



# Can colony resizing represent a strategy for octocorals to face climate warming? The case of the precious red coral *Corallium rubrum*

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**Abstract** Modular colonial benthic organisms exhibit high phenotypic plasticity, which is considered an effective strategy when faced with fluctuations in abiotic and biotic factors. However, when environmental changes occur abruptly, organisms' adaptive capabilities can be limited, leading to the death of some colonies or to mass mortalities. Additionally, a decrease in body size has been proposed as one of the most common responses in both terrestrial and aquatic organisms to face global warming. Here, temperate corals' response to thermal stress was documented using the precious red coral *Corallium rubrum* as a model species. The increased frequency of marine heat waves recorded in the north-western Mediterranean has led to a decrease in the total number of colonies of the analysed populations and reduced colony size in those that have survived, likely through fragmentation and branch loss. The laboratory analyses carried out on collected fragments showed an unexpected swelling, similar to resorption. Additionally, the occurrence of regular sclerite-like protuberances, typical of a normal skeleton surface, suggested a regeneration process. The documented phenomenon supports the hypothesis that *C. rubrum* exhibits an adaptive behaviour via the autotomy

of branches, providing it with an unexpected resilience against climate anomalies thanks to phenotypic plasticity.

**Keywords** Octocorallia · Mesophotic · North-Western Mediterranean Sea · Animal forests · Norm of reaction · Fragmentation

## Introduction

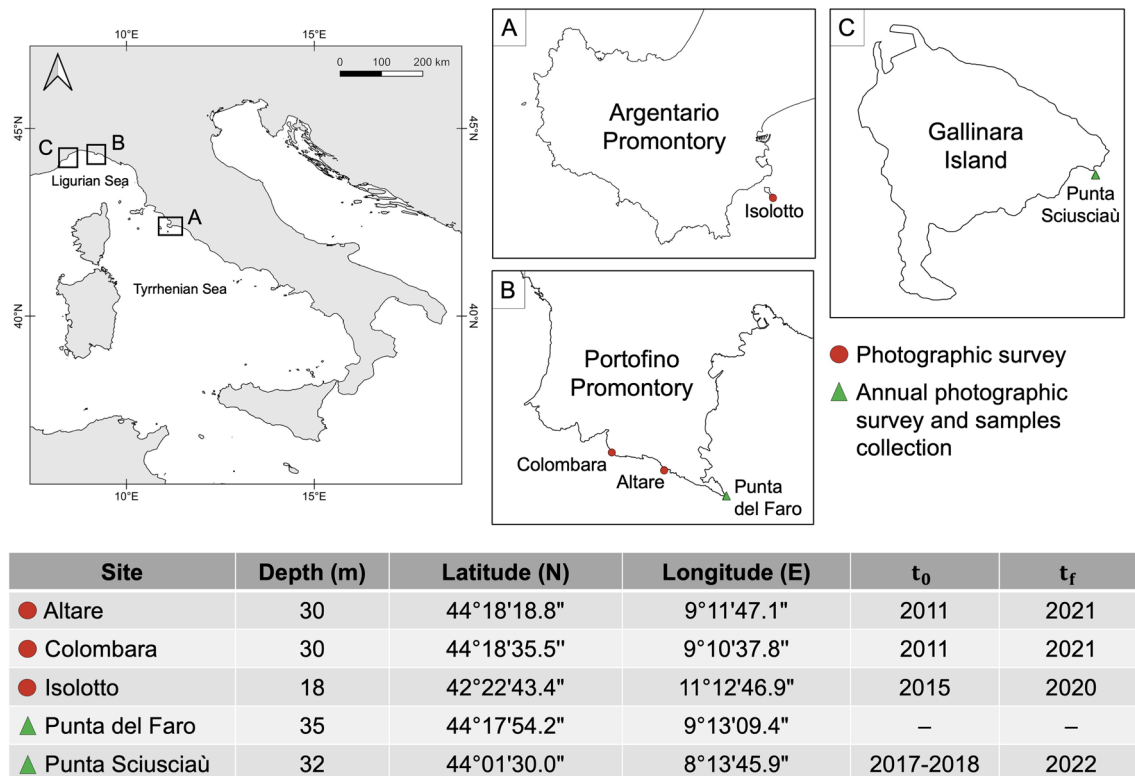
Modular colonial organisms are often characterised by high phenotypic plasticity, defined as the ability of a single genotype to produce, under different environmental stimuli, different phenotypes, including variation in the behaviour, shape, physiology, or sequence of modules produced at a particular stage of growth (West-Eberhard 1989; Padilla et al. 2013). Phenotypic plasticity is a major mechanism of response to environmental variability (e.g. light, depth, water movements, dissolved oxygen, temperature) and biological interactions (e.g. predator–prey interactions, invasion by non-native species), which leads to an increase in biological fitness (Kim et al. 2004; Sánchez et al. 2007; Bonamour et al. 2019; Kielland et al. 2019; Verberk et al. 2021).

The climate crisis (CC) is rapidly altering environmental parameters, as well as the richness, abundance, and distribution of marine organisms (Garrabou et al. 2019, 2022), affecting ecosystems across multiple levels of biological organisation, and inducing short-term changes in organisms' fitness (Crozier et al. 2008; Saers et al. 2011; Di Camillo et al. 2021). Biological mechanisms supporting these responses are likely due to the peculiarity of genotypes, each one presenting its own “reaction norm” (i.e. the direction and degree of response to environmental factors) (West-Eberhard 1989, 2003). Thus, the strong selective pressure experienced by many species may lead to the development of

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**Fig. 1** Map of sites surveyed, with spatial and temporal information for each site.  $t_0$  = initial photographic survey;  $t_f$  = final photographic survey

specific phenotypic responses (Crozier et al. 2008; Poloczanska et al. 2016), at both individual (e.g. growth rate, longevity, excretion rate, food intake, basic metabolism) and population level (e.g. mortality, reproductive rate, recruitment, population structure, distribution) (Madeira et al. 2012).

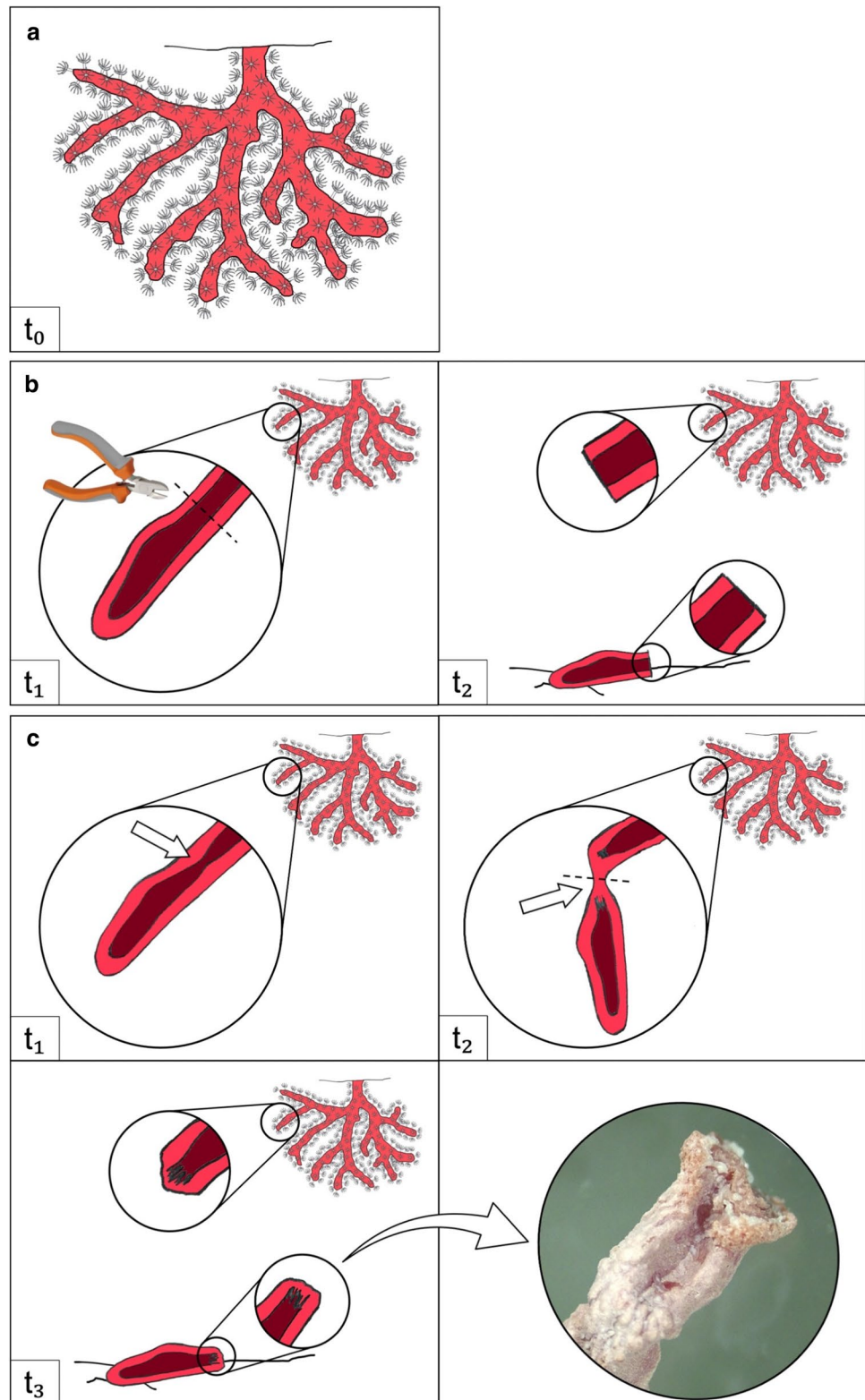
Although phenotypic plasticity is often seen as an important adaptive strategy, when environmental changes occur abruptly or are not spatially homogeneous, the adaptive capabilities of an organism can be limited (Fusco and Minelli 2010; Padilla and Savedo 2013). This is particularly true for aquatic sessile species, in which phenotypic plasticity might be insufficient for their survival, leading to repeated necrotic episodes, to an increase in mass mortality events (MMEs) and, consequently, to a risk of local extinction (Crozier et al. 2008; Di Camillo and Cerrano 2015; Garrabou et al. 2019, 2022).

Temperature and related oxygen concentration are two of the most important variables in the current CC (Madeira et al. 2012; Rubalcaba et al. 2020). It is well known that through developmental plasticity, the body size of many invertebrates is adapted to a given temperature range to optimise their aerobic activity, following the so-called temperature-size rule. This is regulated by a negative correlation between temperature and body size (Audzijonyte et al. 2019; Verberk et al. 2021). In fact, a decrease in body size has been proposed as one of the most recurrent responses of

organisms to climate warming, with a declining rate ranging from 5 to 20% in the last decades (Peter and Sommer 2013; Audzijonyte et al. 2019). As reported by Marfenin (1997) and Elahi et al. (2016), high temperatures and low oxygen availability can trigger a reduction in the final size of various modular organisms as cnidarians and bryozoans.

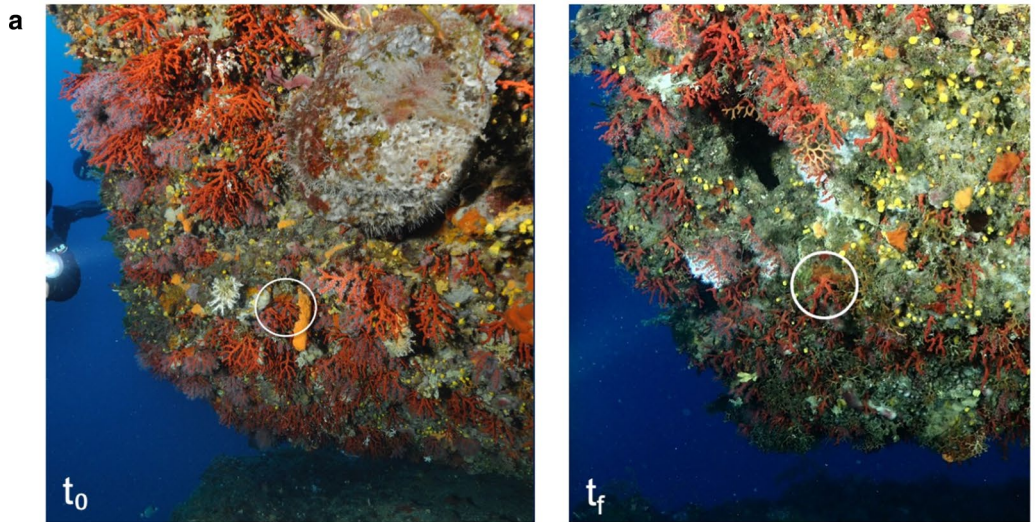
During thermal anomalies and related gorgonian mass mortalities in the Mediterranean Sea, large colonies of sea fans were found to be more affected by thermal stress with a shift towards smaller size classes (Cerrano et al. 2005; Previati et al. 2010). It has been demonstrated that natural or human-induced stresses, especially acute temperature stress, are responsible for fragmentation in various marine benthic taxa (i.e. algae, sponges, corals, mollusks) (e.g. Wulff 1991; Yamashiro and Nishihira 1994; Dahan and Benayahu 1997; Zuschin et al. 2003; Hoeksema and Waheed 2011; Coppari et al. 2019; He et al. 2019). In tropical octocorals, such as *Briareum asbestinum* (Pallas, 1766), *Eunicea flexuosa* (Lamouroux, 1821), *Junceella fragilis* (Ridley, 1884), and *Plexaura* sp., and some Alcyonacea, fragmentation is typically observed and mainly seen as an asexual reproductive strategy (Tursch and Tursch 1982; Lasker 1983, 1984; Walker and Bull 1983; Dahan and Benayahu 1997; Prada et al. 2008). In the Mediterranean gorgonians *Eunicella cavolini* (Koch, 1887) and *Paramuricea clavata* (Risso, 1826), preliminary observations report similar findings, which

**Fig. 2** Schematic representation of the red coral apexes collected at Punta Sciusciaù (Gallinara Island) and Punta del Faro (Portofino MPA) in November 2021. **A**  $t_0$  Red coral colony. **B**  $t_1$  Collection of the apical fragment using a wire cutter;  $t_2$  Highlight of the clean-cut caused by the wire cutters. **C**  $t_1$  Apical fragment naturally detaching from the colony, with the scleraxis starting to be resorbed;  $t_2$  Apical fragment connected to the main colony only by the coenenchyme;  $t_3$  Uncommon swelling caused by the regeneration of the scleraxis, together with a detailed picture taken using a stereomicroscope

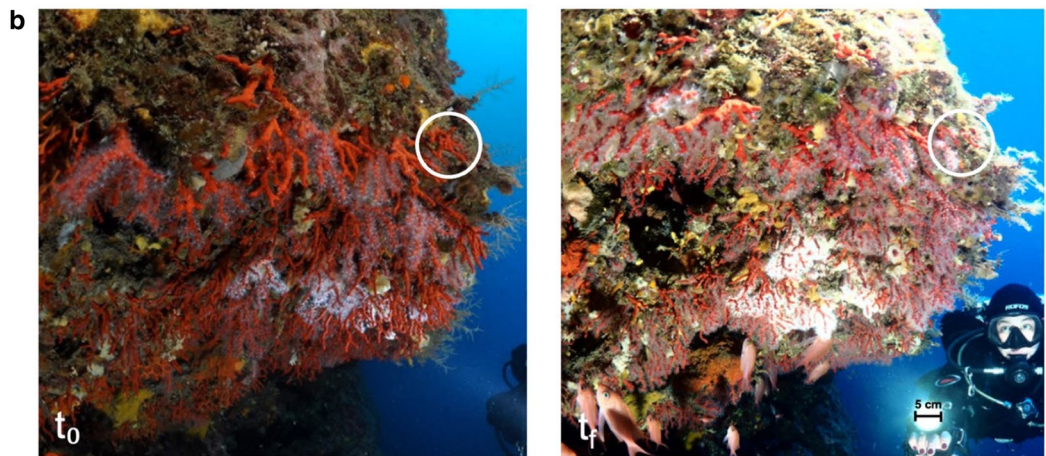


were seen as possible adaptive strategies to overcome stress factors that ensure population survival (Franci et al. 2003; Valisano et al. 2016).

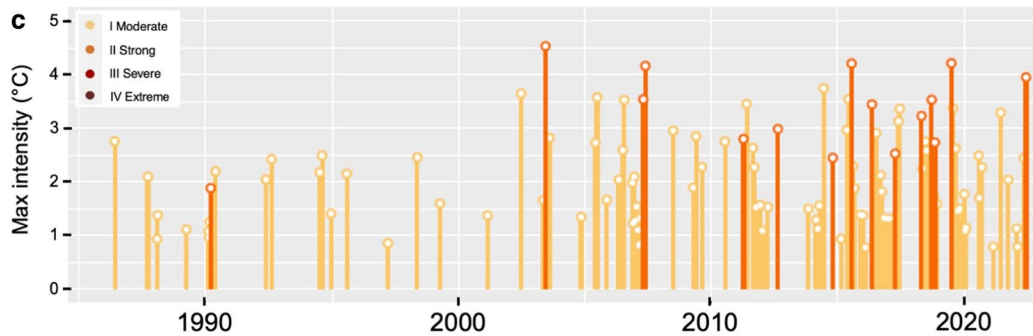
The red coral *Corallium rubrum* (Linnaeus, 1758) is a slow-growing ecosystem engineer of Mediterranean mesophotic benthic communities (Rossi et al. 2008; Benedetti



	$t_0$	$t_f$
Total number of colonies	107	99
Size (av. $\pm$ s.d. %)	- 40.0 $\pm$ 18.1	
Number of apices (av. $\pm$ s.d. %)	- 53.8 $\pm$ 22.9	



	$t_0$	$t_f$
Total number of colonies	123	98
Size (av. $\pm$ s.d. %)	- 48.4 $\pm$ 24.6	
Number of apices (av. $\pm$ s.d. %)	- 43.8 $\pm$ 23.9	



**Fig. 3** Photographic survey conducted in the Portofino MPA at: **A** Altare and **B** Colombara, with the change in the total number, size, and branches of red coral colonies. **C** Maximum intensity of the marine heat waves occurred at the Portofino MPA from 01-01-1986 to 31-12-2021.  $t_0$ =initial photographic survey (2011);  $t_f$ =final photographic survey (2021). av.: average value; s.d.: standard deviation. White circles evidence, as example, the same colony at  $t_0$  and  $t_f$ . The black line inside the torch light indicates the reference size considered to measure the selected colonies

et al. 2016). In the last decades, repeated MMEs mainly linked to thermal anomalies were identified as the major threat for shallow populations of *C. rubrum*, that, coupled with the low growth rates typical of the species (Bavestrello et al. 2009; Cerrano et al. 2013), caused dramatic declines at the basin level (e.g. Cerrano et al. 2000; Perez et al. 2000; Cerrano and Bavestrello 2008; Rossi et al. 2008; Garrabou et al. 2001, 2009). Under laboratory conditions, changes in temperature and salinity were found to induce fragmentation of the coral branch ends, followed by the complete resorption of tissues (Russo 1995). Conversely to the observations made for the other Mediterranean octocorals, this phenomenon was justified as a possible new mechanism of asexual reproduction (Russo 1995; Russo et al. 1997).

In this work, a reduction in the number of colonies, colony size and number of apices in wild and transplanted populations of *C. rubrum* were documented and related to the marine heatwaves (MHWs) occurred over the last 35+ years in various sites. Long-term observations of these populations suggest that autotomy may not only be related to a possible asexual reproductive strategy, but as a potential response of the red coral to stressors, including climate change and temperature increase, thus showing an unexpected resilience thanks to phenotypic plasticity.

## Materials and methods

### Photographic surveys and data analysis

To evaluate phenotypic variations in different red coral populations, *Corallium rubrum* was monitored in four sites: Isolotto (− 18 m), near Porto Ercole in the Argentario Promontory (Tyrrhenian Sea), Altare and Colombara (− 30 m), inside the Marine Protected Area (MPA) of Portofino (Ligurian Sea), and Punta Sciusciaù (− 32 m), at the Gallinara Island (Ligurian Sea) (Fig. 1). The first three sites were monitored only two times, Isolotto in 2015 ( $t_0$ ) and 2020 ( $t_f$ ), while Altare and Colombara in 2011 ( $t_0$ ) and 2021 ( $t_f$ ) (Fig. 1A, 1B). Conversely, at Punta Sciusciaù, a yearly monitoring was conducted, from 2017 ( $t_0$ ) to 2022 ( $t_f$ ) (Fig. 1C).

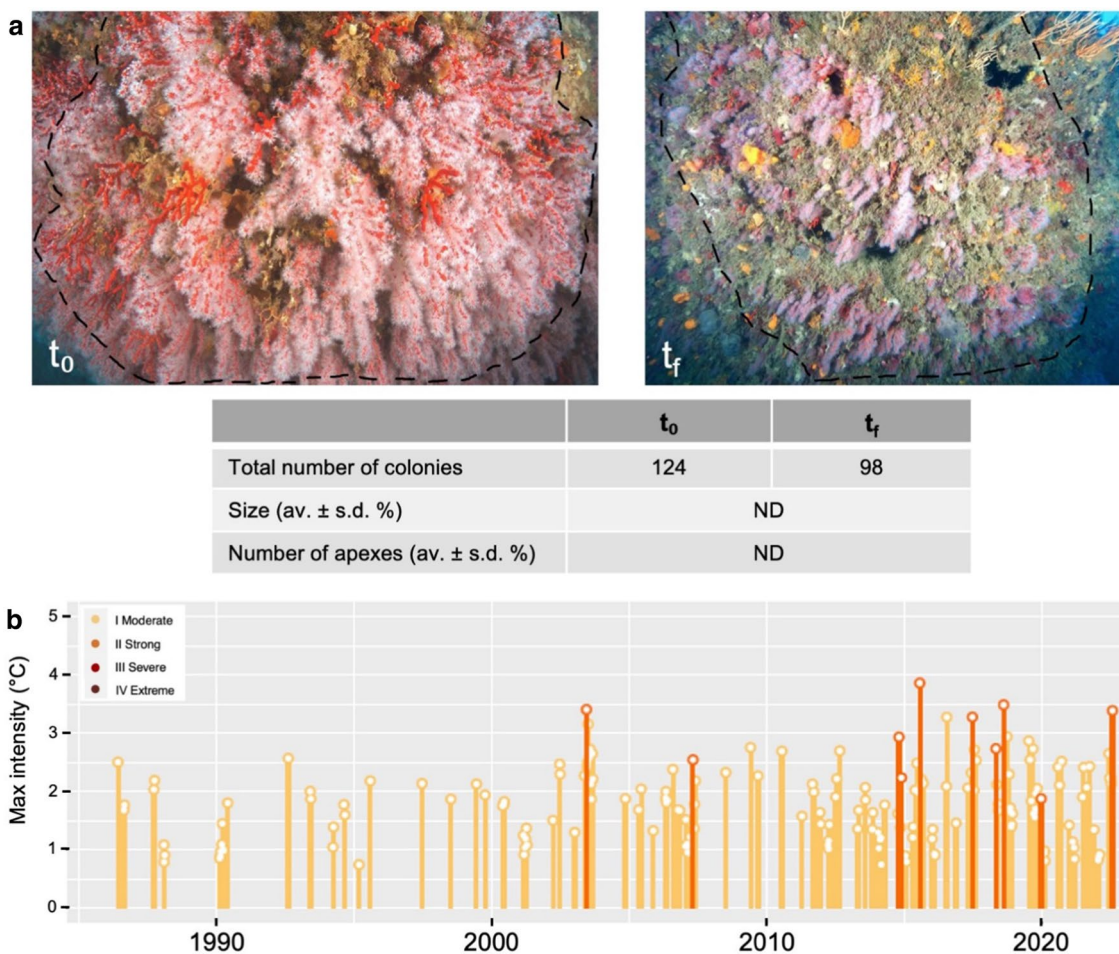
At the Altare and Colombara photos were taken with a Nikon D90, while at Isolotto with a SONY Alpha 6300. At each location, the same rocky cliffs (sensu Musard et al.

2014) were photographed, keeping the same perspective at each monitoring event. From each picture, the total number of colonies was counted, and changes in their number (expressed as percentages) were estimated. Additionally, only from the photos taken in Altare and Colombara, the difference between  $t_0$  and  $t_f$  in colony size (i.e. from the base to the larger branch) and number of apices of 25 colonies were calculated using ImageJ software (Rasband 2012). The height of each colony was evaluated in cm and changes between  $t_0$  and  $t_f$  expressed as an average percentage ( $\pm$  standard deviation, s.d.). Since no metric reference was present in the provided pictures, the colony size was evaluated considering the diver torches, included in each original picture, as a size reference (diameter = 5 cm). Conversely, at the Isolotto, the analysis was prevented due to the nadir perspective of the two photos, preventing the proper calculation of the estimated parameters; thus, only the change in the total number of colonies between monitoring events was evaluated. To test for possible differences in colony size and number of apices between the two timelines, a one-tailed Student *t* test was performed using the R package *ggpubr* (Kassambara 2020).

In the framework of the MERCES project (Marine Ecosystem Restoration in Changing European Seas, <http://www.merces-project.eu/>), 59 fragments of *C. rubrum* were transplanted at 32 m depth at Punta Sciusciaù in Gallinara Island. Transplants were obtained by fragmenting the apical branches of random adult colonies located at 25 m from Punta del Faro (a site included in the Portofino MPA, Ligurian Sea), collecting apical branches of 2–6 cm with an average number of apices per colony of  $5.6 \pm 3.2$  (Villechanoux et al. 2022). Fragments were then transplanted at 32 m depth, within cavities and overhangs, typical of the coralligenous bioconcretions (Ballesteros 2006), in August 2017 ( $n = 45$ ) and June 2018 ( $n = 14$ ). The photographic survey on the translocated colonies was conducted yearly from the transplantation date (August 2017 and July 2018) to August 2022 (Fig. 1). The pattern of branch loss was considered only for colonies that survived until August 2022 ( $n = 25$ ).

### Collection and analysis of apical fragments

To assess possible alterations in the biocalcification pattern of the *C. rubrum* skeleton, in November 2021, 10 apical fragments from ten red coral colonies transplanted in 2017–2018 at Punta Sciusciaù (Gallinara Island) and 10 apical fragments from ten colonies from Punta del Faro (Portofino MPA) (Figs. 1b, c and 2) were collected while SCUBA diving at 32 and 35 m depth, respectively. At Punta Sciusciaù, since fragments were collected from colonies that were also included in the photographic sampling (see paragraph above), the sampled colonies were tagged, and the fragments collected were not included in the lost apex counts.



**Fig. 4** Photographic survey conducted at the Isolotto in the Argentario Promontory. **A** Change in the total number of red coral colonies. **B** Maximum intensity of the marine heat waves occurred at the Argentario Promontory from 01-01-1986 to 31-12-2021.  $t_0$ =initial

photographic survey (2015);  $t_f$ =final photographic survey (2020). Dashed lines delimit the assessed area. av.: average value; s.d.: standard deviation

Fragments were carefully cut with wire cutters (Fig. 2B) and put into sealed plastic bags. At Punta del Faro, by gently touching coral apices it was evident that some of them were loose, and five of them did not need to be cut with wire cutters (Fig. 2C). The collected material was preserved in 90% alcohol until further analysis.

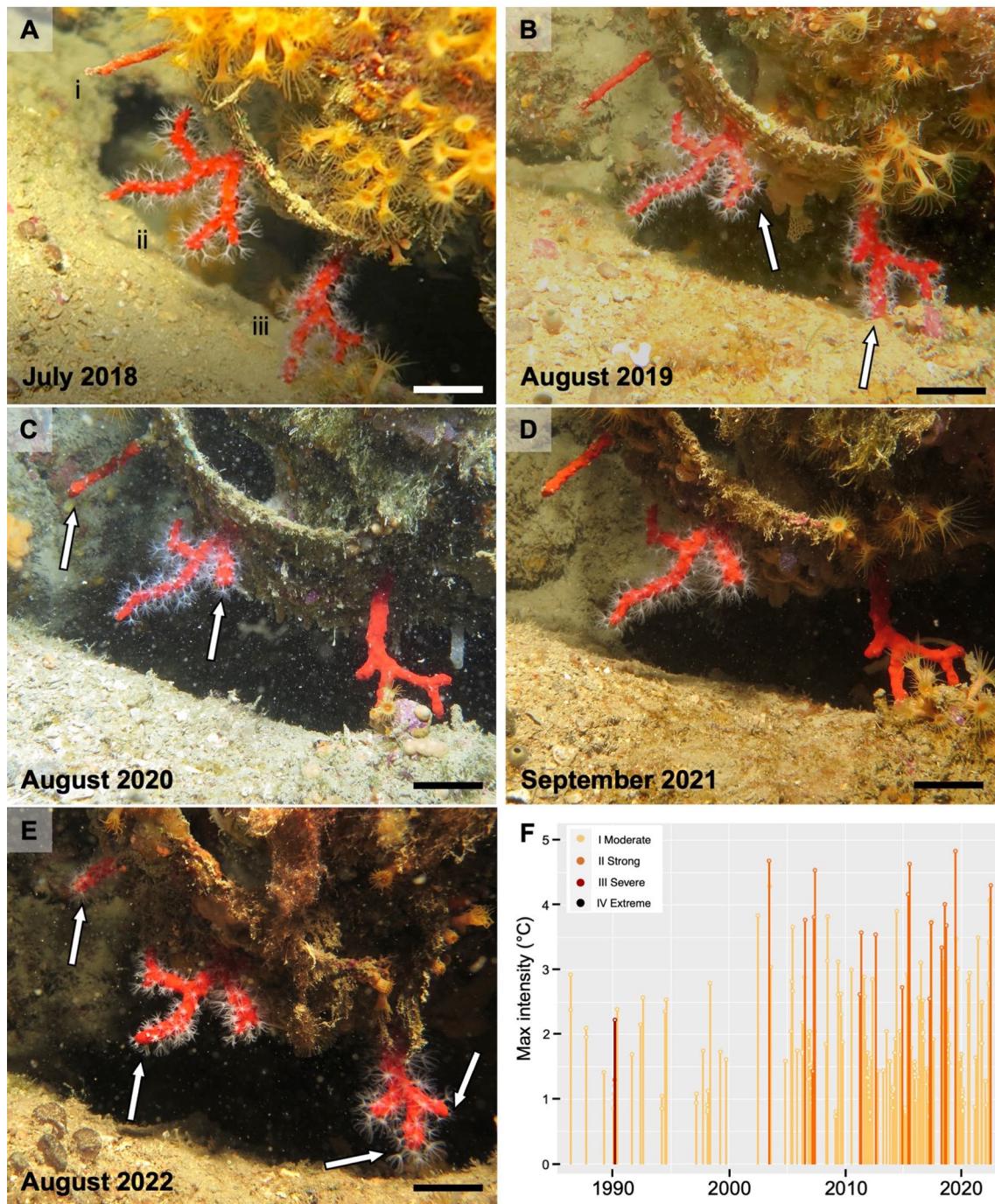
In the collected samples, scleraxis was cleaned in tubes in a 120-volume solution of peroxide oxygen and heated above a flame for 10 min, to accelerate the dissolution of the organic matter. Each scleraxis was separated from their sclerites and rinsed 3 times with reagent grade water (MilliQ) followed by a gradual alcohol concentration rinsing (70%, 80%, 90%, 95%, and 100%) to dehydrate the samples. Samples were initially observed under a Nikon SMZ18 stereomicroscope; then selected fragments were mounted on aluminium stubs using carbon adhesive tabs, coated with gold using a Polaron Range sputter coater and observed under a Philips XL 20 Scanning Electron

Microscope (SEM) to analyse the fine-scale morphology and calcification formation.

#### Detection and classification of MHWs

A MHW is defined as an event in which the sea surface temperature (SST) exceeds, at a certain location, an upper locally determined threshold (90th percentile relative to the long-term climatology) for at least 5 consecutive days. This local threshold is defined using all data within an 11-day window centred on the day from which the climatological mean and percentile are calculated (Hobday et al. 2016).

MHWs were identified from the National Oceanic and Atmospheric Administration (NOAA) Optimum Interpolation Sea Surface Temperature (OISST), a product with a global 1/4 degree gridded dataset of Advanced Very High

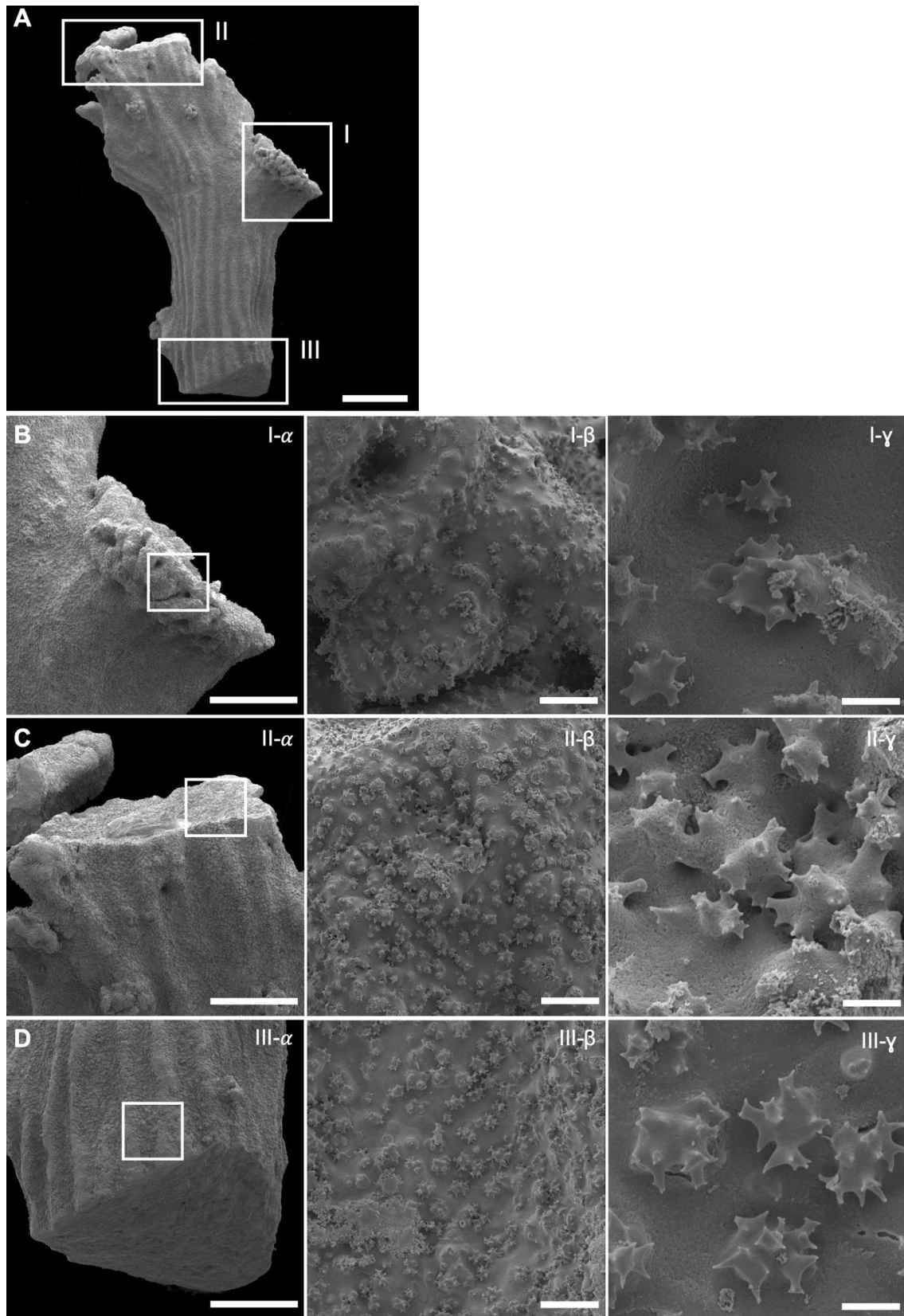


**Fig. 5** A–E Sequence of the annual photographic survey conducted on three transplanted colonies at Punta Sciusciaù in Gallinara Island. **F** Maximum intensity of the marine heat waves occurred at Gallinara

Island from 01-01-1986 to 31-12-2021. The white arrows indicate the loss of ramifications. Scale bars = 2 cm

Resolution Radiometer derived SSTs at a daily resolution, starting on 1 September 1981 (<https://www.ncei.noaa.gov/products/optimum-interpolation-sst>). For the current study, the time series from 01-01-1986 to 13-08-2022 was considered, using the standardised method developed in Hobday et al. (2016, 2018). Each MHW was detected and

described, thanks to the R package *heatwaveR* (Schlegel and Smit 2018), in terms of event duration, frequency, intensity, and cumulative intensity in each surveyed location (Isolotto, Portofino MPA and Punta Sciusciaù) and provided here in the Supplementary Material as Online Resource 1. The same software module allowed us to





**Fig. 6** SEM images of: **A** a fragment of *Corallium rubrum* collected using wire cutters at Punta Sciuscià in Gallinara Island; **B I- $\alpha$**  uncommon swelling, similar to a resorption, suggesting a regeneration process, **I- $\beta$**  uncommon swelling showing a regular pattern of sclerite-like protuberances, **I- $\gamma$**  detail of the regular pattern of sclerite-like protuberances; **C II- $\alpha$**  flat section similar to a cut, possibly caused by the recent detachment of part of the branches, **II- $\beta$**  flat section with an irregular pattern of sclerite-like protuberances, **II- $\gamma$**  detail of the irregular pattern of sclerite-like protuberances; **D III- $\alpha$**  clean-cut caused by the wire cutters, **III- $\beta$**  regular pattern of sclerite-like protuberances in the surrounding area of the clean-cut, **III- $\gamma$**  detail of the sclerite-like protuberances. The white quadrats represent the analysed areas. Scale bars: **A** 2 mm; **B I- $\alpha$** , **C II- $\alpha$** , **D III- $\alpha$**  1 mm; **B I- $\beta$** , **C II- $\beta$** , **D III- $\beta$**  100  $\mu$ m; **B I- $\gamma$** , **C II- $\gamma$** , **D III- $\gamma$**  20  $\mu$ m. Zoom: **A** 17x; **B I- $\alpha$** , **C II- $\alpha$** , **D III- $\alpha$**  60x; **B I- $\beta$** , **C II- $\beta$** , **D III- $\beta$**  400x; **B I- $\gamma$** , **C II- $\gamma$** , **D III- $\gamma$**  2000x

classify each event into four categories (I—moderate, II—strong, III—severe, and IV—extreme), defined by Hobday et al. (2018) as a function of their maximum observed intensity.

The MHWs considered in this study were divided for further analysis into two periods, from 1986 to 2010 (24 years) and from 2011 to 2022 (10 years and 8 months), as the first analysed photo of *C. rubrum* was taken in 2011. Differences in the maximum intensity, cumulative intensity, duration, and frequencies of MHWs were investigated using the non-parametric Kruskal–Wallis analysis of variance between the two periods. Statistical tests were performed using R packages *stats* and *rstatix* (Kassambara 2021; R Core Team 2021).

## Results

### Evaluation of red coral populations over time

The analysed pictures showed a 7% and 20% decrease in the number of colonies from 2011 to 2021 at Altare and Colombara, respectively (Fig. 3), and a 21% decrease from 2015 to 2020 at Isolotto (Fig. 4). A significant reduction in colony size ( $-40.0 \pm 18.1\%$ , at Altare, and  $-48.4 \pm 24.6\%$ , at Colombara) and number of apexes ( $-53.8 \pm 22.9\%$ , at Altare, and  $-43.8 \pm 23.9\%$ , at Colombara) were also recorded in each site located in the Portofino MPA (Student *t* test,  $p < 0.05$ ) (Fig. 3).

At the Punta Sciuscià, a mortality rate of 43% of transplanted colonies was registered in the 5-year monitoring activity. Colonies survived until August 2022 ( $n = 25$ ) were then considered to investigate the pattern of branch loss. All colonies were observed healthy during the five years of the experiments (Fig. 5). However, as in the other locations, a considerable number (76%) displayed a marked reduction in size and suffered from the loss of several branches (Fig. 5). Most of these colonies (73.7%) lost their branches in the first

2 years of the experiment, while the remaining 26.3% lost their branches in the following years.

At all sites, no sign of necrosis or tissue damage was recorded, with colonies presenting open active polyps (Figs. 3, 4, 5).

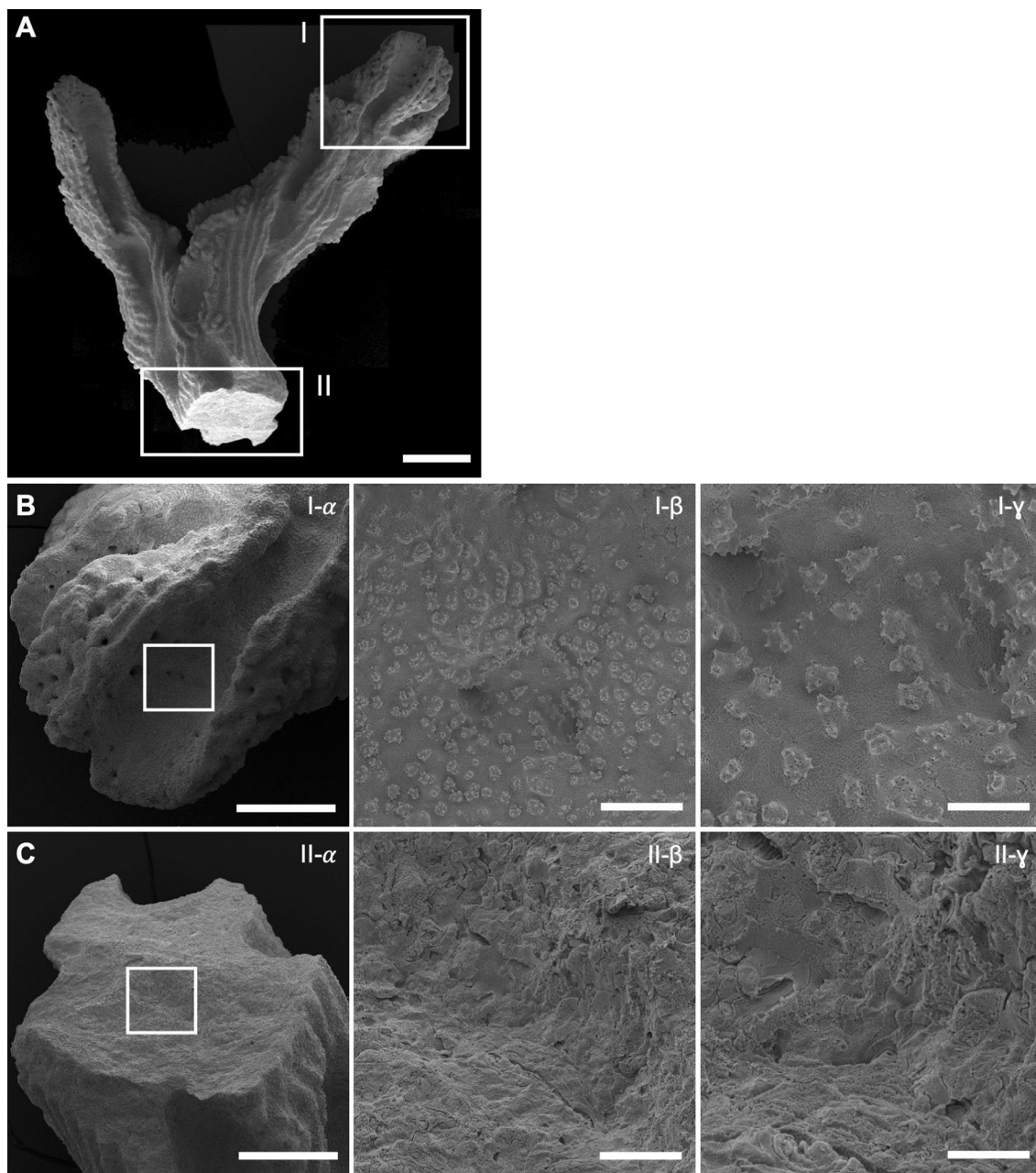
### Analysis of the apical fragments

From the underwater sampling conducted at Punta del Faro in the Portofino MPA in November 2021, two situations were observed: (1) loose coral apexes were hanging directly from the colony, beginning to self-detach on their own (Fig. 2C  $t_1$  and  $t_2$ ), while (2) ten fragments (4 of which still with open polyps) were also found on the substrate, suggesting a recent detachment from the main colonies (Fig. 2C  $t_3$ ). Conversely, at Punta Sciuscià, no apexes were found to be self-detaching and were all collected using wire cutters (Fig. 2B).

In the five loose samples, subsequent stereomicroscope analyses exposed an uncommon swelling at one end of the fragments, like a resorption, suggesting a possible regeneration process (Fig. 2C  $t_3$  stereomicroscope photo). A similar pattern was also observed in the SEM analysis of fragments cut with wire cutters (Figs. 6, 7). In fact, in the latter, most of the examined apexes (12 out of 15) were presenting the same swelling (Figs. 6B I- $\alpha$  and 7B I- $\alpha$ ), with a regular pattern of sclerite-like protuberances (Fig. 6B II- $\beta$  and II- $\gamma$ , Fig. 7B I- $\beta$  and I- $\gamma$ ). Additionally, in some of the fragments (6), the apical portions displayed a flat section similar to a cut (Fig. 6C II- $\alpha$ ), possibly given by the recent detachment of part of the branches and with an irregular pattern of sclerite-like protuberances (Fig. 6C II- $\beta$  and II- $\gamma$ ). On the other hand, the clean-cut caused by the wire cutters were clearly identifiable (Figs. 6D III- $\alpha$  and 7C II- $\alpha$ ), with a regular pattern of sclerite-like protuberances in the surrounding area (Fig. 6D III- $\beta$  and III- $\gamma$ ) and a smooth surface at the bottom of the fragment, with no sign of recalcification (Fig. 7C II- $\beta$  and II- $\gamma$ ).

### MHWs analysis

The MHWs analysis conducted over the past 35 years and 8 months highlighted that Punta Sciuscià and Isolotto displayed the highest number of thermal anomalies, with 184 and 181, respectively, while only 107 were recorded for the Portofino MPA (Online Resource 1). At all sites, most events fell into category I (moderate) (92 for the Portofino MPA, 171 for the Isolotto, and 164 for Punta Sciuscià), while all other events fell into category II (strong) (Figs. 3C, 4B and 5F; Online Resource 1). The only severe (category III) event was recorded during the winter of 1993 in Punta Sciuscià



**Fig. 7** SEM images of: **A** a fragment of *Corallium rubrum* collected using wire cutters at Punta del Faro in the Portofino MPA; **B I- $\alpha$**  uncommon swelling, similar to a resorption, suggesting a regeneration process, **I- $\beta$**  canal of the uncommon swelling showing a regular pattern of sclerite-like protuberances, **I- $\gamma$**  detail of the regular pattern of sclerite-like protuberances; **C II- $\alpha$**  clean-cut caused by the wire

cutters, **II- $\beta$**  smooth surface at the bottom of the clean-cut, **II- $\gamma$**  detail of the smooth surface. The white quadrats represent the analysed areas. Scale bars: **A** 2 mm; **B I- $\alpha$** , **C II- $\alpha$** , **D III- $\alpha$**  1 mm; **B I- $\beta$** , **C II- $\beta$** , **D III- $\beta$**  100  $\mu$ m; **B I- $\gamma$** , **C II- $\gamma$** , **D III- $\gamma$**  50  $\mu$ m. Zoom: **A** 15x; **B I- $\alpha$** , **C II- $\alpha$** , **D III- $\alpha$**  60x; **B I- $\beta$** , **C II- $\beta$** , **D III- $\beta$**  400x; **B I- $\gamma$** , **C II- $\gamma$** , **D III- $\gamma$**  1000x

(Figs. 3C, 4B and 5F; Online Resource 1), and no extreme (category IV) events were recorded.

A general increase in the number of thermal anomalies was observed over the last decade (2011–2022) (Figs. 3C, 4B and 5F; Online Resource 1). In fact, even though no differences were found in the maximum intensity, cumulative intensity, and duration of MHWs between 1986 and

2010 and 2011–2022 (Kruskal–Wallis,  $p > 0.05$ ), their frequency was statistically different (Kruskal–Wallis,  $p < 0.05$ ), with a total number of MHWs recorded during the 24-year period (47 for the Portofino MPA, 80 for the Isolotto, and 76 for Punta Sciuscià) lower than for the following 10 years and 8 months (60 for Portofino MPA, 101 for the Isolotto, and 108 for Punta Sciuscià) in all considered locations

**Table 1** Number of marine heat waves (MHWs) occurred in each of the considered locations, per season and analysed time periods

Site	Season	Total*	1986–2010	2011–2021
Isolotto	Autumn	28	5	23
	Winter	55	27	28
	Spring	55	31	24
	Summer	55	21	34
Portofino MPA	Autumn	22	6	16
	Winter	31	15	16
	Spring	35	16	19
	Summer	32	13	19
Punta Sciusciaù	Autumn	36	10	26
	Winter	66	29	37
	Spring	52	25	27
	Summer	44	15	29

\*Please note that the total number of MHWs summarising all seasons is higher than the actual number recorded in each site since the duration of a discrete event could interest more than one season

(Figs. 3C, 4B and 5F; Online Resource 1). Furthermore, considering the seasonality of the events, autumn showed the lowest number of MHWs at each location, especially during the period of 1986–2010 (Table 1). In the years that followed (2011–2022), MHWs increased in almost all seasons, especially in autumn, equalising or exceeding the number of MHWs recorded for the other seasons (Table 1). Interestingly in Punta Sciusciaù, most of the MHWs occurred in winter in both periods (29 and 37 events in 1986–2010 and 2011–2022, respectively) (Table 1).

## Discussion

According to Stearns (1989), the norm of reaction can be considered adaptive when a phenotype changes function to face a specific environmental signal. Over the past years, MHWs and related MMEs of marine invertebrates have been increasing in frequency, duration, and severity worldwide (e.g. Frölicher et al., 2018; Smale et al. 2019; Mohamed et al. 2021), and the Mediterranean basin is no exception (Garrabou et al. 2019, 2022). In this scenario, it is fundamental to detect how the morphological and physiological plasticity of affected species can support their survival. The current investigation highlighted a significant loss, in terms of number of colonies, colony size and number of apices, within different shallow *Corallium rubrum* populations of the north-western Mediterranean, possibly correlated to the increase in frequency of the MHWs.

Over the last three decades, the north-western Mediterranean has experienced various significant MHWs, of which those of 1999 and 2003 showed the most severe effects, causing MMEs of octocorals with mortality rates of up

to 100% (Cerrano et al. 2000; Perez et al. 2000; Garrabou et al. 2009). Following the previously described episodes and increased frequency of thermal anomalies, especially during the colder seasons, a reduction in the number of colonies of the precious coral was recorded, and the surviving colonies displayed a significant reduction in size, possibly due to fragmentation and the loss of several apical ramifications. Both underwater and laboratory observations suggest that the red coral can undergo to a fragmentation process through an autotomy procedure of the branch ends. Firstly, the scleraxis starts to get resorbed (Fig. 2C t<sub>1</sub>), until the apical fragment is connected to the main colony only by the coenenchymal tissue (Fig. 2C t<sub>2</sub>); then, the complete detachment of the loose fragments is probably triggered by the surrounding water movement (Fig. 2C t<sub>3</sub>). Therefore, the documented phenomenon suggests a reorganisation of the colony shape as an adaptive mechanism of shallow populations against rising temperatures, and could lead to following processes of transgenerational plasticity and a bet-hedging reproductive strategy (e.g. Cumbo et al. 2012, 2013; Putnam and Gates 2015; Chamberland et al. 2017; Torda et al. 2017). For various Mediterranean gorgonians (i.e. *Eunicella singularis*, *E. cavolini*, *C. rubrum*, *Paramuricea clavata*), larger colonies have been documented to be more susceptible to thermal stress, causing a shift in the population structure towards smaller size classes (Cerrano et al. 2005; Previati et al. 2010). However, our study highlights how the same colonies clearly shorten their size over time, displaying a reduction in height due to the loss of several apices, thus leading to a general decrease in the size of the entire population. Nonetheless, further studies are needed to better understand the physiological processes behind the observed phenomenon, also considering its consequences in the reproduction of the species, since larvae production depends not only on the colony age, but also on their size, with smaller colonies producing a lower number of larvae (Santangelo et al. 2003; Tsounis et al., 2006).

From the stereomicroscope and SEM analyses of the scleraxis structures, the fragmentation-like process in *C. rubrum* apical parts was evident. The loose fragments collected at Punta del Faro (Portofino MPA) clearly showed differences in the calcification patterns with respect to the clean-cut ones. The latter have a smooth cut surface, while, in the loose fragments, the surfaces showed irregular patterns with sclerite-like protuberances, typical of the skeleton surface. This structure demonstrated an active process of mineralization acting on the fragmented surfaces, as previously described under laboratory conditions by Russo et al. (1997). The ability of autotomy and resorption of mineral and organic skeletal components is typical in most marine phyla, including Cnidaria (Batson et al. 2020). In the red coral skeleton, various matrix metalloproteinases and collagen-like proteins have been found (Le Roy et al. 2021),

and, due to the role they play in remodelling and mineralization processes, they may be also involved in the scleraxis resorption.

The reorganisation of colony shape through the variation of branch lengths was previously observed under laboratory conditions for *C. rubrum*, as well as for many other cnidarian species (e.g. Tursch and Tursch 1982; Lasker 1983, 1984; Walker and Bull 1983; Dahan and Benayahu 1997; Prada et al. 2008) but explained as a new potential asexual reproduction (Russo 1995; Russo et al. 1997). However, even though the fragments have been observed to produce a thin layer of coenenchyma before detachment, they were generally not able to re-settle (Russo et al. 1997). Additionally, no settlement of the dropped portions was observed during our investigation, suggesting that autotomy as an asexual reproductive strategy needs to be better explored, and could be considered as a way of reorganising the colony as a response to a stress condition (Cerrano and Bavestrello 2008). A similar response has been also hypothesised for *E. cavolini* (Bavestrello and Boero 1986; Franci et al. 2003) and *P. clavata* (Valisano et al. 2016). These observations suggest that, in a warming Mediterranean, future studies on the relationship between size and age of the red coral should also consider the possible resizing of colonies as an additional factor.

Aquatic ecological responses to climatic warming are also linked to other environmental stressors, such as hypoxia (Verbek et al. 2016). Although they have always been considered critical threats, a certain degree of plasticity was documented in various aquatic ectotherms (Hoefnagel and Verberk 2015; Leung et al. 2022). In fact, it has been observed that high temperatures along with limited oxygen availability were responsible for a reduction in growth rates and final size of various organisms, including modular ones (e.g. cnidarians and bryozoans) (Marfenin 1997; Atkinson et al. 2006; Hoefnagel and Verberk 2015; Elahi et al. 2016). It is thus plausible to assume that the reduction in size observed for *C. rubrum* could be caused by the synergic action of temperature and dissolved oxygen availability (Verberk et al. 2021). On the other hand, other studies suggested that limited resources can also play a role in decreasing size of modular colonial organisms, including corals (Kim and Lasker 1998). Since the Mediterranean basin is known to be characterized by trophic depletion during the summer season, limiting food resources especially for filter and suspension feeders (sponges, corals, polychaetes, among others) (Coma et al. 1994), could represent an additional factor driving size in Mediterranean octocorals. Additionally, a high phenotypic plasticity and high levels of biodiversity can also mitigate the effects of other stressors (Leung et al. 2022), as documented for seagrasses at low pH conditions (Gambi et al. 2022). The negative impacts of acidification are also reduced if *C. rubrum* is associated with the natural coralligenous assemblages, displaying higher integrity

of their calcium carbonate sclerites and calcification rates (Rastelli et al. 2020).

We are just starting to scratch the surface in understanding how single species are adapting to climate warming, yet a huge gap in our knowledge remains regarding how these adaptations will affect inter-specific interactions. Even if the single species persists in the environment, its loss in density and size can lead to the Allee effect and/or deeply change the environmental conditions at a small-scale, possibly affecting the entire associated community. To ensure management strategies that will provide and enhance a species-based protection to safeguard ecosystems' diversity, we will need not only to understand the adaptive strategies of a single species, but also how these strategies can impact its associated assemblage.

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#### Declarations

**Conflict of interest** The authors have no relevant financial or non-financial interests to disclose.

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