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Lethal and sublethal effects of thermal stress on octocorals early life-history stages

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Abstract

The frequency and severity of marine heatwaves causing mass mortality events in tropical and temperate coral species increases every year, with serious consequences on the stability and resilience of coral populations. Although recovery and persistence of coral populations after stress events is closely related to adult fitness, as well as larval survival and settlement, much remains unknown about the effects of thermal stress on early life-history stages of temperate coral species. In the present study, the reproductive phenology and the effect of increased water temperature (+4°C and +6°C above ambient, 20°C) on larval survival and settlement was evaluated for two of the most representative Mediterranean octocoral species (*Eunicella singularis* and *Corallium rubrum*). Our study shows that reproductive behavior is more variable than previously reported and breeding period occurs over a longer period in both species. Thermal stress did not affect the survival of symbiotic *E. singularis* larvae but drastically reduced the survival of the non-symbiotic *C. rubrum* larvae. Results on larval biomass and caloric consumption suggest that higher mortality rates of *C. rubrum* exposed to increased temperature were not related to depletion of endogenous energy in larvae. The results also show that settlement rates of *E. singularis* did not change in response to elevated temperature after 20 days of exposure, but larvae may settle fast and close to their native population at 26°C (+6°C). Although previous experimental studies found that adult colonies of both octocoral species are mostly resistant to thermal stress, our results on early life-history stages suggest that the persistence and inter-connectivity of local populations may be severely compromised under continued trends in ocean warming.

KEYWORDS
brooding, energetic consumption, gorgonians, larvae, marine heatwaves, reproductive phenology, settlement

1 | INTRODUCTION

In the last few decades, global climate change, and ocean warming in particular, has been recognized as one of the most important threats to marine biodiversity (Halpern et al., 2015). Coral communities have been severely affected by a dramatic increase in the frequency and intensity of mass mortality events linked to increased global temperatures and marine heatwaves (e.g., Baird & Marshall, 2002;

Garrabou et al., 2022; Hughes et al., 2017). This increase in the frequency and intensity of mass mortality events is ubiquitous and has been observed in tropical, subtropical, temperate and polar seas (e.g., Barnes & Souster, 2011; Garrabou et al., 2019; Kemp et al., 2011). Moreover, ocean warming has also induced an earlier arrival of spring conditions affecting numerous marine ecosystems and biological processes (Loeb et al., 1997; Parmesan, 2006; Walther et al., 2002). An earlier arrival of spring conditions can significantly affect coral reproductive phenology and, consequently, the success of future populations (IPCC, 2007; Shefy et al., 2018; Shlesinger & Loya, 2019). Since many corals play a structural role increasing the diversity of marine ecosystems (Dayton et al., 1974; Jones et al., 1994; Thrush & Dayton, 2002), changes in their reproductive processes could also have the potential to result in a drastic loss of biodiversity at both the community and ecosystem levels.

Ocean warming is predicted to increase under the expected 1–5°C rise in mean global seawater temperature by 2100 (IPCC, 2022). However, the distribution of excess heat will not be uniform across all the oceans. The Mediterranean Sea is recognized as a "hotspot" for ocean warming, ranking among the fastest-warming ocean regions in the world (Garrabou et al., 2022; Marbà et al., 2015). The sea surface temperature of the Mediterranean shows a nearly continuous warming trend at a rate of 0.41°C per decade, which is three to six times higher than the warming rate of oceans globally (Cramer et al., 2018; Garrabou et al., 2021; Pisano et al., 2020). To our knowledge, despite this fast warming, consequences on coral reproductive phenology have never been studied before in the Mediterranean Sea. In addition, increases in the frequency and intensity of extreme heatwaves in the Mediterranean Sea have also been detected through field observations and are expected to continue in future projections (Adloff et al., 2015; Darmaraki et al., 2019), inducing mass mortality events primarily on benthic invertebrate taxa (e.g., Cerrano et al., 2000; Garrabou et al., 2009; Pérez et al., 2000). About 50% of all recorded mass mortality events in the Mediterranean Sea have occurred in Cnidarians, principally octocorals (Garrabou et al., 2019), which are the most conspicuous ecosystem engineering species in the rocky bottoms of the Mediterranean Sea (Ballesteros, 2006). Field and experimental studies have evaluated the immediate and delayed impacts of temperature increases on adult octocoral colonies (e.g., Coma et al., 2006; Ezzat et al., 2013; Gómez-Gras et al., 2019; Linares et al., 2005), including sublethal impacts on their reproduction effort (Arizmendi-Mejía et al., 2015; Linares, Coma, & Zabala, 2008). To date, however, only one study has examined the effects of thermal stress on embryonic and larval stages of a Mediterranean octocoral, *Paramuricea clavata* (Kipson et al., 2012), overlooking the possible effects on settlement rates.

Studies on temperature effects on coral larvae have increased markedly in the last few years. However, most of these studies have focused on hexacoral tropical species, whereas octocoral species have been largely neglected. Although octocoral species are present across large depth ranges and in all oceans worldwide, the effects of thermal stress on their early life-history stages have been studied in only two tropical, one temperate, and one deep-sea species (Conaco & Cabaitan, 2020; Da-Anoy et al., 2020; Kipson et al., 2012; Liberman et al., 2021; Rakka et al., 2021). These studies suggest that octocoral larvae have tolerance to thermal stress. Larvae of the deep-sea octocoral *Dentomuricea aff. Meteor* exposed to high temperature (+2°C) had similar survival as larvae at ambient temperature (Rakka et al., 2021). Larvae from two tropical and one temperate octocoral species showed tolerance to temperature conditions expected by 2100 (+3°C; Conaco & Cabaitan, 2020; Da-Anoy et al., 2020; Kipson et al., 2012; Liberman et al., 2021). In these studies, larval survival was only affected by thermal stress under high larval densities (Conaco & Cabaitan, 2020) or after a prolonged exposure (27 days; Kipson et al., 2012). However, this limited knowledge makes difficult to project how octocoral larvae will perform in the future under thermal stress, and more research is needed to include more species with different life-history traits (e.g., thermal tolerance in symbiotic and brooded octocoral larvae has never been examined).

The aim of this study is to provide new knowledge on the reproductive phenology and larval thermotolerance in two of the most representative octocoral species in the Mediterranean Sea, by answering the following questions: (1) How long is their breeding period? (2) How variable is the amount of larvae released during the breeding period? (3) How are larval survival and settlement affected by thermal stress? (4) How does thermal stress affect the metabolic balance of larvae in terms of biomass and energy consumption? To answer these questions, we monitored the breeding period of octocorals *Eunicella singularis* and *Corallium rubrum*, and used an experimental approach to examine the larvae performance at 20°C (control), 24°C (a temperature observed during Mediterranean heatwaves in the last few years) and 26°C (a temperature expected to occur during Mediterranean heatwaves in the near future).

2 | MATERIALS AND METHODS

2.1 | Target species

In the Mediterranean Sea, *E. singularis* (Esper, 1794) and *C. rubrum* (Linnaeus, 1758; Figure 1a,b) are two of the most representative octocorals in coastal areas (Ballesteros, 2006). Both species are long-lived, slow-growing, and endemic to the Mediterranean Sea; however, they can also be found along rocky shores of the neighboring Atlantic Ocean (Costantini et al., 2010; Cúrdia et al., 2013). The white gorgonian *E. singularis* is the only Mediterranean octocoral exhibiting symbiosis with photosynthetic dinoflagellates (Carpine & Grasshoff, 1975; Rossi, 1959; Weinberg, 1976), whereas the red coral *C. rubrum* is an aposymbiotic species considered to be one of the most overharvested precious corals due to its use for the jewelry industry (Santangelo et al., 2004; Tsounis et al., 2010). Both *E. singularis* and *C. rubrum* are gonochoric species and internal brooders, releasing lecithotrophic larvae (planulae) once a year in June–July and

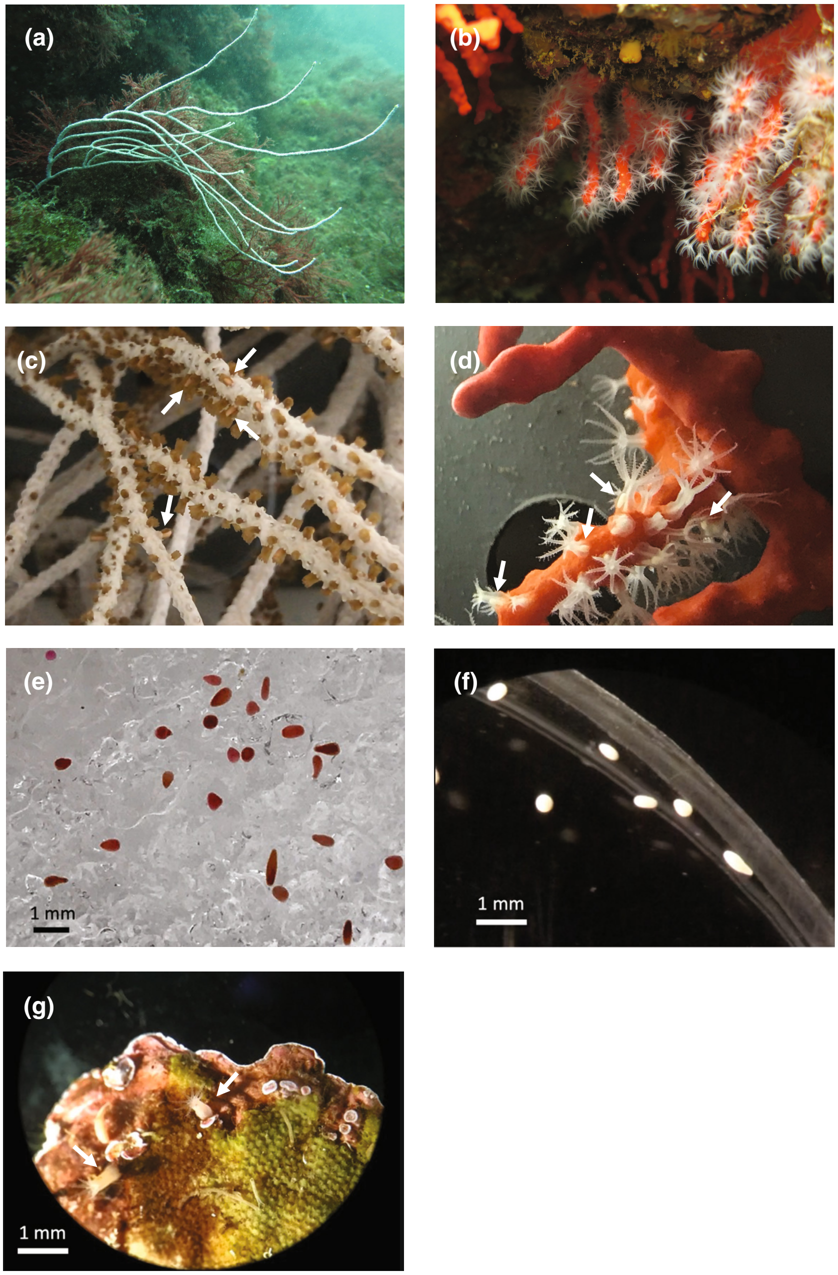

FIGURE 1 Adult colonies of *Eunicella singularis* (a) and *Corallium rubrum* (b) used in the present study. Expanded polyps during the brooding period event for *E. singularis* (c) and *C. rubrum* (d) (arrows indicate the larvae ready to be spawned). Pink larvae of *E. singularis* (e) and white larvae of *C. rubrum* (f). New recruits of *E. singularis* (g)

July–August, respectively (Ribes et al., 2007; Santangelo et al., 2003; Torrents & Garrabou, 2011; Weinberg & Weinberg, 1979). While *C. rubrum* releases non-symbiotic ciliated larvae, *E. singularis* larvae, like the adult colonies, contain algal symbionts that belong to the *Symbiodinium* genus (phylotype that was previously assigned to temperate clade A; Forcioli et al., 2011; Weinberg, 1979). The larval size of *C. rubrum* is ~1 mm along the major axis and 0.3 mm along the minor axis (Lacaze-Duthiers, 1864), whereas *E. singularis* larval axis dimensions are ~2.5 and 0.5 mm, respectively (Weinberg & Weinberg, 1979). Planulae of both species have a pelagic larval duration of approximately 1 month (Martínez-Quintana et al., 2015; Theodor, 1967; Weinberg & Weinberg, 1979). Larval competence (i.e., period during which pelagic larvae are able to settle) is approximately 8 days for *E. singularis* and 20 days for *C. rubrum* (Zelli et al., 2020).

2.2 | Specimen collection and maintenance

Ten colonies of *E. singularis* and 10 colonies of *C. rubrum* were collected at the end of June 2020, prior to the expected time of larvae release. Collections were performed by SCUBA diving in the Natural Park of Cap de Creus (42°19′37″N; 003°18′39″E, NW Mediterranean Sea, Spain), under permit FUE-2020-01576039 issued by the Generalitat de Catalunya, Department of Territory and Sustainability. Colonies of *E. singularis* were collected at depths of 13–16 m, whereas colonies of *C. rubrum* were collected at depths of 25–35 m. To ensure their sexual maturity, collections were limited to colonies of *E. singularis* larger than 20 cm (Ribes et al., 2007) and *C. rubrum* larger than 5 cm (Tsounis et al., 2006). The collected colonies were maintained in seawater at 19 ± 1.0°C and transported (within 2 h from sampling) to the University of Barcelona.

Colonies of each species were maintained separately in 8 L tanks and kept at ambient temperature (20 ± 0.2°C) in a temperature-controlled experimental chamber (Conviron Gen2000). Since *E. singularis* colonies contained symbiotic algae, a 12 h:12 h light: dark cycle was established with irradiance matching the light intensity for the population at the field site (150 μmol photons m^{-2} s^{-1}), whereas *C. rubrum* colonies were maintained in dark conditions. Seawater temperature and light intensity were monitored using a HOBO logger (MX2202) in each tank. Continuous water movement was provided by air bubbling, and one-third of the seawater volume was renewed daily within each tank.

2.3 | Larval release and collection

Tanks were inspected daily to detect larval release, starting on June 24 for *E. singularis* and July 12 for *C. rubrum*. Larval release was not artificially stimulated by physical or chemical factors. When the breeding period initiated, tanks were inspected for larvae twice a day until no more larvae were detected. All the larvae released in the morning before 8 am were counted and considered to be released during the previous night, whereas larvae counted before 9 pm were considered to be released during the day. Larvae were collected from the tanks using 3-ml plastic Pasteur pipettes.

2.4 | Experimental design

To assess the effects of seawater temperature on larvae survival and settlement, the collected larvae of both species (*E. singularis* and *C. rubrum*) were maintained under three temperature treatments: 20°C (control), 24°C, and 26°C (±0.2°C in each treatment). These temperature treatments were selected to represent extreme conditions in the Mediterranean Sea that (1) have already been observed during heatwaves in the last few years (24°C; T-MEDNet database, www.t-mednet.org; Garrabou et al., 2021, 2022), and (2) are expected to occur for periods as long as 3 weeks in duration by 2050 (25–26°C; Galli et al., 2017). Each treatment was maintained using 15 L water baths (one water bath for each temperature and species) inside a temperature-controlled experimental chamber (Conviron Gen2000). The temperature of each water bath was maintained with a titanium heater (Aqua Medic AM-300) connected to an electronic controller (Aqua Medic TH-100) with submersible pumps (Sicce Nano 2000) for water circulation, and temperature was recorded every 10 min using a HOBO logger. For each species and treatment, 10 larvae were placed into each of 10 replicated glass beakers containing 300 ml of 0.2 μm filtered seawater to estimate survival (100 larvae in each of the three temperature treatments, and 300 larvae in total for each species). Five additional glass beakers (300 ml) for each species with approximately 70 larvae were maintained in each treatment and sampled after 5 days of exposure to assess larval biomass and energetic consumption (see below). This sample timing was chosen based on previous observed survival of Mediterranean gorgonian larvae (Kipson et al., 2012) to allow for detection of sublethal effects. Since the breeding period of both species occurs over the course of several days and the number of larvae released per day was lower than the total number of larvae necessary for the experiments, the sampling of larvae was conducted across different days. When more than 30 larvae were collected per day, larvae were placed into their own beaker glass for each treatment (10 larvae for each treatment). In each glass, a piece of coralline algae *Lithophyllum stictaeforme* (~5 cm^2) was added as suitable substrate for settlement (Zelli et al., 2020). Since larvae of *E. singularis* contain symbiotic algae, a 12 h:12 h light: dark cycle was maintained with the same irradiance as for the parental colonies (150 μmol photons m^{-2} s^{-1}), whereas larvae of *C. rubrum* were maintained in dark conditions. In each glass beaker, two-thirds of total seawater volume were replaced daily.

2.5 | Larval survival and settlement rates

For each temperature treatment and species, larval survival was assessed every day by counting the number of larvae in each glass beaker ($n = 10$ for each treatment and species) for a total of 20 consecutive days, since the heatwaves are expected to occur for periods as long as 3 weeks in duration (Galli et al., 2017). Settlement rate and post-settlement survival were also assessed by counting the number of larvae settled in each glass beaker every day throughout the 20-day observation period.

2.6 | Larval biomass and energy consumption

To examine larval biomass and energy consumption, five filters with 10 larvae for *E. singularis* and 15 larvae for *C. rubrum* were used in each analysis and treatment. Larvae were collected just after release and 5 days after exposure to the respective temperature treatment. Larvae were fixed on pre-combusted (5 h at 450°C) GF/F filters and immediately frozen in liquid nitrogen and stored at −80°C. Samples were then freeze-dried for 24 h at −110°C at a pressure of 100 mbar. Larval biomass was assessed by measuring the organic carbon content of each filter using a C/N autoanalyzer (Perkin-Elmer 2040). Biomass was reported per larva by dividing the value of each filter by 10 for *E. singularis* and by 15 for *C. rubrum*. Energetic content was analyzed by combustion calorimetry using differential scanning calorimetry (DSC; Mettler Toledo DSC-822e). The DSC temperature was programmed to increase from 30°C to 450°C (10°C min^{-1}) in a synthetic air atmosphere (50 ml min^{-1}). The daily average energy consumption of larvae under each temperature treatment was calculated according to the following equation: $El = (Ec_1 - Ec_2)\ \Delta t^{-1}$, where El is the daily average energy consumption, Ec_1 is the larval energy content in calories just after release, Ec_2 is the larval energy content after exposure to each temperature (in calories), and Δdt is the number of days of exposure (i.e., 5 days). El was reported per larva by dividing the El equation-value by 10 for *E. singularis* and by 15 for *C. rubrum*.

2.7 | Statistical analyses

Estimates of the survival function probabilities for each temperature treatment and species were obtained from the observed larval survival using the Kaplan–Meier product-limit method (Kaplan & Meier, 1992). The Kaplan–Meier method was also applied to examine survival in larvae released at the beginning and the middle of the release period. The unsettled larvae (i.e., still alive) remaining at the end of the experiment represented censored data, since they did not reach the outcome of interest during the study (i.e., death or settlement) and their future survival was not determined. In the analysis, a value of 0 was assigned to these censored data, whereas a value of 1 was assigned to all larvae with complete endpoint observations (i.e., a recorded time-point of larval death or settlement during the study). Log-rank test was used to test the differences in larval survival among temperature treatments. This is a non-parametric test based on the rank ordering of survival times that can be applied to censored data. Survival analysis was performed with the *survival* (Therneau, 2015) and *survminer* packages (Kassambara et al., 2019) in R version 3.5.0 (R Core Team, 2019). To analyze the settlement probabilities of larvae (response variables) according to larval age (explanatory continuous variable) and temperature treatment (explanatory discrete variables), a generalized linear model (GLM) was fitted for each species. Settlement probabilities were also analyzed in larvae released during the beginning and the middle of the release period. Since the data of all parameters were over-dispersed (i.e., residual deviance was significantly higher than the residual degrees of freedom, which is often the case when a data set contains many low and many high values), the negative binomial model was used with the "log link" function to correct for over-dispersion of the data. GLMs were performed via the *foreign*, *ggplot2*, and *MASS* packages in R. For each species, biomass and energy consumption was compared among the three temperature treatments by two-way analysis of variance (ANOVA) followed by Tukey's test for pairwise comparison. Before performing ANOVAs, normality of data residuals and variance homogeneity were tested with Shapiro–Wilk and Bartlett tests, respectively.

3 | RESULTS

3.1 | Larval release

Larval release of *E. singularis* started on July 3 (2 days before full moon) and ended on August 1st (Figures 1c and 2a). Similar number of larvae released was observed during the day (from 8 am to 9 pm) and night (from 9 pm to 8 am). The number of larvae released increased gradually, reaching its maximum on July 15, 12 days after the first larval release (Figure 2a). The maximum larval release occurred for 1 week with 297 ± 68 larvae day^{-1} (mean ± SD) and then decreased gradually over a period of 10 days. *Corallium rubrum* released larvae for approximately 1 month, starting on July 21 (1 day after new moon) and ending on August 20 (Figures 1d and 2b), without any difference between the number of larvae released during day or night. During the first week, *C. rubrum* released a moderate number of larvae every day (65 ± 17 larvae day^{-1}, mean ± SD), reaching a maximum of 140 larvae on day eight. The maximal larval release occurred over the next 11 days with 110 ± 25 larvae day^{-1} (mean ± SD) and then reduced drastically during the following 13 days (20 ± 12 larvae day^{-1}).

3.2 | Larval survival

At the end of of experiment, survival of *E. singularis* larvae (Figure 1e) showed similar trends among 20°C (control), 24°C and 26°C treatments (Figure 3a; Kaplan–Meier survival analysis, log-rank test, $p > .05$). However, during the first 10 days, larvae showed lower survival at 26°C than in the control and 24°C treatments (Kaplan–Meier survival analysis, log-rank test, $p < .05$). During the first day of the experiment, the probability of survival was maintained at around 90% in all treatments. In the second day of exposure, the differences among treatments increased. After 5 days, survival dropped from 88% to 41% at 26°C, whereas in the control and 24°C treatments it decreased to 64%. Median larval survival (i.e., time from larval release at which 50% of the initial number of larvae had died

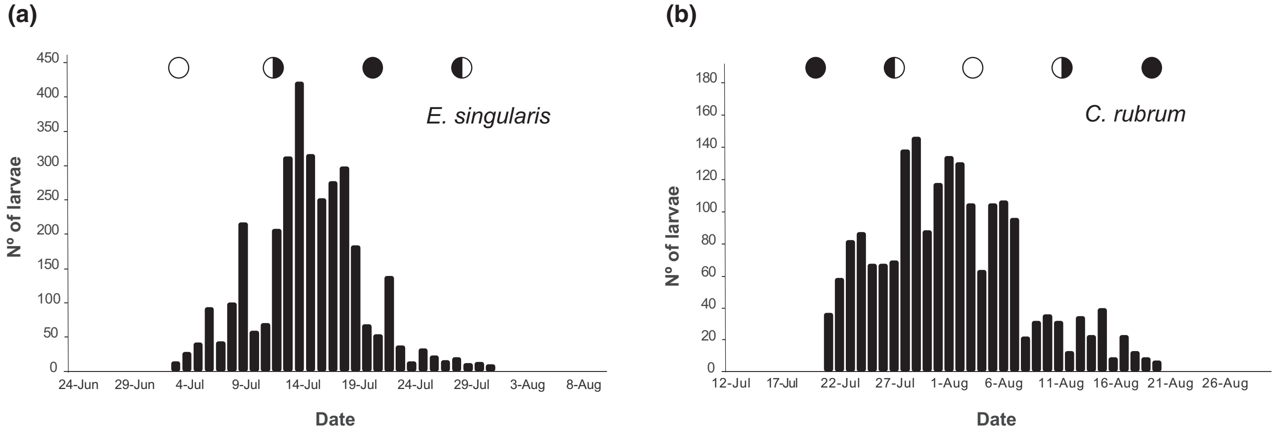

FIGURE 2 Number of larvae released per day (a) *Eunicella singularis* and (b) *Corallium rubrum*. Moon symbols represent lunar phases (full, last quarter, new and first quarter). The range of *x*-axes indicates the days that colonies were inspected to detect larvae released (from June 24 to August 8 for *E. singularis* and from July 12 to August 26 for *C. rubrum*).

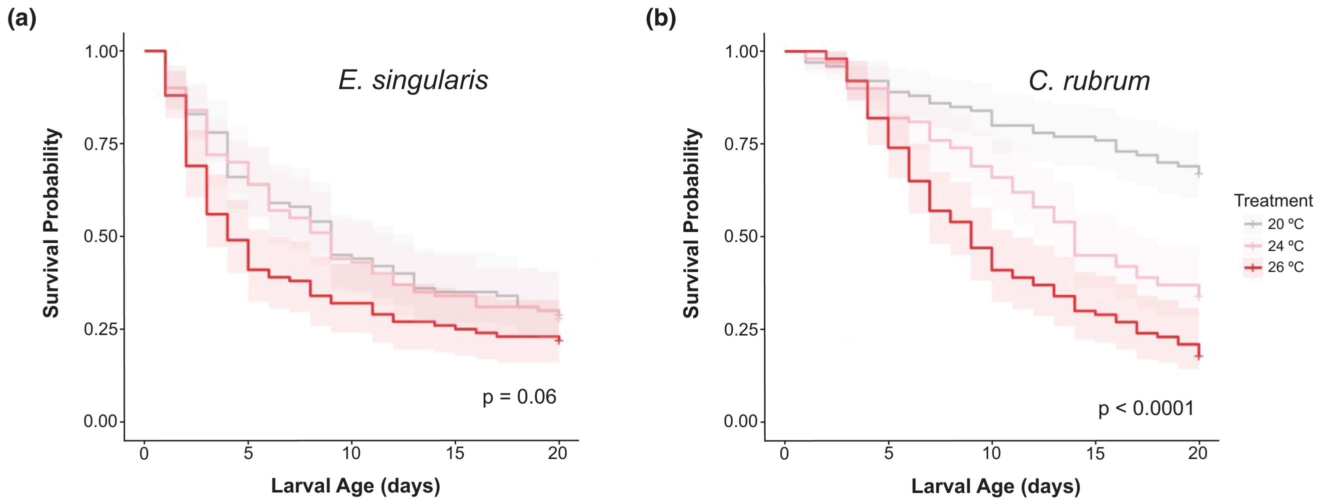

FIGURE 3 Kaplan–Meier estimated larval survival probabilities for (a) *Eunicella singularis* and (b) *Corallium rubrum* in the control (20°C, grey line), 24°C (pink line) and 26°C (red line) treatments. All replicates are pooled and the total number of larvae per treatment was 100. Shading represents 95% confidence intervals.

or settled) was 3–4 days under 26°C and 8–9 days for the other two treatments. Larval survival was not related with the date of larval release in the control and 24°C treatments (Kaplan–Meier survival analysis, log-rank test, $p > .05$; Figure S1). However, at 26°C larvae released at the beginning of the breeding period showed lower survival than larvae released later in the breeding period (when we observed the maximum number of larvae released; Kaplan–Meier survival analysis, log-rank test, $p < .05$; Figure S1). Survival of *C. rubrum* larvae (Figure 1f) showed significant differences among the three temperature treatments (Kaplan–Meier survival analysis, log-rank test, $p < .001$; Figure 3b). At the control temperature, survival gradually decreased to 67% at the end of the 20 days experiment, whereas larval survival was reduced under 30% and 18% at 24°C and 26°C, respectively. Larvae of *C. rubrum* did not show any abrupt change on survival probability according to the days of exposure in any treatment. Median larval survival was 8–9 days at 26°C, 13–14 days at 24°C and >20 days for control conditions. Similar to *E. singularis*, the larval survival in *C. rubrum* was not related with the timing of larval release in the control and 24°C treatments (Kaplan–Meier survival analysis, log-rank test, $p > .05$; Figure S2). However, at 26°C, larvae released at the middle of the breeding period showed higher survival than larvae released at the beginning of the breeding period (Kaplan–Meier survival analysis, log-rank test, $p < .01$; Figure S2).

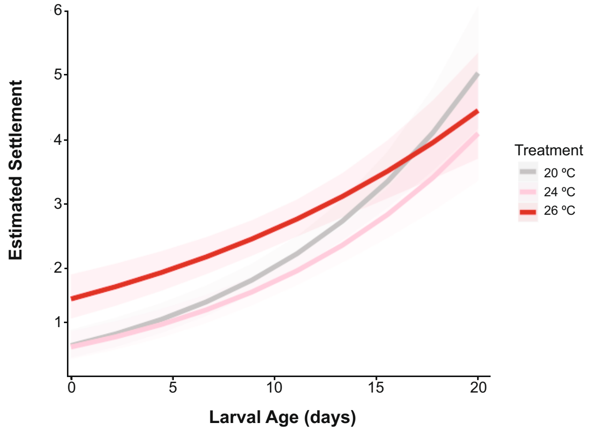

FIGURE 4 Estimated number of settlements of *Eunicella singularis* in the control (20°C, grey, $n = 100$), 24°C (pink, $n = 100$) and 26°C (red, $n = 100$) treatments. Shading represents 95% confidence intervals.

3.3 | Settlement rates

Settlement rates of *E. singularis* (Figure 1g) were generally not affected by temperature treatments, being 50 ± 7.8% at 20°C, 41 ± 5.7% at 24°C and 45 ± 7% at 26°C of larvae settled at the end of the experiment (mean ± SE). However, the highest temperature (26°C) had a positive effect on settlement rate in the first 10 days of larval age (GLM, $p < .01$; Figure 4; Table S1). Settlement probability was strongly related to the time when larvae were released during the breeding period (Figure S3). Larvae released at the beginning had lower probabilities of settlement success in all treatments compared with larvae released during the middle of breeding period (GLM, $p < .01$; Table S2). In *C. rubrum* no larval settlement was observed during the experiment in any treatment.

3.4 | Larval biomass

In *E. singularis*, larval biomass just after release was 57.8 ± 5.3 μg C per larvae (mean ± SD). After 5 days of exposure, the biomass was 56.4 ± 6.6 μg C per larvae under control conditions, whereas at 24°C and 26°C it was 51.7 ± 9.0 and 43.8 ± 4.1 μg C per larvae, respectively (Figure 5a). The results only showed significant differences

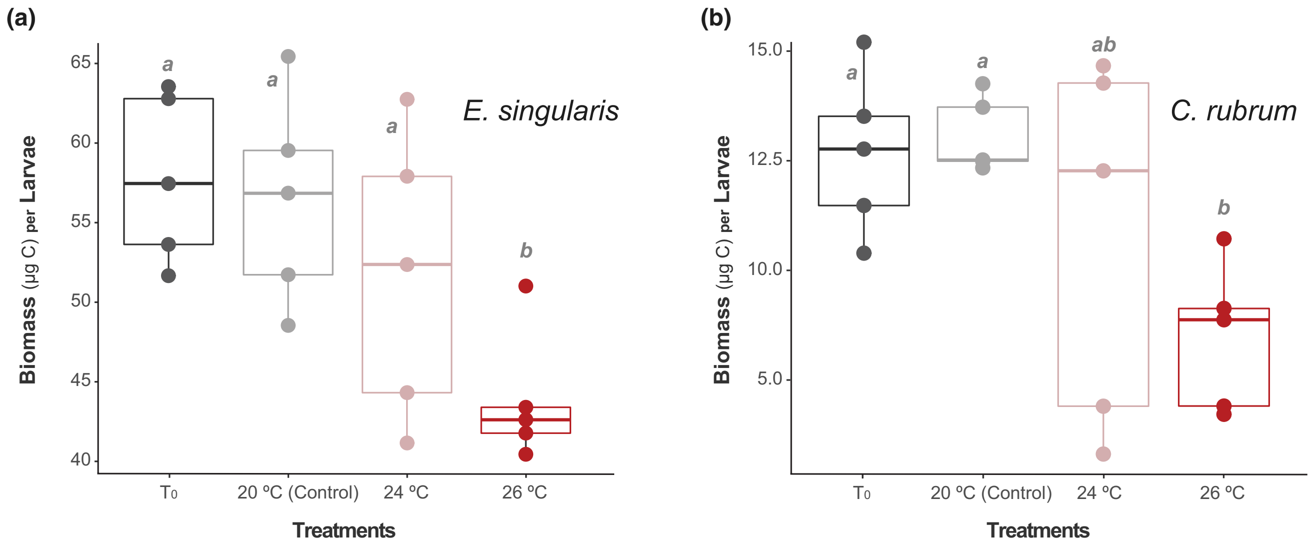

FIGURE 5 Box-plot with overlaying data points of larval biomass (µg C per larvae) in (a) *Eunicella singularis* and (b) *Corallium rubrum* just after larval release (to black bar $n = 5$) and after 5 days of exposure in the control (20°C, grey bar, $n = 5$), 24°C (pink bar, $n = 5$) and 26°C (red bar, $n = 5$) treatments. Bars marked with the same letters are not significantly different (Tukey post hoc, $p > .05$).

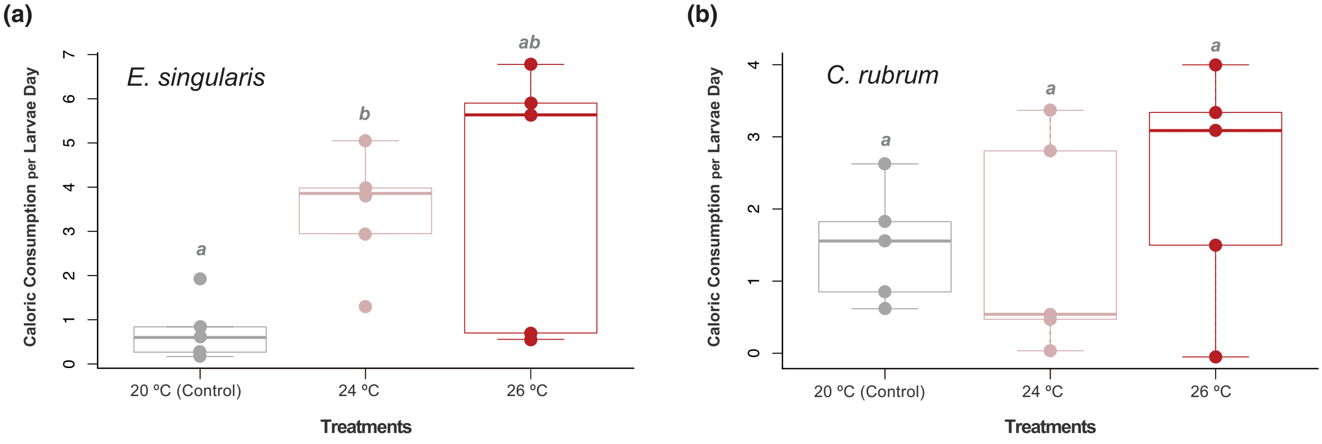

FIGURE 6 Box-plot with overlaying data points of caloric consumption per day of (a) *Eunicella singularis* larvae and (b) *Corallium rubrum* larvae in the control (20°C, $n = 5$), 24°C ($n = 5$) and 26°C ($n = 5$) treatments after 5 days of exposure. Bars marked with the same letters are not significantly different (Tukey post hoc, $p > .05$).

between the control and 26°C treatments ($p < .01$). Larval biomass of *C. rubrum* just after release was 13.1 ± 0.9 µg C per larvae, whereas after 5 days of exposure the biomass was 12.7 ± 1.8, 10.8 ± 4.2 and 8.5 ± 1.7 µg C per larvae under the control, 24°C and 26°C treatments, respectively (Figure 5a). Similar to *E. singularis*, the biomass of *C. rubrum* larvae significantly differed between the control and 26°C treatments ($p < .001$, Figure 5b).

3.5 | Larval energy consumption

Larvae of *E. singularis* had an energetic value of 67.9 ± 7.2 Cal per larvae just after release (mean ± SD). Energy consumption of the larvae increased with temperature, representing a daily energy loss of 0.8 ± 0.7, 3.4 ± 1.4 and 3.9 ± 3.0 Cal per larvae and day^{-1} under the control, 24°C and 26°C treatments, respectively (Figure 6a). Daily energy consumption showed significant differences between larvae under the control and 24°C ($p < .01$), whereas no significant differences were found among the treatment at 26°C and the other temperatures ($p > .05$). *C. rubrum* larvae presented an energetic value of 22.4 ± 5.8 Cal per larvae just after release. The daily energy loss of *C. rubrum* larvae was similar between the control and 24°C treatments, being 1.5 ± 0.8 and 1.4 ± 1.5 Cal per larvae and day^{-1}, respectively (Figure 6b). Daily energy consumption increased to 2.4 ± 1.6 Cal per larvae and day^{-1} under 26°C; however, results did not show significant differences among treatments ($p > .05$).

4 | DISCUSSION

Octocoral species play a paramount role as ecosystem engineers in Mediterranean benthic communities, as well as around the world (Gili & Coma, 1998; Velásquez & Sánchez, 2015; Wild et al., 2011), and are considered one of the main three-dimensional constituents of the "marine animal forests" (sensu Rossi, 2013). Internal brooder species, such as the Mediterranean *E. singularis* and *C. rubrum*, represent more than 40% of all octocoral species with known reproductive strategies (Kahng et al., 2011). Despite their importance, compared with broadcast coral species, reproductive characteristics such as the duration, number of events and larval release intensity of brooders remain largely unknown.

4.1 | Breeding characteristics

In this study, the breeding period in *E. singularis* took place in one single event lasting 4–5 weeks, longer than 2–3 weeks previously reported for the same species by Theodor (1976). Initially, it had been assumed that larvae were released in approximately equal amounts during the entire breeding period, showing no correlation with the lunar phase (Weinberg, 1979). However, our results showed a gradual increase of larvae released, reaching its maximum 12 days after the breeding period started. The maximum release of larvae was concentrated in the period between the last quarter and the new moon. However, additional observations are needed to further explore this possible relationship between larval release and lunar phase, as has been observed in other Mediterranean octocoral species such as *P. clavata* (Linares, Coma, Mariani, et al., 2008). Similar to *E. singularis*, larval release of *C. rubrum* occurred over a single event for approximately 4–5 weeks, without any difference in the number of larvae released between day and night. The breeding period duration was longer than the 1–2 weeks previously reported for this species (Lacaze-Duthiers, 1864; Vighi, 1970). Weinberg (1979) suggests a possible correlation between new moon and maximum intensity of larval release in *C. rubrum*; however, our results show the maximum release between the last quarter and the new moon. Therefore, our study shows that breeding of *E. singularis* and *C. rubrum* occurs over a longer period and reproductive behavior (i.e., release of larvae) is more variable than previously reported. Our results could also indicate a phenological shift in the duration of the breeding season over the last 50 years. This possible phenological shift could be caused by the on-going ocean warming, since a longer spawning season has been positively correlated with longer exposure to warmer waters in several broadcasting coral species studied across latitudinal gradients (De Putron & Ryland, 2009; Mangubhai & Harrison, 2009; Oliver et al., 1988). Indeed, the sea surface temperature of the Mediterranean has warmed by 1.48°C on average for the entire basin over the last four decades, corresponding to an increase of 0.41°C per decade, which is three to six times higher than the warming rate of oceans globally (Cramer et al., 2018; Garrabou et al., 2021; Pisano et al., 2020). During the brooding period (April to July), satellite observations from the last few decades showed a significant increase in seawater temperature with the peak increase occurring in June (0.08°C year^{-1}; Nykjaer, 2009).

Since reproductive events have evolved to occur at optimal times to maximize the survival of the next generation (Stearns, 1992), rapid shifts in reproductive phenology could threaten the long-term viability of populations (Charmantier et al., 2008; Edwards & Richardson, 2004). Shefy et al. (2018) showed an increase in the duration of the larval release period of *Stylophora pistillata* from 2–3 to 5–6 months in the past four decades, which could be caused by anthropogenic and environmental impacts. In broadcast corals of the Red Sea, shifts in the timing of gamete release have been found due to environmental changes with potential consequences for coral reproductive success (Shlesinger & Loya, 2019). Our results show that the breeding periods of the studied corals span over longer time periods than previously documented which could be the result of different environmental cues in their current habitat. Future studies should focus on looking at the plasticity in reproductive breeding behavior of the adult colonies under ocean warming conditions, and performing longer larval experiments to obtain a better understanding of the resilience of parental colonies and offspring to thermal stress.

4.2 | Effects of thermal stress on larval survival and energy reserves

The two Mediterranean octocoral species studied here showed a contrasted response in larval survival under thermal stress treatments that simulated marine heatwave events caused by on-going global climate change. Whereas +4°C and +6°C increases in temperature did not cause significant negative effects in the symbiotic *E. singularis* larvae, the survival of non-symbiotic *C. rubrum* larvae was drastically reduced (Figure 3). Until now, the temperature effects on larvae from octocorals at shallow depths (5–30 m) have only been studied in the surface brooders *Heliopora coerulea*, *P. clavata* and *Rhytisma fulvum* (Conaco & Cabaitan, 2020; Da-Anoy et al., 2020; Kipson et al., 2012; Liberman et al., 2021). In these species, larvae showed some tolerance to elevated temperature that was explained by the absence of symbionts in larvae tissues. Conversely, in the present study, the symbiotic larvae of *E. singularis* showed higher resistance to temperature increases than *C. rubrum* non-symbiotic larvae. The thermotolerance observed in *E. singularis* larvae contrasts with results from several hexacoral species showing that thermal stress weakens endosymbiont interactions in coral larvae and reduces larval survivorship (Edmunds et al., 2001; Graham et al., 2017; Randall & Szmant, 2009; Schnitzler et al., 2012; Serrano et al., 2018). The thermotolerance of *E. singularis* symbiotic larvae is in line with the performance of adult colonies of the same species which do not show any evidence of coral bleaching when exposed to thermal stress (26°C; Ferrier-Pagès et al., 2009).

The higher resistance of *E. singularis* larvae observed in this study may be partly due to their large larval size (Figure 5; e.g., Baria et al., 2015; Chamberland et al., 2017; Conaco & Cabaitan, 2020). Larger larvae are more likely to contain higher endogenous energetic reserves provided maternally than smaller larvae (de Putron et al., 2017; Hartmann et al., 2013; Marshall & Keough, 2008). It is generally assumed that metabolic rates, and consequently energy consumption, increase with temperature, which may lead to higher mortality rates as lecithotrophic larvae deplete their endogenous energy reserves faster (e.g., Edmunds et al., 2001; Kipson et al., 2012; Pechenik, 1987). However, our results on larval biomass and caloric consumption of *C. rubrum* suggest that the earlier mortality rates caused by increased temperature were not related to depletion of endogenous energy. Although survival of *C. rubrum* larvae decreased as temperature increased, energy consumption was similar between all treatments (Figure 6). The earlier mortality of *C. rubrum* larvae may be related to the parental environment. Although *C. rubrum* colonies at ~30 m can experience high temperature variability and can experience maximum temperatures similar to those found at 5 m depth (Viladrich et al., 2016), colonies of *C. rubrum* at 25–30 m experience cooler waters than *E. singularis* at 13–16 m for a substantial amount of time and thus may be less adapted to high temperature stress. Other potential causes of high mortality of *C. rubrum* larvae, that represent important directions for future research, include disruption of routine metabolic function (Pechenik, 1987), damage to membrane structures disrupting transport systems into and between cells (Hofmann & Todgham, 2010), molecular responses such as metabolic depression (Rodriguez-Lanetty et al., 2009), and increased mitochondrial ROS formation (Keller et al., 2004). Our results show that larval biological responses to thermal stress are complex, and they cannot only be explained by larval size, presence of symbionts in the larvae, and/or brood quality (i.e., biomass and energy consumption), as previously suggested (e.g., Cumbo et al., 2013; Putnam et al., 2010). Finally, our results also show that larval survival to thermal stress depends on the day of release in both species studied (Figures S1 and S2). This highlights the importance to consider the day of larvae release and shifts in reproductive phenology to better project the success and viability of future coral populations (Cumbo et al., 2012; Edmunds et al., 2001; Isomura & Nishihira, 2001; Putnam et al., 2010).

4.3 | Effects of thermal stress on settlement

Low recruitment rates may undermine the long-term viability of coral populations with consequences that may scale up to the community or the ecosystem level. However, we still have a limited understanding about how thermal stress impacts on coral larvae might affect the transition from larva to juvenile. Some studies have shown negative impacts of elevated temperature on coral larvae settlement (e.g., Bassim & Sammarco, 2003; Conaco & Cabaitan, 2020), while others have found that short-duration stressors had little to no ecological consequence for larvae (e.g., Edmunds et al., 2001; Ross et al., 2013). Our results show that coral settlement rates in *E. singularis* were similar between temperature treatments after 20 days, however, larvae in the high-temperature treatment (26°C) settled faster. This suggests that if larvae are exposed to thermal stress in the field, they may settle fast and close to their native populations, decreasing their potential for long-distance dispersal and connectivity (Costantini et al., 2016). Our results are consistent with other studies that have suggested that warmer temperatures can reduce coral larval swimming and facilitate settlement (Kipson et al., 2012; Putnam et al., 2008; Serrano et al., 2018). However, as mentioned above, the day of larvae release can also be a strong factor determining settlement probability (Figure S3). On the other hand, larvae of the octocoral *C. rubrum* did not settle in any of the treatments after 20 days despite having coralline algae *L. stictaeforme* to provide positive settlement cues for this species (Zelli et al., 2020). However, high variability in *C. rubrum* settlement and recruitment among years and sites have been observed in the field, suggesting settlement and recruitment rates by pulses (Bramanti et al., 2003, 2007; Garrabou & Harmelin, 2002; Santangelo et al., 2012). Garrabou and Harmelin (2002) reported that the annual recruitment observed on 10 panels (4000 cm^2) over 22 years was limited to a single recruitment event at the beginning of the study and long-term monitoring of red coral populations across different marine protected areas showed very low recruitment rates observed for this species (Montero-Serra et al., 2019). Recently, it has been suggested that this high inter-annual variability of settlement and recruitment rates could be related to non-selective transfer of energy reserves (i.e., lipids) from maternal colonies to larvae in *C. rubrum* (Viladrich et al., 2021), resulting in a strong dependence of recruitment on the nutritional condition of maternal colonies (Dunstan & Johnson, 1998; Yoshioka, 1996).

4.4 | Ecological consequences and management implications

The ability to predict the vulnerability and resilience of corals at different life stages during extreme events is essential for understanding the effect of global climate change on species distributions (Woods et al., 2016), estimating the potential for adaptation and designing effective management strategies (Figueiredo et al., 2014). Some coral species will be able to persist; other will change their distribution or disappear due to global climate change, causing a shift in species composition. Our results on early life-history stages of the octocoral *E. singularis* combined with previous experimental studies looking at the high thermal resistance of adult colonies (Ezzat et al., 2013; Previati et al., 2010) suggest that *E. singularis* may be a winner species under future climatic conditions in the Mediterranean Sea. However, our results also show that thermal stress can induce a faster settlement, which may result in lower larval dispersal capacity and, consequently, reduced genetic connectivity among populations (Cowen et al., 2000). Persistence of precious red coral population is at higher risk if heatwaves continue, and severe conservation and management plans are not applied. Although adult colonies of *C. rubrum* seem to be experimentally resistance to heat stress events

(Previati et al., 2010; Torrents et al., 2008), the impact of recurrent heatwaves can cause collapse of their populations (Gómez-Gras et al., 2021; Montero-Serra et al., 2019). In addition, the present study reveals how ocean warming may have serious consequences on larval survival, limiting the introduction of new individuals in the population or the possibility to colonize new areas. The viability of *C. rubrum* populations is further aggravated since red coral is one of the corals most valued for use in the jewelry industry, and consequently has been and is still overexploited in several Mediterranean countries (Tsounis et al., 2010). Low thermotolerance of larvae, coupled with uncontrolled harvesting and the impact of recurrent marine heatwaves, could bring red coral populations to local extinction. To better understand the future of benthic communities of the Mediterranean Sea, our study provides empirical data that can be used to project population dynamics and demography of both octocoral species under the expected future global climate change scenarios based on matrix models and integral projection models (Bramanti et al., 2015; Doak et al., 2021; Linares & Doak, 2010; Montero-Serra et al., 2019). So, management and conservation actions should be based on the outcomes of these simulations to preserve these endemic species together with their associated biodiversity.

AUTHOR CONTRIBUTIONS

Núria Viladrich conceived the idea, planned the experiments, carried out the experiments and analysed the data. Cristina Linares and Jacqueline L. Padilla-Gamiño encouraged Núria Viladrich to investigate thermal stress effects on octocoral larvae and supervised the findings of this work. Núria Viladrich took the lead in writing the manuscript and Cristina Linares and Jacqueline L. Padilla-Gamiño contributed to writing, provided critical feedback and helped shape the manuscript.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study, as well as the code used for the analyses, are openly available in the Zenodo repository through the link https://doi.org/10.5281/zenodo.6496490.

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