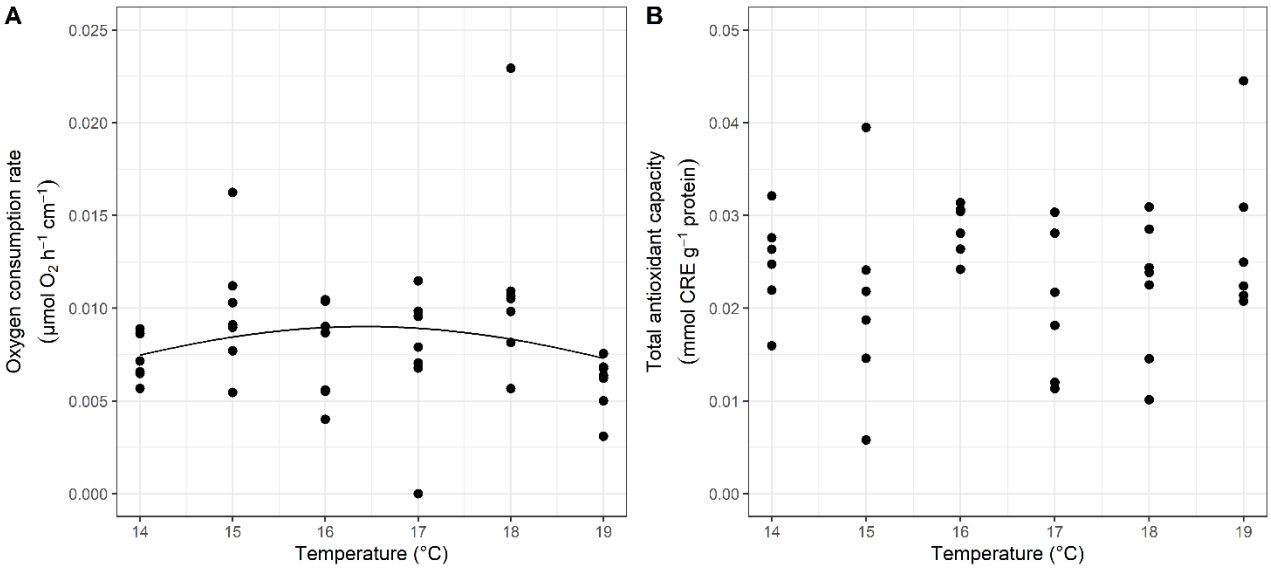

Figure 2. Effects of temperature on *Antipathella subpinnata* (**A**) Oxygen consumption rate (µmol O_2 h^{-1} cm^{-1}), (**B**) Total antioxidant capacity (mmol Copper Reducing Equivalents g^{-1} protein).

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

SDMs showed high performance scores, with AUC of 0.999 ± 0.001, TSS of 0.738 ± 0.017 and COR of 0.972 ± 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 ± 2.49% (mean ± se) for group 1, 98.19 ± 2.81% for group 2, 99.60 ± 1.47% for group 3 and 96.69 ± 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

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

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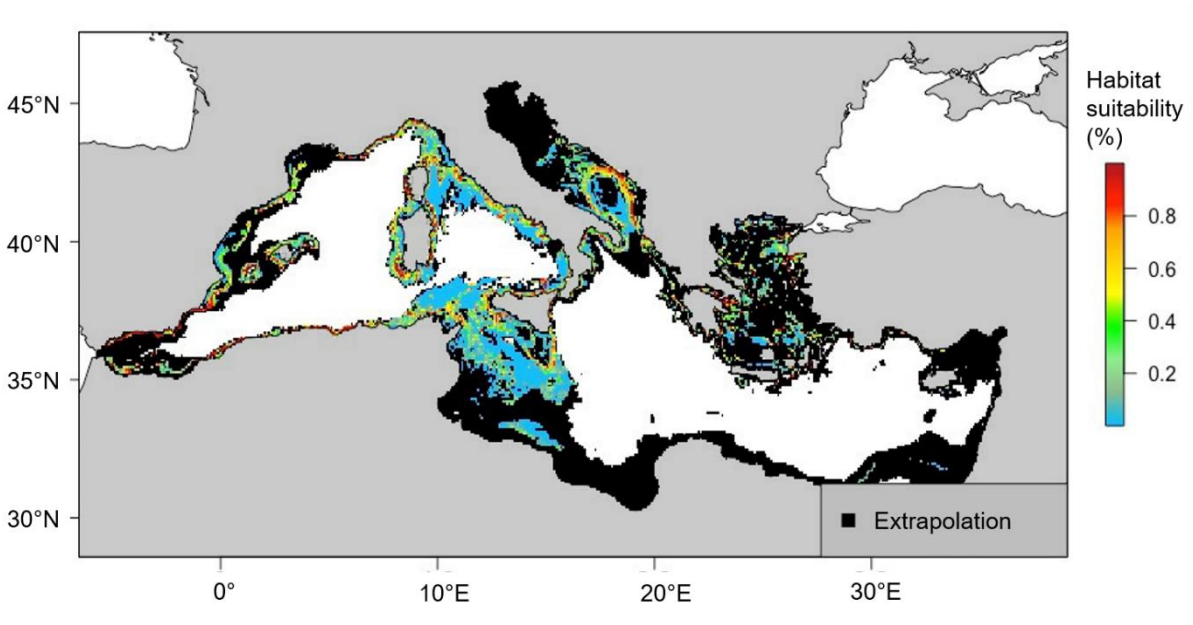

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355 **Figure 3.** Distribution model predictions of the likelihood of presence of *Antipathella subpinnata* (between 0 and 1) under
356 current environmental conditions (2000-2014) for the Mediterranean Sea. Model results are the average of 50 model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

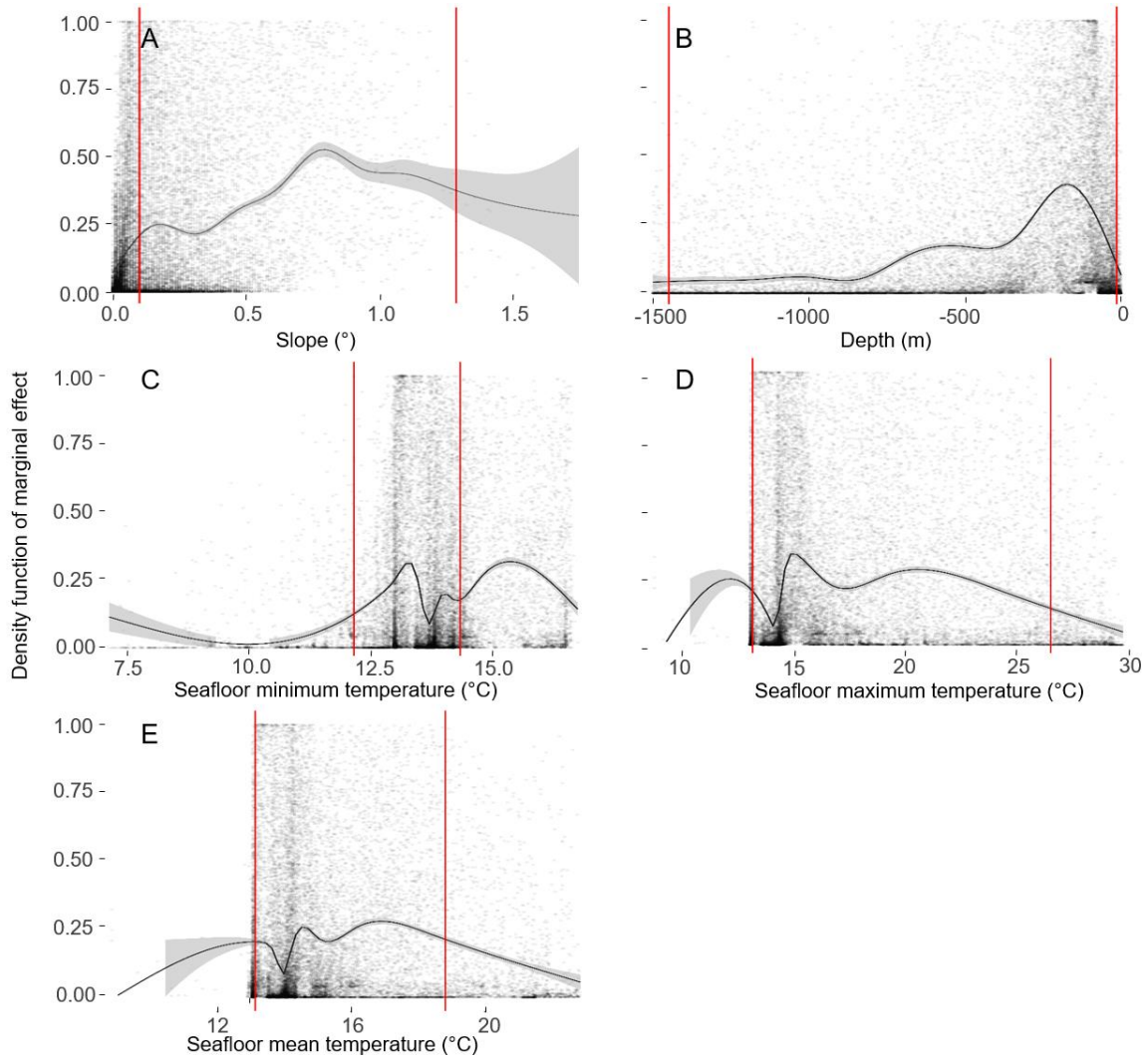
360

361 The two main descriptors contributing to the species distribution model are slope (45.9 ± 13.2%) and
362 depth (43.9 ± 13.6%), which together contributed to 89.8% (Table 2). In contrast, environmental
363 descriptors characterizing seafloor temperature only contributed for 5.4%, including 2.4 ± 0.8% for
364 minimum, 1.7 ± 0.8% for maximum and 1.3 ± 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 ± SD (%)
Slope	45.9 ± 13.2
Depth	43.9 ± 13.6
Minimum seafloor temperature	2.4 ± 0.8
Mean sea surface chlorophyll-*a* concentration	1.9 ± 0.7
Maximum seafloor temperature	1.7 ± 0.8
Mean seafloor current	1.6 ± 0.6
Mean seafloor oxygen	1.4 ± 0.4
Mean seafloor temperature	1.3 ± 0.6



377

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

382

383 ## 4. Discussion

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

388 tolerance experiments should also be incorporated (Buckley et al., 2010). For these reasons, we
389 combined experimental and modelling approaches to investigate the effects of increasing
390 temperatures on the branched antipatharian *A. subpinnata* from the Mediterranean Sea. Results from
391 spatial predictive modelling indicated that the distribution of *A. subpinnata* is driven by a combination
392 of interacting factors rather than by a single leading environmental descriptor. For depth, the upper
393 and lower bathymetric limits estimated by the model at 60 and 600m respectively, match with
394 observations from Bo et al. (2008). Ocean current is also important for antipatharians as it provides
395 them with suspended food particles (Genin et al., 1986; Warner, 1981). However, hydrodynamic
396 preferences vary between species. The unbranched species from Indonesia were shown to
397 preferentially select sites with higher hydrodynamics than branched species (Tazioli et al., 2007), as
398 further supported by higher bending resistance in unbranched species (Dugauquier et al., 2021). This
399 may explain the preferences of *A. subpinnata* to relatively gentle slopes and moderate current speeds.
400 For temperature, mean temperature correlating with its distribution ranged between 14.3 and 15.9°C
401 (with a maximum at 14.9°C) and the upper limit of the range of maximum temperature was 18°C,
402 suggesting that *A. subpinnata* can thrive at 18°C for several days. Such a narrow temperature interval
403 may either indicate that the species is not physiologically able to survive at temperatures outside this
404 range, or that other factors involved in the areas where temperatures are not in this range prevent the
405 establishment of *A. subpinnata.* SDM projections also highlighted the areas with favourable
406 environmental conditions for *A. subpinnata* but where no occurrences have been recorded to date in
407 the Mediterranean Sea. These model outputs could help guide future exploration and sampling efforts
408 as well as providing further validation of the model. In addition, some areas in the Mediterranean Sea
409 where high probability of presence were identified by the model to coincide with areas of some of the
410 historical taxonomic determinations that could not be used in the presence data to build the model as
411 they were doubtful and/or lacked georeferencing data (Bo et al., 2008). Examples include specimens
412 near Gibraltar (Alboran Sea; Ellis & Solander, 1786) and along the Algerian coast (Vafidis & Koukouras;
413 1998). This provides additional data supporting the model.

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

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

464 are thus the result of abiotic and biotic interactions (Tazioli et al., 2007; Wagner et al., 2012). In tropical
465 shallow habitats, antipatharians compete for space with zooxanthellate scleractinians (Tazioli et al.,
466 2007) and macrophytes (Kahng & Kelley, 2007). Larvae or bailed-out propagules' settlement could be
467 inhibited by the mechanical action of the macrophytes sweeping the substrate. In case of successful
468 settlement, they would probably be outcompeted by surrounding macrophytes and scleractinians
469 which are characterized by faster growth rates. We suggest that the competition for space with
470 crustose coralline algae and other habitat-forming species (sponges and Anthozoans) may also explain
471 the distribution of *A. subpinnata* in the Mediterranean Sea. The actual distribution of *A. subpinnata*
472 would therefore not be the consequence of physiological limitations, as suggested by Bo et al. (2008),
473 but rather the result of interspecific competition and probably also larval dispersal (completely
474 unknown for this species).

475 As a consequence of global warming, mean shallow-water temperature (0-150m) in the Mediterranean
476 is expected to increase by 3.7°C under the most pessimistic scenario (RCP 8.5; Soto-Navarro et al.,
477 2020). Even under this extreme scenario, seawater temperature will remain within the large thermal
478 tolerance window of *A. subpinnata,* suggesting that it should not suffer from deleterious physiological
479 impacts, if results obtained here over short-term (15 days) also apply to longer term. How thermal
480 tolerance estimated under experimental conditions can be extrapolated to natural settings is an
481 ongoing debate. It is noteworthy that the duration and intensity of the experimental assay influence
482 the observed response (Sinclair et al., 2016). For example, the mechanisms influencing performance
483 at acute and chronic time scales may be quite different, and TPC shape can change with acclimation
484 (Schulte et al., 2011). Rezende et al (2014) demonstrated that the temperature range that an organism
485 can tolerate is expected to narrow down with the duration of the thermal challenge. With this in mind,
486 it could be that we did not observe any effects over 15d but would have if exposure had been longer
487 (>15d). Despite this, none of the endpoints recorded during the experiment seem to indicate a sign of
488 stress, neither at the physiological, nor at the subcellular level (antioxidant response). In addition, the
489 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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CRediT (Contribution Roles Taxonomy) author statement

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