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RESEARCH

Sex matters: female black corals experience higher stress under different current velocities

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Abstract Black coral forests play a vital role in mesophotic and deep-water environments, providing habitat and refuge for numerous organisms. Their presence and distribution are influenced by hydrodynamic conditions. Yet, insight into the effect of current velocity on the survival and overall condition of black corals, and how this may differ between sexes during the reproductive period, is lacking. Here, we investigated how the current velocity affected male and female nubbins of *Antipathella wollastoni*, throughout a 5-week experiment, under three treatments: no (0 cm s^{-1}), low (mean ± SE = 5.3 cm s^{-1} ± 0.27) and high current (10 cm s^{-1} ± 0.42). We studied both the nubbin state (*i.e.* mortality, tissue necrosis and propagule production) and their physiology (*i.e.* total antioxidant capacity, TAC). We found higher tissue necrosis and mortality in the no-current treatment. Responses were significantly sex-conditioned across all treatments. All male nubbins survived the experiment and exhibited minimal tissue necrosis (mean ± SE = 4.72% ± 0.77), whereas 33.3% of female nubbins died and showed significantly higher tissue necrosis (37.05% ± 8.57). Propagule release was up to fourfold higher under high current compared to low, whereas nubbins in the no-current treatment produced almost none, likely due to the rapid onset of necrosis preventing the use of this escape response. The findings emphasize the importance of current velocities to rear black corals under controlled conditions, especially given the increased vulnerability of female nubbins during the reproductive period.

Resume Los bosques de coral negro desempeñan un papel vital en entornos mesofóticos y de aguas profundas, proporcionando hábitat y refugio para numerosos organismos. Su presencia y distribución están influenciadas por las condiciones hidrodinámicas. Sin embargo, faltan conocimientos sobre el efecto de la velocidad de la corriente en la supervivencia y el estado general de los corales negros, y sobre cómo esto podría variar entre sexos durante el período reproductivo. En este estudio investigamos cómo la velocidad de la corriente afectó a fragmentos macho y hembra de *Antipathella wollastoni*, durante un experimento de 5 semanas, con tres tratamientos: sin corriente (0 cm/s), corriente baja (media ± EE = 5,3 ± 0,27 cm/s) y corriente alta (10 ± 0,42 cm/s). Estudiamos tanto el estado de los fragmentos de coral (es decir, mortalidad, necrosis del tejido y producción de propágulos) como su fisiología (es decir, capacidad antioxidante total, TAC). Observamos mayor necrosis del tejido y mortalidad en el tratamiento sin corriente. Las respuestas estuvieron significativamente condicionadas por el sexo en todos los tratamientos. Todos los fragmentos macho sobrevivieron al experimento y presentaron una necrosis mínima (media ± EE = 4,72% ± 0,77), mientras que el 33,3% de los fragmentos hembra murieron y mostraron una necrosis significativamente mayor (37,05% ± 8,57). La liberación de propágulos fue hasta cuatro veces mayor en el tratamiento de corriente alta, en comparación con el de baja, mientras que los fragmentos en el tratamiento sin corriente casi no produjeron ninguno, probablemente debido a la aparición rápida

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de necrosis impidiendo el uso de esta estrategia de escape. Estos hallazgos destacan la importancia de la velocidad de la corriente para el cultivo de corales negros en condiciones controladas, especialmente dado que los fragmentos hembra son más vulnerables durante el período reproductivo.

Keywords Antipatharia · *Antipathella wollastoni* · Sex-associated differences · Mortality · Propagules · Reproductive season

Introduction

Marine animal forests (MAFs) create three-dimensional habitats, supporting high biodiversity by providing shelter and food to a wide variety of species (Rossi et al. 2017; Bosch et al. 2023; Navarro-Mayoral et al. 2024). These ecosystems are mostly dominated by megabenthic suspension feeders, such as sponges, bivalves, and corals (Rossi et al. 2017). Among these, antipatharians, commonly known as black corals, are some of the most widely distributed (Wagner et al. 2012a), ranging from tropical to polar latitudes and covering a wide bathymetric range, from shallow waters (ca. 2 m; Parrish and Baco 2007) to abyssal depths (ca. 8,600 m; Pasternak 1977; Molodtsova et al. 2008). In environments where benthic heterogeneity is limited, antipatharians form dense underwater forests, particularly at mesophotic depths (ca. 30 to 150 m; de Matos et al. 2014; Bo et al. 2019; Chimienti et al. 2020).

The presence of black corals is determined by several abiotic factors, including bottom topography, sedimentation, light, temperature, or current conditions (Wagner et al. 2012a). Most black coral species require a hard substrate to firmly attach the basal plate of their flexible proteinaceous skeletons, which is why they are usually found on rocky bottoms (e.g. Grigg 1965; Genin et al. 1986; Bo et al. 2008; Guinotte and Davies 2014; Yesson et al. 2017; Czechowska et al. 2020; Cosme de Esteban et al. 2024). Additionally, they avoid areas with high sediment cover, as abundant suspended sand particles can create abrasion in the black corals' tissue (Grigg 1965; Tazioli et al. 2007; Fraser and Sedberry 2008). Moreover, their preference for low-light environments can be influenced by competition with photosynthetic organisms, which can explain their occurrence inside caves, beneath crevices or on steep vertical walls (Oakley 1988; Kim et al. 1992; Parrish and Baco 2007; Morgulis et al. 2022). Temperature is another factor predicting the occurrence of black corals, as each species is thought to have an optimal range that defines its vertical distribution within the water column (Roberts et al. 2009; Guinotte and Davies 2014; Yesson et al. 2017; Lavorato et al. 2021; Godefroid et al. 2023).

Hydrodynamic conditions (*i.e.* currents) are one of the main elements shaping the distribution and density of black corals (Tazioli et al. 2007; Huff et al. 2013). As sessile organisms, they mostly rely on currents to supply nutrients and oxygen, capture prey, and remove sediment and waste (Grigg 1965; Warner 1981; Tazioli et al. 2007; Roberts et al. 2009; Rakka et al. 2020). In addition, some water flow is needed for the proper exchange of gases and metabolites between the surrounding water and corals' tissues (Patterson and Sebens 1989), which is essential for basic functions, such as growth and reproduction (e.g. Atkinson et al. 1994; Lesser et al. 1994; Khalesi et al. 2007; Mass et al. 2011). Black corals are generally found in environments where currents oscillate between 5 and 15 cm s^{-1}; they can also be found in areas with stronger currents but in lower densities (Warner 1981; Gennin et al. 1986; Oakley 1988; Yesson et al. 2017; Chimienti et al. 2020). Preferences for certain current conditions are likely linked to colony morphology, with branched species (e.g. arborescent or bush-like) being more abundant in areas with slow, unidirectional currents or avoiding direct exposure to stronger currents. Meanwhile unbranched species (e.g. whip or wire-like) dominate in areas with high multidirectional currents, or where they are more directly exposed (Warner 1981; Genin et al. 1986; Tazioli et al. 2007; Morgulis et al. 2022). This is likely related to their contrasting feeding strategy, with branched species bending over to maintain a large food capture area, and unbranched species maintaining a vertical position, optimizing food capture by exposing most of their surface area to particle-rich currents (Dugauquier et al. 2021).

In recent years, the number of studies aiming at understanding how environmental factors shape coral distribution and survival has increased, driven by the ongoing and rapid reorganization of biological assemblages in the Anthropocene (Hillebrand et al. 2018; Blowes et al. 2019). For instance, as studies show, thermal stress can lead to increased tissue necrosis or production of bailout propagules, highlighting the negative impact of rising temperatures on black coral colonies (Godefroid et al. 2022a, 2023, 2024; Gouveia et al. 2023). Although currents are recognized as a vital factor for the survival of black coral species, most studies have focused on describing in situ current conditions and their influence on species distribution (e.g. speed and direction; Yesson et al. 2017; Chimienti et al. 2020; Morgulis et al. 2022). To date, limited research has explored the effects of currents on the feeding biology of black coral species, specifically its ability to capture zooplankton under varying current flow regimes (e.g. *A. wollastoni*; Rakka et al. 2020). Furthermore, the potential differences between male and female colonies remain unexplored, even though most black coral species are gonochoric, exhibiting a distinct reproductive period that coincides with the warmest seawater temperatures of the year (Wagner et al. 2011, 2012b;

Rakka et al. 2017; Terrana et al. 2019). Across other gonochoric anthozoans, sex-associated differences have been observed during the reproductive period, with lower survival, growth or calcification rates for female individuals (e.g. Linares et al. 2008; Holcomb et al. 2012; Arizmendi-Mejía et al. 2015; Cruz-Ortega et al. 2020; Cabral-Tena et al. 2024). These differences are critical to understand the long-term effect of different stressors on population dynamics, as a shift in sex ratios could compromise sexual reproduction (Holcomb et al. 2012; Cabral-Tena et al. 2013). Thus, there are limited data on the effect that currents have on the overall health status of black corals and possible sex-related differences during the reproductive period. This knowledge is important to better understand their population dynamics and distribution, but also for developing controlled reproduction programmes for restoration activities, especially in the context of rapid global change and habitat degradation.

In this study, an ex situ experiment was conducted, under controlled current conditions, focusing on *Antipathella wollastoni* (Gray 2023). This black coral species is commonly found in the Canarian Archipelago and other islands of the Macaronesian region, occurring at depths ranging from 25 to over 1000 m and forming extensive MAFs, particularly at mesophotic depths (Bianchi et al. 2000; Ocaña and Brito 2004; Braga-Henriques et al. 2013; Czechowska et al. 2020; Feldens et al. 2023). This study explored how three different current velocities affected the mortality, tissue necrosis and Total Antioxidant Capacity (TAC) of *A. wollastoni*, and whether these coral responses varied with sex. We also assessed whether bailout propagule production varied with current velocity.

Material and methods

Collection and maintenance of coral fragments

Several colonies of *A. wollastoni* were tagged using SCUBA diving, at 32 m depth, during July and August 2023, on the east coast of Gran Canaria Island (Canary Islands, eastern Atlantic Ocean; 28°01′56″W, 15°22′32″N). Subsequently, samples were taken to determine the sex of the colonies through histological analysis, following the procedure described by Rakka et al. (2017). The collection of nubbins for the experiment took place between October 26 and 27, 2023; during the species' reproductive period (Fig. S1; Rakka et al. 2017). In total, 9 nubbins (mean height ± SE = 73.02 mm ± 0.15) were collected from each of 6 different tagged colonies, three males and three females (a total of $n = 54$). Nubbins were then transported in cool boxes with seawater from the collection site to the Parque Científico Tecnológico Marino de Taliarte (Telde, Gran Canaria) (*ca*. 30 min) to maintain the original temperature and minimize any additional stress.

In the laboratory, nubbins were initially acclimated in an 80 L aquarium, connected to a semi-open circuit (ca. 1 h), ensuring gradual adjustments and preventing abrupt changes in seawater chemistry. After acclimation, all nubbins were attached to tagged PVC supports using EPOXY resin (Aquascape Construction Epoxy, D-D The Aquarium Solution). One nubbin from each colony was then transferred to each of the nine experimental aquariums ($n = 6$, 30 L, salinity 36.8‰), where they were kept at a temperature of 23 °C, matching the site of collection (Fig. 1c). All aquaria were connected to a 300 L sump tank. Seawater was pumped from the nearby shore, first passing through a 150 µm filter sock before entering the sump, which was equipped with a skimmer (Aqua Ocean Pro, SKP900) and a biofilter media (Marine PURE Block). The seawater in the sump was cooled to 23 °C using a chiller (Hailea, model HC-2200BH) before being distributed to the nine aquaria. Overflowing water was directed back to the sump through PVC pipes for filtration. To maintain stable seawater parameters, the semi-open circuit renewal rate was adjusted to *ca.* 10–15% per week, while individual tanks had a higher renewal rate, with complete water replacement every hour. Throughout the experiment, seawater parameters were monitored, including temperature, oxygen, nitrates, nitrites, phosphate and ammonium to ensure optimal seawater quality. Each 30 L aquarium was equipped with its own individual blue light fluorescent tube (900 lm, Leddy Tube Marine D & N, AQUAEL) simulating the natural light conditions at the collection depth and maintaining the natural photoperiod (12 h/12 h, light/dark regime). Coral nubbins were fed twice a day (morning and evening) with live rotifers enriched with *Nannochloropsis* sp.

Current experiment

The experiment comprised three treatments: (i) no current, (ii) low current, and (iii) high current, with three replicates each, resulting in a total of 9 experimental aquaria (Fig. 2). In the no-current treatment, the aquaria had no water movement, except for the hourly water replacement in the semi-open circuit. The remaining aquaria were equipped with a wave maker (Jebao, Smart Wave Maker MOW-3), capable of generating a uniform circular current. To ensure uniformity in current exposure for each coral nubbin, they were fixed equidistant from the aquarium walls on a coral rack (Fig. 1c). Current speed measurements were taken using an electromagnetic current meter (JFE Advantech, AEM1-DA), at each coral nubbin position, to define low (mean ± SE = 5.42 cm s^{-1} ± 0.28) and high intensity current treatments (10.78 cm s^{-1} ± 0.42), which were maintained constant for one month (Table S1). The selected current velocities were

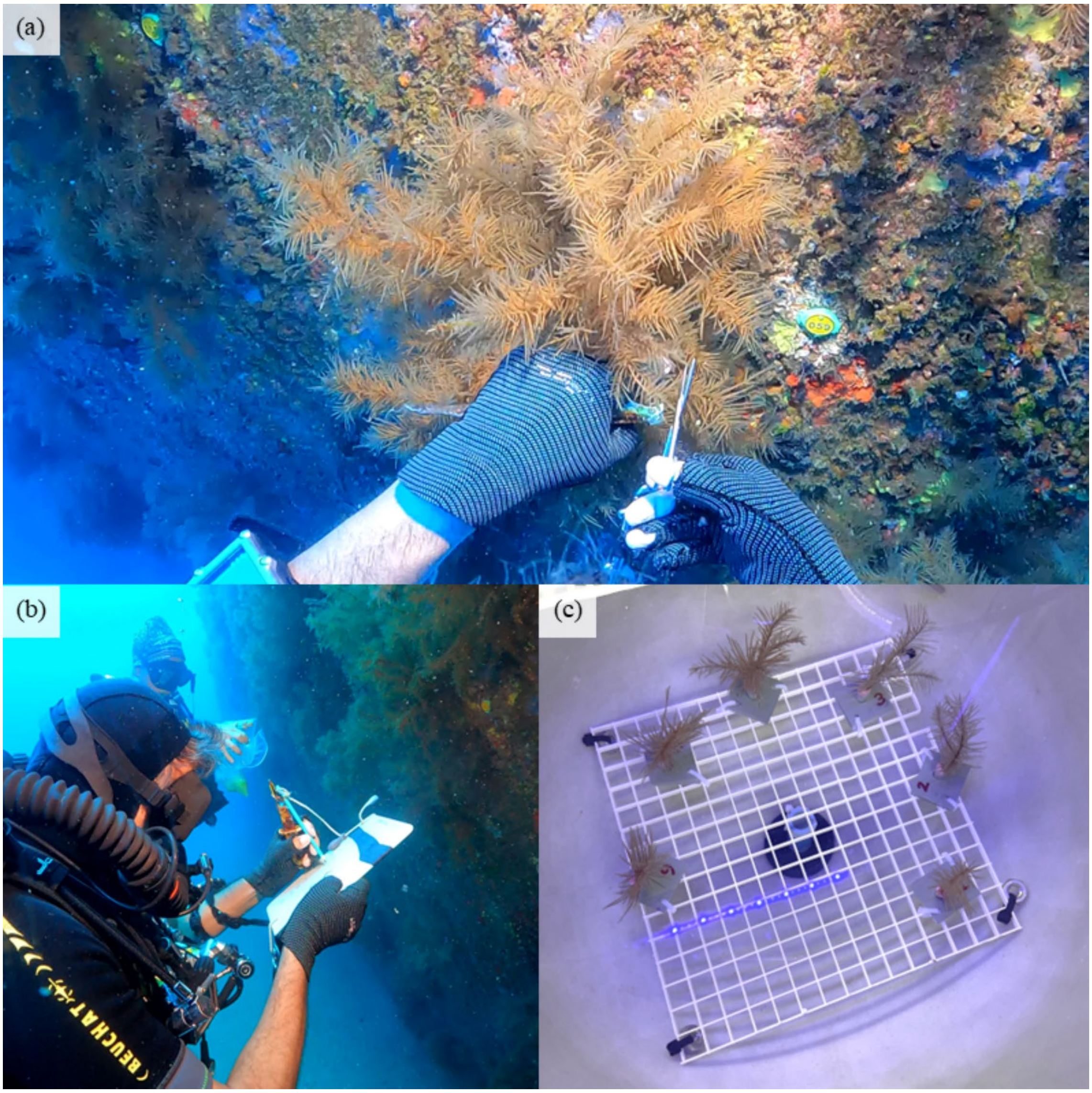

Fig. 1 Collection of *A. wollastoni* nubbins from the previously marked "donor colonies" in the natural environment (**a**, **b**). Arrangement of coral nubbins inside an experimental aquarium (**c**)

based on unpublished in situ measurements from a black coral forest primarily composed of *A. wollastoni* off Lanzarote Island (Otero-Ferrer, pers. comm.), as well as on published data from *Antipathella subpinnata* in the Mediterranean (Chimienti et al. 2020). Additionally, subsequent current measurements taken in 2024 and 2025, in the same study site off the eastern coast of Gran Canaria, further confirmed that these velocities fall within the natural range for the study species (Fig. S2).

Coral nubbins were checked daily to observe (i) tissue necrosis, (ii) mortality and (iii) production of bailout propagules. Tissue necrosis (*i.e.* the partial loss of live tissues around the skeleton) was monitored, with pictures taken every three days for each individual nubbin, using an underwater camera (Olympus, Tough TG-6) (Gouveia et al. 2023). These images were analysed using the Software ImageJ (Schneider et al. 2012), and tissue necrosis reported as a percentage: tissue necrosis (%) = (area of necrosed ramifications/total area of all ramifications) * 100. Mortality (*i.e.* 100% tissue loss) was checked daily for all nubbins and reported on a binary scale (dead/alive) (Godefroid et al. 2023). Bailout propagules produced by the nubbins were collected daily by vacuuming the bottom of the aquaria (as all were negatively buoyant) using a pipette connected to a thin silicon tube. The vacuumed water was collected in a 500 ml container and then examined under a stereo microscope (Leica EZ4 W). Propagules were quantified with a manual counter and preserved in 2 ml Eppendorf tubes

Fig. 2 Scheme of the experimental set up, with the three different treatments: no current (**a**), low current (**b**), and high current (**c**). Coral nubbins in orange and brown corresponding to females and males, respectively

with formaldehyde, for each individual aquarium (Coppari et al. 2020; Gouveia et al. 2023). Differentiating propagules from male and female nubbins was not possible; however, the thinning of the coenosarc and the dissociation of the polyp tissue from the skeleton were only apparent in the female nubbins presenting necrosis (Fig. 3c, d), with some propagules still containing oocytes when observed under the stereomicroscope (Fig. 3a, b). Nevertheless, it was not possible to confirm all propagules were just released by female nubbins.

At the end of the experiment, samples were taken from each live coral nubbin for biomarker analysis. Three randomly selected branchlets, 2–3 cm in length, were cut from each coral nubbin, placed in a 1.5 ml tube containing 400 µl of phosphate buffer (50 mM) and stored at -80 °C until further preparation of samples (Godefroid et al. 2022b). To detach the tissue from the skeleton, a micropestle was used, maintaining the samples on ice. The tissue homogenate was then centrifuged for 10 min at 4 °C (10,000 × g, Sigma Centrifuge 2-16KL) and the obtained supernatant was transferred into a new 1.5 ml tube and stored again at – 80 °C until further analysis (Godefroid et al. 2022b). Total protein content and total antioxidant capacity (TAC) were determined using commercial reagent kits, following the manufacturer's instructions, as reported in Godefroid et al. (2022a, b). In brief, total protein content was determined for biomarker normalization using the Pierce™ BCA Protein Assay Kit (ThermoFisher Scientific Inc., USA) based on the Bradford assay, using bovine serum albumin (BSA) as standard (2 mg mL^{-1}). Subsequently, TAC was measured using OxiSelect™ Total Antioxidant Capacity Assay Kit (Cell Biolabs Inc, USA) with a standard of uric acid. This is an electron-transfer based assay (Huang et al. 2005), based on the reduction of Copper II to Copper I by an antioxidant (here, uric acid), which further reacts with a coupling chromogenic reagent that produces a colour with a maximum absorbance at 490 nm. The degree of colour change is correlated with the sample's antioxidant concentrations. Absorbance was measured with a microplate reader (Multiskan GO Spectrophotometer, Thermo Fisher Scientific) and compared to uric acid standard curves. Finally, results were normalized to the protein content and expressed as 'mM Copper Reducing Equivalents per g of protein'.

Data analysis

Generalized linear mixed-effect models (GLMMs) were fitted to univariate response variables, including tissue

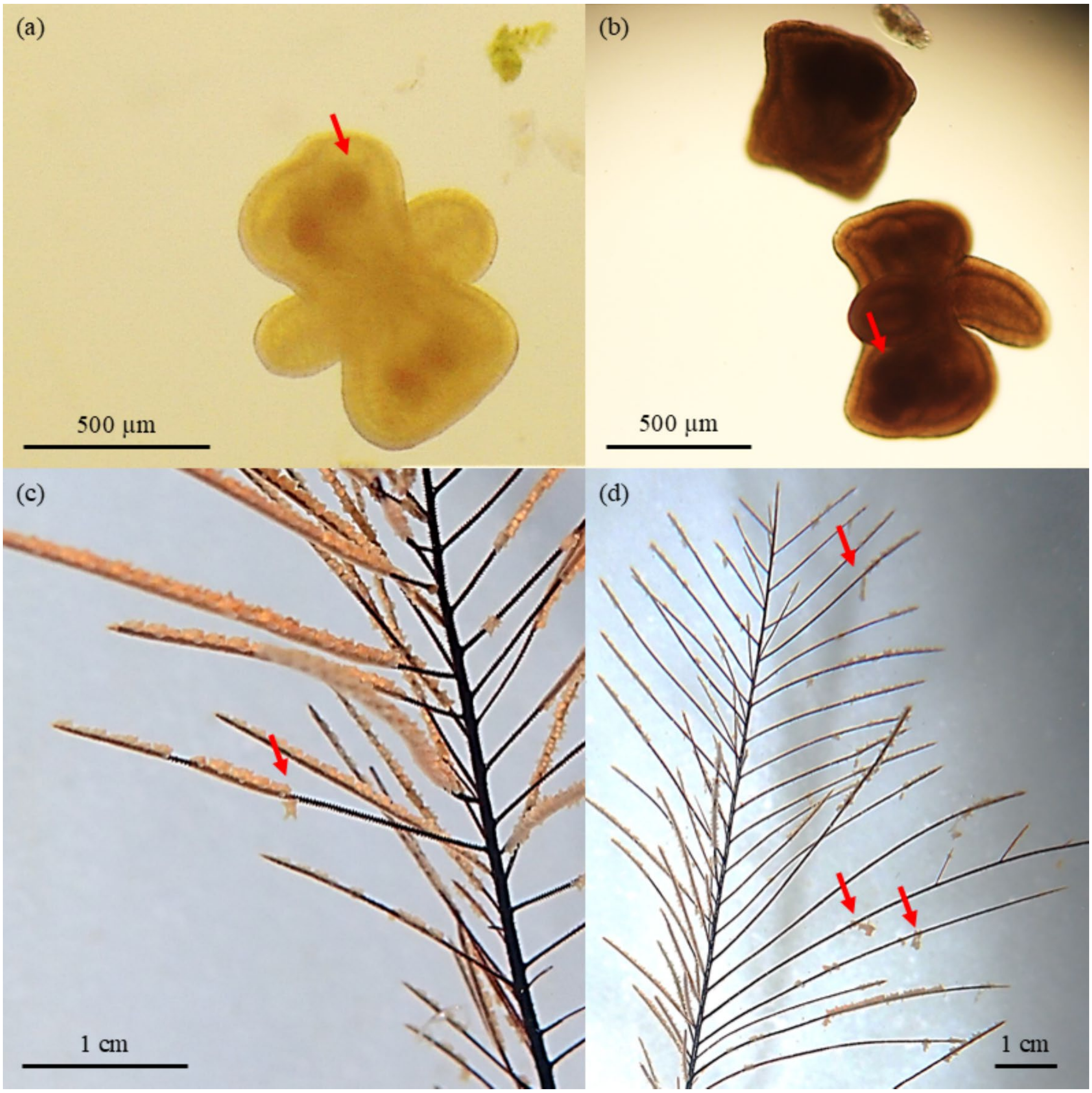

Fig. 3 Stereomicroscope images of propagules released by nubbins of *A. wollastoni* during the experiment (**a**), with oocytes still inside (**b**, red arrows), and polyp bailout in a female nubbin presenting necrosis (**c**), where dissociation of polyp tissue from the skeleton is observed (**d**, red arrows)

necrosis, mortality, number of bailout propagules and TAC. All models were fitted using the 'glmmTM' package in R (RStudio Team, 2022). The experimental design included two fixed factors: 'treatment' (three levels: no current, low current, and high current) and 'sex' (two levels: males and females). Random effects included 'donor colony' (nested within sex), 'tank' and 'time'. The experimental period was divided into three phases: initial (1–13 days), intermediate (14–22 days), and end (23–34 days), to address temporal dependence and facilitate the detection of changes over time.

Tissue necrosis was modelled using a 'beta' error distribution structure with a 'log' link function. Fixed effects included treatment and sex, and random effects included donor colony, tank and time. Due to the high variability observed among female nubbins, an additional independent model was fitted for this group to assess the individual effect of donor colony, using the same structure of predictors.

Mortality was analysed with a 'binomial' error distribution structure with a 'log' link function. Treatment and sex were included as fixed effects, while donor colony and tank were included random effects. Time was excluded from this model, as mortality was assessed only at the end of each experimental phase.

The number of bailout propagules was analysed using a 'negative binomial' error distribution structure with a 'log' link function. Treatment was included as a fixed effect, and tank and time as random effects. Sex and donor colony were excluded, as the individual origin of propagules could not be determined.

TAC was modelled with a 'Gaussian' error distribution structure with a 'log' link function. Treatment and sex were included as fixed effects, and donor colony and tank as random effects. Time was excluded, as TAC was measured only once per colony, at the conclusion of the experiment, providing a single value per colony.

For each response variable, all possible combinations of fixed effects, including interaction terms, were used to generate candidate models. The most parsimonious model was selected based on the Akaike information criterion (AIC). Additionally, marginal and conditional R^2 values were calculated to quantify the variance explained by the fixed effects alone (marginal R^2) and by the entire model, including both fixed and random effects (conditional R^2). Model fit was assessed through visual inspection of diagnostic residual plots, including Q-Q plots (Harrison et al. 2018).

Results

Temporal patterns of tissue necrosis

The percentage of tissue necrosis differed significantly between treatments and sexes throughout the experiment, particularly in both the intermediate and end phases (Fig. 4, Table 1). Overall, necrosis was significantly higher in the no-current treatment compared to both low- and high-current treatments across all three experimental phases (Table 1). This pattern, however, was significantly conditioned by sex in the end phase. Thus, females exhibited the highest increase in tissue necrosis (mean ± SE = 37.05% ± 8.57), with several nubbins reaching 100%, while all males maintained values < 15% (4.72% ± 0.77; Fig. 4, Table 1). The random effect of the individual colony became increasingly important in the intermediate and end phases, explaining a substantial portion of the variability (Conditional $R^2 = 0.35$ and 0.81, respectively; Figs. S3 and S4, Table S2). Male nubbins exhibited minimal necrosis over time, with no significant differences between treatments (Fig. 4). In contrast, female nubbins showed high values of tissue necrosis that varied significantly between treatments throughout the experiment (Fig. 4, Table 2 and S3). Specifically, during the initial phase, the best-fitting model included time and tank as random effects, but neither explained any variability (Table S3). By comparison, during the intermediate and end phases, the random effect of donor colony became increasingly important, explaining most of the variability (Conditional $R^2 = 0.40$ and 0.75, respectively; Fig. S4, Table S3), consistent with the pattern observed in the overall model for tissue necrosis in *A. wollastoni* nubbins (Table S2).

Temporal patterns of mortality

The mortality of *A. wollastoni* nubbins was significantly higher in females than in males during both the intermediate ($P = 0.02$) and end ($P = 0.01$) phases; 33.3% of females ultimately died, while no mortality was observed in males (Fig. S5, Table S7). In the initial phase, several females in the no-current treatment presented high levels of necrosis, but only one of them died (Figs. 4a and S5a). During the intermediate phase, necrosis escalated in the no-current treatment, resulting in the death of three additional female nubbins. In contrast, necrosis increased more gradually in the low- and high-current treatments, leading to three deaths overall (Figs. 4b and S5b). In the end phase, necrosis continued, causing one additional death in both the no-current and low-current treatments (Figs. 4c and S5c). Although no statistically significant differences were detected between treatments (Tables S4 and S7), some clear trends were observed: mortality was highest in the no-current treatment (55.6%), followed by the low- and high-current treatments (22.2% each, Fig. S5).

Production of bailout propagules

Bailout propagules were released by *A. wollastoni* nubbins over the different phases of the experiment, in all replicated aquaria of the three treatments. From the intermediate phase onward, the number of propagules released varied significantly between treatments, with the high-current treatment presenting the greatest release, followed by low- and no-current treatments (Fig. 5, Table 3). In the initial phase, all treatments presented high propagule release (> 100 propagules/aquarium), particularly in the high-current treatment. During this phase, most of the variability was explained by the random effects of tank and time (Conditional $R^2 = 0.55$, Table S5). This tendency changed during the intermediate and end phases. Nubbins in the no-current treatment almost stopped producing propagules (< 40 propagules/aquarium), while an increase was observed in the other two treatments (Fig. 5b, c). Particularly, the high-current treatment showed the most pronounced rise in the intermediate phase (up to 900 propagules/aquarium, Fig. 5b). From this phase onward, there was also a random effect of tank, although it explained only a small proportion of the total variability (Table S5).

Total antioxidant capacity

The total antioxidant capacity did not differ significantly among treatments; however, the data suggest a trend towards lower values in the low-current treatment (mean ± SE = 0.44 mM CRE g protein^{-1} ± 0.05) compared to no current (0.47 ± 0.05) and high current (0.58 ± 0.08; Fig. S6, Tables S6 and S8). Similarly, no

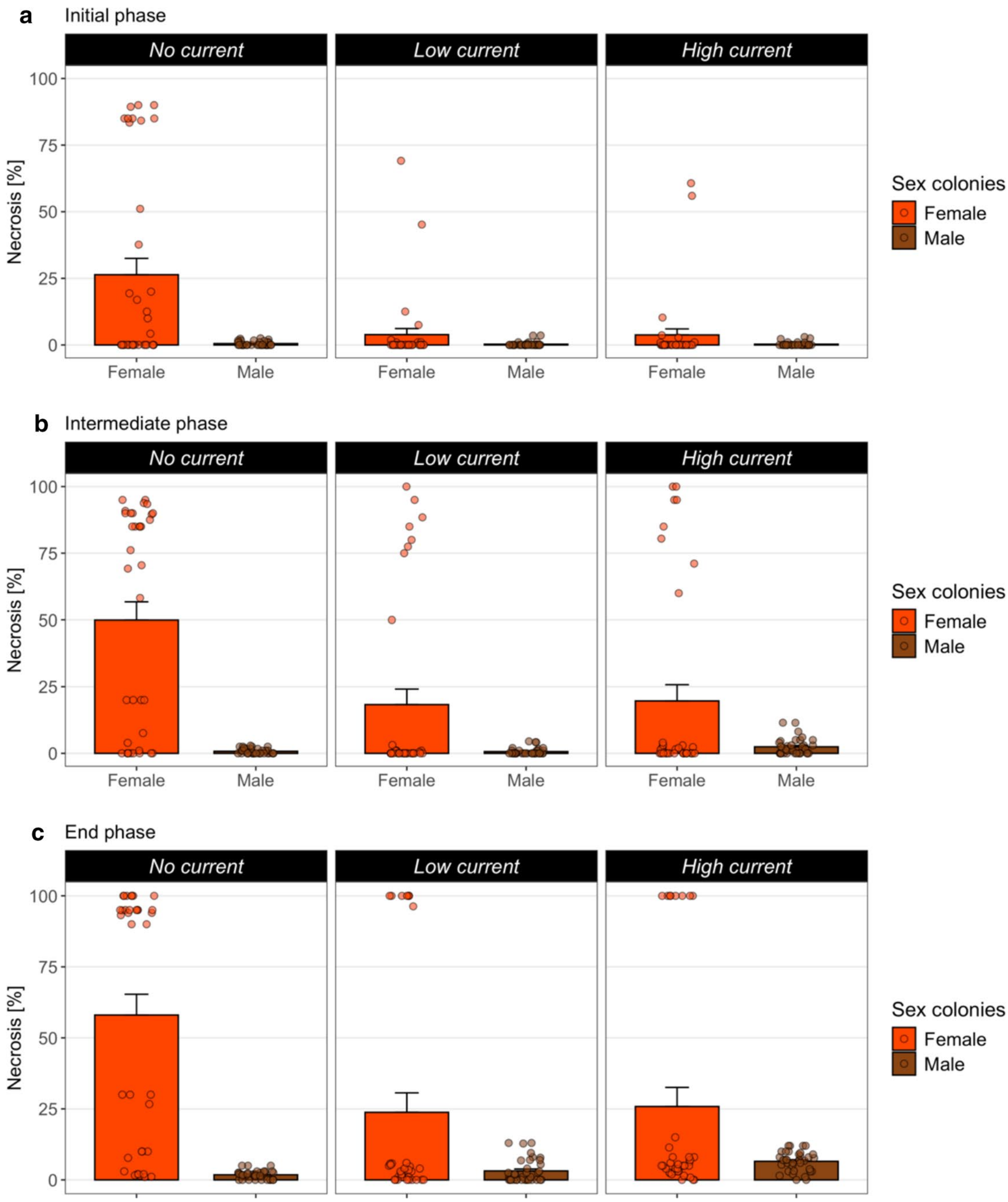

Fig. 4 Tissue necrosis in male and female nubbins of *A. wollastoni* under different current treatments (no current, low, and high) throughout experimental phases: initial (**a**), intermediate (**b**), and end (**c**)

significant differences were observed between male and female nubbins, and no random effect of the donor colony was detected (Table S6 and S8). Nevertheless, some patterns can be observed: males showed a slight tendency towards higher TAC with increasing current (no current: 0.42 ± 0.06; low current: 0.49 ± 0.09; high current: 0.65 ± 0.16), whereas females tended to exhibit the lowest TAC values in the low-current treatment (0.38 ± 0.04), followed by high (0.50 ± 0.06) and no current (0.55 ± 0.08). As a result, females showed a tendency for higher TAC production than males in the no-current treatment, while the opposite pattern was observed under the other two conditions (Fig. S6).

Table 1 Results from the best-fitting GLMMs for each experimental phase assessing tissue necrosis in *A. wollastoni* (see Table S2 for model selection)

	Estimate	SE	*z* value	*P*
Initial phase				
Intercept (Ref. levels: No current, Female)	−1.62	0.18	−9.11	**<2 e^{-16}**
Treatment (High)	−0.66	0.23	−2.93	**0.003**
Treatment (Low)	−0.65	0.23	−2.88	**0.003**
Sex (Male)	−0.69	0.23	−3.04	**0.002**
Treatment (High)*Sex (Male)	0.59	0.32	1.85	0.06
Treatment (Low)*Sex (Male)	0.56	0.32	1.77	0.07
Intermediate phase				
Intercept (Ref. levels: No current, Female)	−0.33	0.36	−0.90	0.37
Treatment (High)	−0.64	0.34	−1.88	**0.04**
Treatment (Low)	−0.87	0.34	−2.55	**0.01**
Sex (Male)	−1.32	0.51	−2.61	**0.008**
Treatment (High)*Sex (Male)	0.88	0.46	1.90	0.05
Treatment (Low)*Sex (Male)	0.84	0.46	1.82	0.06
End phase				
Intercept (Ref. levels: No current, Female)	0.67	0.62	1.08	0.28
Treatment (High)	−0.88	0.29	−3.04	0.002
Treatment (Low)	−1.13	0.29	−3.95	**7.72 e^{-05}**
Sex (Male)	−2.28	0.87	−2.61	**0.009**
Treatment (High)* Sex (Male)	1.27	0.40	3.18	**0.001**
Treatment (Low)* Sex (Male)	1.13	0.39	2.87	**0.004**

The intercept corresponds to the reference levels for each fixed factor (*i.e.* 'treatment' and 'sex'). To enable pairwise comparisons, each treatment level was used as the reference (intercept) in separate models. Only models showing statistically significant differences are presented. Significant differences ($P<0.05$) are highlighted in bold. (*) Denotes interaction between factors. Abbreviations: Ref. levels = reference levels

Table 2 Results from the best-fitting GLMMs for each experimental phase assessing tissue necrosis of female nubbins of *A. wollastoni* (see Table S3 for model selection)

	Estimate	SE	*z* value	*P*
Initial phase				
Intercept (Ref. level: No current)	−1.28	0.19	−6.58	**4.77 e^{-11}**
Treatment (High)	−0.59	0.24	−2.44	**0.01**
Treatment (Low)	−0.58	0.24	−2.40	**0.01**
Intermediate phase				
Intercept (Ref. level: No current)	−1.29	0.19	−6.58	**4.77 e^{-11}**
Treatment (High)	−0.59	0.24	−2.44	**0.01**
Treatment (Low)	−0.58	0.24	−2.44	**0.02**
End phase				
Intercept (Ref. level: No current)	0.48	0.64	0.74	0.46
Treatment (High)	−0.61	0.30	−1.99	**0.04**
Treatment (Low)	−0.82	0.30	−2.73	**0.006**

The intercept corresponds to the reference level of fixed factor (*i.e.* treatment). To enable pairwise comparisons, all treatment levels were used as the reference (intercept) in separate models. Only models with significant differences are presented. Significant differences ($P<0.05$) are highlighted in bold. Abbreviations: Ref. levels = reference levels

Discussion

In our study, current intensity had a significant influence on the health of black coral nubbins of *A. wollastoni*, highlighting its critical role in shaping their ecological dynamics. Notably, females were more affected by current velocity than males. This observation suggests a sex-related response, documented here for the first time in antipatharian corals. Throughout the experiment, females proved to be more sensitive, presenting the highest necrosis and mortality. They were specially affected in the no-current treatment, where they presented the most rapid increase in necrosis. In contrast, males showed fewer signs of stress across all treatments, with very low necrosis and no observed mortality. Bailout propagules were observed across all treatments over time, with abundance increasing notably at high current velocities. Finally, current intensity had no effect on the total antioxidant capacity of the nubbins, although some trends could be observed in the data, as values were slightly lower in the low-current treatment, and female nubbins tended to show slightly higher values in the no-current treatment, where they also exhibited the highest necrosis.

Given the fundamental role of currents in supporting the exchanges between a coral's internal compartments and its surrounding environment (Thomas and Atkinson 1997;

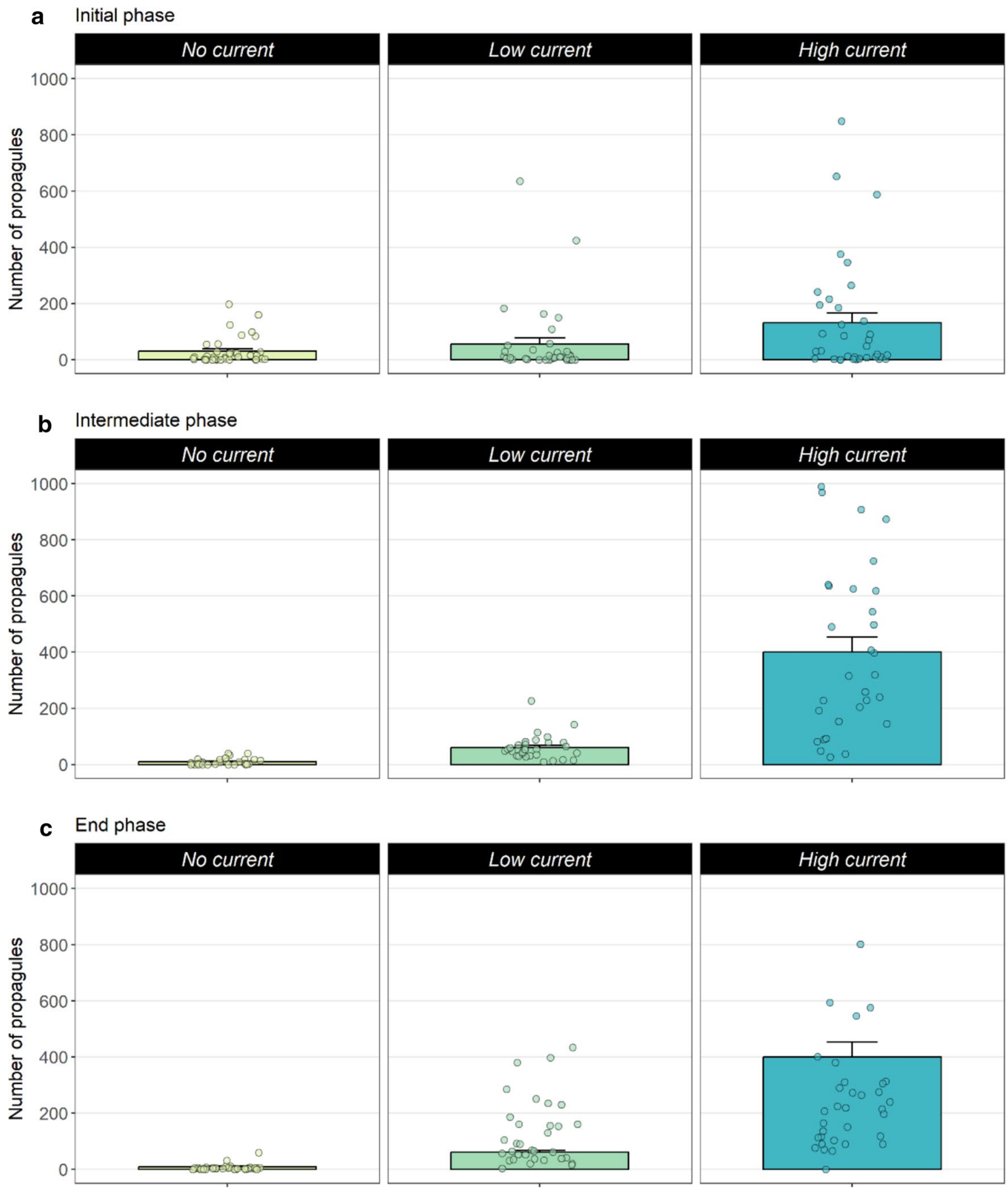

Fig. 5 Bailout propagules released by *A. wollastoni* nubbins exposed to different current flow treatments (no current, low current, and high current) throughout experimental phases: initial (**a**), intermediate (**b**), and end (**c**)

Khalesi et al. 2007; Nakamura 2010; Mass et al. 2011), it is not surprising that in the absence of current, higher stress levels (*i.e.* necrosis) were observed, an effect that was particularly pronounced in female nubbins. The preference of branched or arborescent black coral species for low-current environments (Tazioli et al. 2007; Morgulis et al. 2022) was reflected in our studied species, as a lower production of bailout propagules and a tendency towards reduced TAC were observed in coral nubbins under the low-current treatment. Conversely, constant and elevated currents may increase stress responses in this species, triggering the escape strategy of bailout propagules, caused by the faster detachment of polyps and coenosarc (Sammarco 1982), and promoting higher oxidative stress. This was indicated by the increased production of propagules and the tendency for higher TAC values in the high-current treatment.

Table 3 Results from the best-fitting GLMMs for each experimental phase assessing the number of bailout propagules expelled by *A. wollastoni* nubbins (see Table SX for model selection)

	Estimate	SE	*z* value	*P*
Initial phase				
Intercept (Ref. level: High)	3.62	0.73	4.90	**9.55 e^{-07}**
Treatment (No current)	0.53	0.93	0.57	0.56
Treatment (Low)	−0.87	0.91	−0.95	0.34
Intermediate phase				
Intercept (Ref. level: High)	5.99	0.45	12.76	**< 2 e^{-16}**
Treatment (No current)	−4.04	0.64	−6.15	**7.4 e^{-10}**
Treatment (Low)	−1.73	0.65	−2.68	**0.007**
Intercept (Ref. level: No current)	1.80	0.47	3.82	**0.0001**
Treatment (High)	4.04	0.65	6.15	**0.0004**
Treatment (Low)	2.30	0.65	3.51	**7.4 e^{-10}**
End phase				
Intercept (Ref. level: High)	5.49	0.26	20.59	**< 2 e^{-16}**
Treatment (No current)	−3.65	0.38	−9.50	**< 2 e^{-16}**
Treatment (Low)	−0.94	0.38	−2.48	**0.01**
Intercept (Ref. level: No current)	1.85	0.28	6.53	**6.52 e^{-11}**
Treatment (High)	3.65	0.38	9.50	**< 2 e^{-16}**
Treatment (Low)	2.99	0.38	7.03	**2.01 e^{-12}**

The intercept corresponds to the reference level of the fixed factor (*i.e.* 'treatment'). To enable pairwise comparisons, all treatment levels were used as the reference (intercept) in separate models. Only models with significant differences are presented. Significant differences ($P < 0.05$) are highlighted in bold. Abbreviations: Ref. levels = reference levels

Additionally, one female nubbin died earlier in this treatment compared to those in the low-current treatment, which may further support the hypothesis that elevated current velocities increase physiological stress. These patterns suggest a potential influence of current velocity on survival, although the limited number of mortality events and the fact that mortality was assessed only at the end of each phase may have reduced the power to detect significant differences. While these findings provide valuable insights, they present certain limitations when extrapolating to the natural environment. The experimental set up does not fully replicate the complexity of natural current regimes, which are often characterized by temporal variability and irregular oscillations, including intermittent periods of higher flow. Reproducing such conditions ex situ remains technically challenging, and further data are needed to accurately simulate natural current variability.

Several gonochoric anthozoans have shown differences in the overall health state between male and female colonies during the reproductive season, likely due to their distinctive physiological demands (e.g. Cerrano et al. 2005; Holcomb et al. 2012; Arizmendi-Mejía et al. 2015; Mozqueda-Torres et al. 2018). For instance, the Mediterranean gorgonian *Paramuricea clavata* showed a skewed sex ratio after a mass mortality event caused by a heat wave, showing a higher vulnerability of females to temperature (Cerrano et al. 2005; Linares et al. 2008). This was corroborated by an experimental study, where female colonies of this gorgonian showed necrosis before males and significant reductions in fertility and number of gonads, when exposed to thermal stress (Arizmendi-Mejía et al. 2015). There are also examples of sex-based differences in growth or calcification rates across various species of scleractinian corals, where female colonies showed lower rates in response to stress factors, such as increased temperature (Cruz-Ortega et al. 2020; Cabral-Tena et al. 2024), elevated pCO_2 (Holcomb et al. 2012) or salinity changes (Cabral-Tena et al. 2013). Despite the varying stressors across studies, the outcomes are consistently similar, with female colonies being less capable of coping with stress. They are particularly vulnerable during the reproductive period showing a lower health performance over time (e.g. increased mortality or necrosis, and lower growth or calcification rate). In this study, the differences observed between sexes in tissue necrosis and mortality could be influenced by the timing of the experiment, which was conducted during the reproductive season, when gametes are fully developed and ready to spawn (Rakka et al. 2017). It is known that female invertebrates dedicate more energy to gamete production than males (Hayward and Gilloly 2011). For instance, some gonochoric scleractinian corals produce a greater mass of lipid-rich eggs compared to testes, increasing the energy expenditure of female colonies in gametogenesis (Hall and Hughes 1996; Leuzinger et al. 2003; Harrison 2011). Therefore, this higher energy allocation for reproduction in female colonies may contribute to their increased sensitivity to a stress factor. Moreover, it could partially explain the random effect of donor colony observed in the models for tissue necrosis, as colonies with higher fecundity may also exhibit greater vulnerability. However, we cannot confirm whether this random effect is driven by fecundity, as these data were not available for the donor colonies used in this study.

The increased female sensitivity to current conditions observed in *A. wollastoni* is particularly relevant, as it provides the first documented evidence of sex-related differences in Antipatharia, especially considering that most species within the group are gonochoric (Wagner et al. 2011; Waller et al. 2023; Lavorato et al. 2024). The lack of studies addressing sex differentiation in corals has been noted, with several authors highlighting the need to distinguish between sexes to better understand coral responses to environmental stressors (Cabral-Tena et al. 2013, 2024; Arizmendi-Mejía et al. 2015; Mozqueda-Torres et al. 2018; Cruz-Ortega et al. 2020). Sex-specific responses may have important ecological implications, particularly when females are more vulnerable to environmental stress. In our study, this increased susceptibility was evident under no-current conditions, where female colonies experienced more severe tissue necrosis. Such vulnerability in females can ultimately lead to skewed sex ratios and reduced reproductive success, with potential consequences for population resilience (Holcomb et al. 2012; Cabral-Tena et al. 2013). As these differences were observed during the reproductive season, which coincides with annual peak seawater temperature (Rakka et al. 2017), they are specially concerning in the context of rising sea surface temperatures within the Canary Current Upwelling System and the potential occurrence of extreme thermal events, such as marine heatwaves (Frölicher and Laufkötter 2018; Mills et al. 2024).

Another sign of stress observed across the experiment was polyp bailout, which is a common strategy to escape unfavourable conditions among anthozoans; this is produced when the polyp tissue completely separates from the skeleton (Sammarco 1982; Shapiro et al. 2016; Rakka et al. 2019; Schweinsberg et al. 2021; Gouveia et al. 2023). It has been largely studied across scleractinian corals, where it has been observed under different stressors, such as increased temperatures (e.g. Fordyce et al. 2017), reduced pH (Kvitt et al. 2015), increased salinity (e.g. Shapiro et al. 2016), or low food availability (Serrano et al. 2017). More recently, it has been described as a stress response in two black coral species, where polyp bailout was induced by the manipulation and rearing conditions in *A. subpinnata* (Coppari et al. 2020), and as a response to increasing temperature in *A. wollastoni* (Gouveia et al. 2023). The polyp bailout observed here was most likely related to the increased sensitivity of females to the different current treatments and rearing conditions, as those stressors previously mentioned as possible causes of this response were controlled. The only unexpected response occurred in the no-current treatment, where only a few propagules were released, despite it being the most stressful treatment for the nubbins. This suggests that the rapid onset of necrosis and the subsequent death of the nubbins, along with the absence of water movement, prevented them from utilizing this escape response. Additionally, we detected a random effect of the tank, which decreased in importance towards the end of the experiment. This effect may reflect variability in the number of polyps present in each nubbin. Although all fragments were standardized by size, it was not possible to ensure an identical polyp count across individuals, which could have introduced additional variability in propagule production.

Total antioxidant capacity is commonly used as a proxy for oxidative stress in anthozoans (e.g. Marangoni et al. 2019; Godefroid et al. 2022a; Tignat-Perrier et al. 2022; Gouveia et al. 2023; Strand et al. 2024). In black corals, this response has been studied in thermal stress experiments, where antioxidant capacity has generally been observed to increase under rising temperatures (Godefroid et al. 2022a, b; Gouveia et al. 2023). In our case, TAC measured at the end of the experiment showed no clear trend but was slightly lower in the low-current treatment, where nubbins showed fewer stress signs. The high variability among individual nubbins, a common feature in studies using this technique (e.g., Godefroid et al. 2022a; Tignat-Perrier et al. 2022; Gouveia et al. 2023; Strand et al. 2024), could have influenced the results, and the absence of multiple time points throughout the experiment may have hindered the identification of response trends. Comparing experimental TAC with values from wild colonies across seasons could help identify potential variations due to environmental factors.

This study highlights the critical role of current conditions in ensuring the survival of black corals and provides the first documented evidence of sex-related physiological differences in this group. Low, constant current velocities (around 5 cm s^{-1}) appear to be the most suitable for minimizing stress responses under rearing conditions, offering practical guidance for both experimental design and conservation efforts. Understanding the impact of environmental stressors is particularly important given the fundamental role of black coral forests in mesophotic ecosystems. This is especially true when considering sex-specific responses, as females may be more vulnerable during the reproductive period, when energy demands are the highest and seawater temperature reaches its annual peak. These insights contribute valuable ecological knowledge to a taxonomic group for which physiological studies remain scarce.

To build on these findings, future research should aim to recreate more realistic, oscillatory current regimes in laboratory settings. This will require more detailed in situ data to accurately replicate natural conditions. Additionally, understanding how different black coral morphologies are adapted to specific current regimes could inform species-specific restoration strategies. It is also essential to examine sex-related differences beyond the reproductive period, when energy allocation may be similar across sexes, to determine whether such differences persist year-round. Incorporating sex differentiation into experimental frameworks may help explain previously unaccounted variability in coral responses to environmental stress. We believe this work can serve as a valuable reference for future research on black corals under rearing conditions, offering also a basis for the implementation of reproduction programmes, supporting future active restoration efforts amid ongoing habitat fragmentation, biodiversity loss, and global environmental changes.

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Author's contribution Conceptualization was performed by FOF, LPC, SNM; method design by FOF, LPC, SNM; sample collection by FOF, LPC, SNM, CGH; laboratory work by LPC, SNM, FOF, CGH; data analysis by SNM, FT, LPC, FOF; image analysis by LPC; TAC analysis by LPC, SNM, FOF, MG; interpretation of data by SNM, LPC, FT, FOF, MG; funding acquisition by FOF, FT, RH; supervision by FOF; writing—original draft preparation by LPC; writing—review and editing by all authors.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Conflict of interest All authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest or non-financial interest in the subject matter or materials discussed in this manuscript. The contents of this document are the sole responsibility of the authors and can, under no circumstances, be regarded as reflecting the position of the EU, nor of the OFB and AFD.

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