










Local-scale climatic refugia offer sanctuary for a habitat-forming species during a marine heatwave

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Funding information

Ministerio de Economía, Industria y Competitividad, Gobierno de España, Grant/Award Number: CGL2016-76341-R and FPI (BES-2017-079907); European Maritime and Fisheries Fund EMFF, Grant/Award Number: EASME/EMFF/2017/1.2.1.12/S4/01/SI2.789059; UK Research and Innovation, Grant/Award Number: MR/S032827/1; Horizon 2020 Framework Programme, Grant/Award Number: 689518; Generalitat de Catalunya, Grant/Award Number: 2017 SGR 1521; Universitat de Girona, Grant/Award Number: IFUdG-2016 and MPCUdG2016/097; European Regional Development Fund, Grant/Award Number: CGL2016-76341-R; "la Caixa" Foundation, Grant/Award Number: LCF/BQ/ES17/11600001

Handling Editor: Kathy Van Alstyne

Abstract

1. Gradual climate change and discrete extreme climatic events have driven shifts in the structure of populations and the distribution of species in many marine ecosystems. The most profound impacts of recent warming trends have been generally observed at species' warm edges and on large conspicuous species. However, given that different species and populations exhibit different responses to warming, and that responses are highly variable at regional scales, there is a need to broaden the evidence to include less conspicuous species and to focus on both local- and regional-scale processes.
2. We examined the population dynamics of canopy-forming seaweed populations situated at the core range of their distribution during a regional marine heatwave (MHW) event that occurred in the Mediterranean Sea in 2015, to determine between-site variability in relation to the intensity of the MHW. We combined field observations with a thermo-tolerance experiment to elucidate mechanisms underlying observed responses.
3. Despite our study populations are located in the species core range, the MHW was concomitant with a high mortality and structural shifts in only one of the two surveyed populations, most likely due to differences in habitat characteristics between sites (e.g. degree of shelter and seawater transfer). The experiment showed high mortalities at temperatures of 28°C, having the most severe implications for early life stages and fertility, which is consistent with warming being the cause of population changes in the field. Crucially, the regional-scale quantification of the MHW (as described by satellite-derived SSTs) did not capture local-scale variation in MHW conditions at the study sites, which likely explained variation in population-level responses to warming.
4. *Synthesis.* Enclosed and semi-enclosed seas, such as the Mediterranean Sea, often highly impacted by human perturbations, are also global hotspots for ocean warming and are highly susceptible to future MHWs. Our findings highlight that local-scale variability in the magnitude of extreme climatic events can lead to local extinctions of already fragmented populations of habitat-forming seaweeds, even towards the species' core range. However, our results highlight the potential for

local-scale climatic refugia, which could be identified and managed to safeguard the persistence of canopy-forming seaweeds.

KEYWORDS

canopy-forming seaweeds, *Carpodesmia*, climate change, climatic refugia, coastal ecosystems, *Cystoseira*, *Ericaria*, marine heatwaves

1 | INTRODUCTION

Anthropogenic stressors are increasingly impacting natural environments, eroding the resilience of ecosystems and leading to a reorganization of biodiversity at the global scale (Crain et al., 2008; Elmqvist et al., 2003; Folke et al., 2002; Millennium Ecosystem Assessment (MEA), 2005). Among these stressors, climate change is expected to become one of the most important drivers of global ecological change (Bellard et al., 2012). Indeed, there is already compelling evidence that gradual climate change has modified species distributions and altered the structure and functioning of entire ecosystems (Parmesan, 2006; Pecl et al., 2017; Poloczanska et al., 2013). Many species have shifted their geographical distributions in response to warming by colonizing new habitats (Crozier, 2003; Hickling et al., 2005; Parmesan et al., 2000; Tanaka et al., 2012; Vergés et al., 2014), and by losing previously occupied areas through local extinctions (Derocher et al., 2004; Moritz et al., 2008; Smale & Wernberg, 2013; Tanaka et al., 2012). Although many climate-driven range shifts occur gradually (Chen et al., 2011; Parmesan & Yohe, 2003), extreme climatic events, which are increasing in frequency as a consequence of anthropogenic climate change (Coumou & Rahmstorf, 2012; Oliver et al., 2018), can cause rapid distributional shifts (Battisti et al., 2006; Smale & Wernberg, 2013) and abruptly alter local ecosystem structure and functioning (Parmesan et al., 2000; Parmesan & Yohe, 2003; Thibault & Brown, 2008; Wernberg et al., 2013).

Marine species may be particularly vulnerable to the effects of both chronic and acute warming, as their ecophysiology and geographical distributions are strongly constrained by temperature (Pinsky et al., 2019; Sunday et al., 2012). In fact, marine heat waves (MHWs), defined as a discrete and prolonged anomalous warm water event in a particular location (Hobday et al., 2016), have recently been attributed to devastating impacts on marine biodiversity and ecosystem services and functions (Garrabou et al., 2009; Mills et al., 2013; Oliver et al., 2017; Wernberg et al., 2016). However, the speed, extent and magnitude of species' range shifts following MHWs, as well as their capacity to recover, are highly variable and may be dependent on species' traits and on local and regional factors (Krumhansl et al., 2016; Smale et al., 2019; Sunday et al., 2015). For example, sessile species including corals and seaweeds are more sensitive to MHWs than mobile species (Smale et al., 2019), often exhibiting sharp declines after exposure to anomalously high temperatures (Brown & Suharsono, 1990; Garrabou et al., 2009; Wernberg et al., 2016).

Brown seaweeds (which include the orders Fucales and Laminariales) are dominant habitat-formers on intertidal and subtidal rocky shores in temperate and cold regions (Schiel & Foster, 2006),

where they provide a large number of ecosystem functions (Steneck et al., 2002). It is clear that some seaweed populations, and the ecosystems they underpin, have been impacted by both recent MHWs and longer-term warming trends (Smale, 2020; Straub et al., 2019). However, most research conducted to date on subtidal communities has focused on the impacts of MHWs on large conspicuous species that are continuously distributed across extensive areas of temperate coastline, particularly kelps (e.g. Arafah-Dalmau et al., 2019; Casado-Amezúa et al., 2019; Duarte et al., 2013). Given that different species and populations of seaweeds have exhibited inconsistent responses to recent warming (Lima et al., 2007; Straub et al., 2019), there is a need to broaden the evidence base to include less conspicuous subtidal habitat-formers with more restricted and/or discontinuous distributions. Moreover, most evidence of MHW impacts on seaweeds stems from populations persisting at the warm edge, where thermal thresholds are more likely to be exceeded (but see Bennett et al., 2015; King et al., 2019), while range centre and cold-water range edge populations have remained largely unaffected (Jones et al., 2010; Smale & Wernberg, 2013; Smale et al., 2019). However, regional variability in the responses of seaweed populations to recent environmental change is far larger than any global trend, highlighting the importance of local- and regional-scale processes (Krumhansl et al., 2016; Müller et al., 2009).

In this context, little is known about the impacts of ocean warming, and specifically MHWs, in areas with historically high human impacts where, for example, previously widespread canopy-forming algae have become extinct or reduced to remnant, fragmented and isolated populations (e.g. Mariani et al., 2019; Thibaut et al., 2005, 2016). Coastal environments in the Mediterranean Sea have been modified by human activities for millennia (Lotze et al., 2011) and, concurrently, are considered to be very sensitive to recent and future climate change (Giorgi, 2006). In fact, several Mediterranean MHWs have triggered deleterious impacts on populations of benthic invertebrates and seagrasses (Cebrian et al., 2011; Cerrano et al., 2000; Coma et al., 2009; Crisci et al., 2011, 2017; Garrabou et al., 2001, 2009; Linares et al., 2005; Marbà & Duarte, 2010; Verdura et al., 2019).

Species of the genus *Cystoseira sensu lato* (including *Ericaria* Stackhouse, *Cystoseira* C. Agardh and *Gongolaria* Boehmer; Molinari-Nova & Guiry, 2020) are the main subtidal canopy-forming seaweeds inhabiting shallow water Mediterranean rocky habitats (Ballesteros, 1992; Feldmann, 1937; Giaccone & Bruni, 1973; Verlaque, 1987). Assemblages dominated by these seaweeds exhibit similar functional properties to kelp forests, and represent the highest level of Mediterranean seaweed complexity (Ballesteros, 1988, 1989, 1990a, 1990b; Clayton, 1990; Pinna et al., 2020). Like other

canopy-forming seaweeds around the world, several *Cystoseira sensu lato* populations have experienced marked declines, mainly as a consequence of changes in water quality (Munda, 1974, 1982; Rodríguez-Prieto & Polo, 1996; Soltan et al., 2001), habitat destruction (Gros, 1978; Thibaut et al., 2005) and overgrazing by sea-urchins (Sala et al., 1998, 2012; Verlaque, 1987). However, even after general and widespread declines, isolated populations remain in certain locations and in certain habitats, such as rock pools (Iveša et al., 2016), leading to fragmented, discontinuous distributions (Blanfuné et al., 2016; Mariani et al., 2019; Thibaut et al., 2016). These patchy distributions may represent a serious challenge for the conservation of these species when faced with acute warming-related perturbations.

Here we provide evidence of a MHW event occurring in summer 2015 along the Catalan coast coupled to a high mortality event on a *Ericaria crinita* population from one of our study sites, which compromised the viability of this remnant population. However, another population remained unimpacted, with in situ temperature data

indicating that warming was less severe, thereby suggesting that the site was acting as a climatic refuge. By means of a thermo-tolerance experiment, we determine the direct effect of thermal stress on individuals' performance and survival at different life stages (e.g. adults and recruits). We discuss our findings and the future implications for management and conservation of a critical habitat-forming species.

2 | MATERIALS AND METHODS

2.1 | Target species and study site

Ericaria crinita (Duby) Molinari-Novoa and Guiry is a perennial caespitose seaweed that can thrive under a wide range of thermal regimes and is distributed throughout the entire Mediterranean Sea (as *Cystoseira crinita*; Ribera et al., 1992; Sales et al., 2012; Figure 1), where it is mainly restricted to the upper sublittoral zone

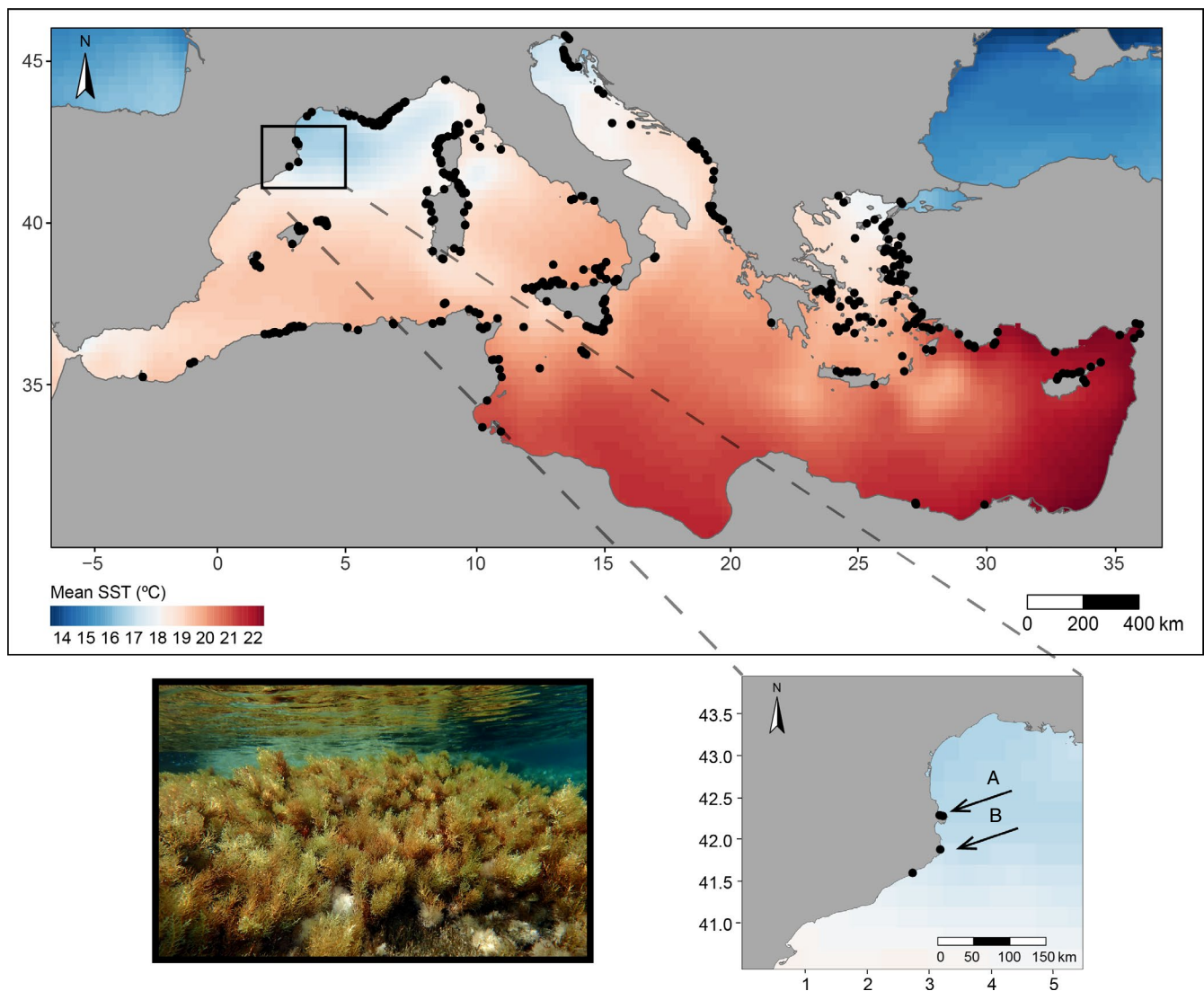


FIGURE 1 Annual mean sea surface temperature (SST; in °C) in the Mediterranean Sea (1982–2019 period, data NOAA). Black dots show the approximate distribution of *Ericaria crinita* throughout the Mediterranean Sea. Bottom figures show a typical stand of *E. crinita* (left) and locations of the two study sites (right; A = Port de la Selva; B = Palamós)

in relatively wave-sheltered and well-illuminated environments (Molinier, 1960; Sales & Ballesteros, 2009, 2010, 2012). Individuals are formed by a discoid base from which several erect axes grow (Gómez-Garreta et al., 2000) making a dense canopy of up to 30 cm. The life cycle is monophasic diploid, in which meiosis takes place during the formation of gametes (n) and the zygote ($2n$) develops into the only diploid vegetative phase of the life cycle (Gómez-Garreta et al., 2000; Rodríguez-Prieto et al., 2013). Individuals are monoecious, with male and female gametes housed within the same conceptacle, which are grouped in terminal receptacles (Rodríguez-Prieto et al., 2013). Reproduction is oogamic (large non-motile eggs and biflagellate sperm) and fertilization is external (Gómez-Garreta et al., 2000). After the fertilization, the large and free-living zygote (~ 70 – $100 \mu\text{m}$) rapidly sinks to the bottom where it is fixed during the first 12–24 hr (Orfila, 2014). Reproductive structures in both population are present all year around but are better developed and more abundant from April to November (Gómez-Garreta et al., 2000; Silva, 2019). The growth pattern is seasonal as described in Ballesteros (1992) and Sales and Ballesteros (2012).

The approximate distribution of *E. crinita* and sea surface temperature (SST) from 1980 to 2019 (Figure 1) were obtained as described in the online Supporting Information S1. *Ericaria crinita* was widespread in rocky shores from the north-western Mediterranean at the beginning of the 20th century but has largely disappeared from several areas (Blanfuné et al., 2016; Mariani et al., 2019; Thibaut et al., 2005) due to different environmental pressures such as habitat destruction and overgrazing by sea urchins. However, the regression has left remnant populations along the previous distribution range of the species (Blanfuné et al., 2016; Mariani et al., 2019). For this study, we have selected two remnant populations of *E. crinita* found at Port de la Selva and Palamós, Northern Catalonia (Figure 1). The Port de la Selva population inhabits a permanent submerged rock pool measuring $5 \times 2 \text{ m}$ and $< 1 \text{ m}$ depth, which offers calm and sheltered conditions. *Ericaria crinita* makes a permanent belt between the surface and 0.6 m depth. The rock pool is constantly connected to the open sea but the exchange of water in/out of the pool is somewhat restricted by its geomorphological structure. The Palamós population, located $\sim 50 \text{ km}$ south of Port de la Selva, is the largest remaining in northern Catalonia (Mariani et al., 2019), occupying an area of 40 m^2 . *Ericaria crinita* thrives among rocks within a shallow, open and semi-exposed mixed substrate habitat, also between the surface and 0.6 m depth, where water exchange is unrestricted.

2.2 | Monitoring natural populations and temperature records

Populations were monitored from 2014 to 2017. Density (total number of individuals/ 0.04 m^2) and size-class distribution (length from the basal disc to the tip of the highest axis of each individual) of each population were monitored in at least 20 randomly distributed $20 \times 20 \text{ cm}^2$ quadrats. Recruits were easily recognizable in the field because of their small size ($< 0.5 \text{ cm}$ length) and morphology.

Populations were sampled once or twice per year. Port de la Selva population was sampled in April 2014 and 2015, November 2015, April and November 2016 and February 2017 and similarly, Palamós population was sampled in August 2014, November 2015, July and December 2016 and March 2017.

Satellite sea surface temperature (SST) are commonly used as a proxy for coastal temperatures since they are highly correlated with in situ sea temperature (IST; Brewin et al., 2018). However, considerable site-specific differences between SST and IST have been detected within shallow coastal benthic habitats and, as such, SST may be inappropriate for capturing small-scale variability or extreme temperature events in some settings (Smale & Wernberg, 2009; Stobart et al., 2016). Therefore, we used both in situ and satellite-driven temperature records to examine the intensity and duration of the anomalously warm water event detected during summer 2015. In situ sea temperatures at both study sites were obtained by deploying one high-resolution (hourly records, $\pm 0.21^\circ\text{C}$ accuracy) temperature logger (HOBO Water Temp Pro v2) at each site, at 0.3 m depth during the period 2014–2016. Data loggers were attached to the bottom using a permanent epoxy glue (IVEGOR; Garrabou et al., 2018). Satellite-driven temperature data were obtained over the 1985–2016 period from the NOAA's OISST dataset (Reynolds et al., 2007).

The climatology experienced at each site, and in particular the occurrence of MHW events during the study periods, was described from daily mean temperature time series following the definition developed by Hobday et al. (2016) using the HEATWAVE package (Schlegel & Smit, 2018) in R (R Core Team, 2019). Both satellite-derived and in situ daily mean sea temperatures were compared with a baseline 30-year climatology (i.e. from 1985 to 2016) described by satellite-derived SSTs. MHWs were defined as periods when daily mean temperatures exceeded the 90th percentile (relative to the baseline climatology) for at least 5 consecutive days (Hobday et al., 2016). Moreover, the number of days per year (2014, 2015 and 2016) in which in situ maximum temperatures exceeded different thermal values were counted and compared between the two study sites (from 24 to 29°C).

2.3 | Seaweed collection and experimental set up

Effects of thermal stress on *CE crinita* were experimentally tested on both adults and recruits. Three different temperature treatments were selected based on actual temperatures experienced in situ by populations at the study sites during summer: 21°C (ambient), 24°C (peak summer temperatures) and 28°C (anomalously high, experienced during MHWs). Specifically, the mean temperature ($\pm SD$) obtained for each treatment during the experiment period was 20.98 ± 0.57 , 24.4 ± 0.33 and $28.17 \pm 0.56^\circ\text{C}$.

2.3.1 | Adults

In all, 22 adult individuals with no signs of stress (necrosis, herbivory, high epiphytism, etc.) were randomly collected in May 2017, using

a chisel and a hammer to ensure the complete collection of the individual together with the basal disc. To avoid any pre-conditioning of individuals exposed to previous mortality events while ensuring similar environmental conditions as at the study sites, we collected *E. crinita* from Palamós (Figure 1), where deleterious effects of MHWs were not recorded. After collection, individuals were immediately transported to the laboratory, where they were cleaned to remove epiphytes and organic matter. Subsequently, a set of 18 individuals were selected and distributed among treatments, ensuring comparable size and biomass of individuals across the different treatments. The individuals were distributed into nine different 12 L tanks of seawater (two individuals per tank) held at 18°C, coinciding with in situ temperature at the sampling season, for 3 days for initial acclimation to laboratory conditions. After this period, temperatures were gradually increased at a maximum rate of 1.5°C per day until the target experimental temperatures were attained, at which point the experiment commenced and ran for 30 days. Three tanks with two individuals each were used as replicates for each treatment (2 individuals \times 3 tanks \times 3 temperatures), with individuals held in a closed-water circuit with aeration. All tanks had a daily water replacement rates of 2 L per tank and once per week the entire 12 L volume of each tank was replaced. The temperature of each tank was regulated with a seawater temperature controller (Teco TK 500). To simulate in situ light conditions, four fluorescent lamps (two Master TL-D 36W/386 of Philips and two Actinic BL TL-K 40W/10-R of Philips) supplying 180–200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ of PAR and UV were set at 0.8 m height above the water surface. This irradiance corresponds to the irradiance at photosynthesis saturation levels for *E. crinita* (Sant, 2003). The photoperiod was 14:10, coinciding with natural light conditions of the season in which the experiment took place.

Three different response variables were used to examine temperature effects on adults: (a) biomass, (b) optimum quantum yield (F_v/F_m) of photosystem II (PSII) and (c) carbon and nitrogen content (C:N). Changes in biomass were estimated by comparing wet weight of individuals at the different sampling times to the initial weight. F_v/F_m was used as an indicator of PSII performance to assess photosynthetic efficiency under thermal stress (Graiff et al., 2015; Saada et al., 2016). One measurement per individual was performed at the apical part of a secondary branch with no signs of necrosis. Fronds were dark incubated for 15 min using the specific underwater clips for dark-acclimation after which F_v/F_m measurements were obtained using pulse amplitude modulated (PAM) fluorometry (using a Diving-PAM Underwater fluorometer). C:N ratios were obtained from five random individuals of the natural population at the beginning of the experiment and from five individuals per treatment at the end of the experiment. Ten grams (wet weight) coming from the apical part of the secondary branches of each individual were dried at 60°C for 48 hr. The dried samples were ground using a ball mill (mill, Retsch MM20) for 20–25 min at a frequency of 25/s. Two subsamples of 3–4 mg (balances, Sartorius M2P) from each individual were packed into tin capsules (5 \times 8 mm) and manually closed. The capsules were combusted at 930°C (elemental analyser Perkin-Elmer EA2400-II) and C and N contents were quantified as a weight percentage using acetanilide as standard.

2.3.2 | Settlement and survival of early stages

Over 100 fertile branches of *E. crinita* were collected from Palamós and immediately returned to the laboratory, where they were stored at 5°C in dark conditions for 12–24 hr to stimulate release of gametes. For each temperature treatment, three culture boxes were prepared and three replicate microscope slides were placed within each box (i.e. 3 slides \times 3 boxes \times 3 treatments). In total, 12 fertile branches were placed in each culture box with sterilized sea water and growth medium (Von Stoch modified by Guiry & Cunningham, 1984). After 3 days, following the formation and attachment of zygotes, fertile branches were removed. Lighting was achieved as described above (but using two PAR radiation fluorescent lamps, supplying 100 $\mu\text{mol m}^{-2} \text{s}^{-1}$) and the growth medium was renewed twice a week with the experiment lasting for 19 days.

Temperature effect on zygotes settlement was assessed by quantifying the density of settled zygotes per each slide 3 days after the deployment of fertile branches within culture boxes. Finally, the survival rate of recruits was quantified on days 1, 3, 5, 9, 12 and 19, as the proportion of viable recruits relative to those observed on the first day.

2.4 | Data analysis

For the analysis of the data obtained from both adult and recruit experiments, the use of mixed-effects models (MM) is appropriate because they allow inclusion of both fixed and random effects as predictor variables. In our case, the use of crossed and nested random effects allows us to control for the lack of independence among observational units and to handle in the same model clustered data and repeated measures across time (Bates et al., 2015; Bolker et al., 2009; Harrison et al., 2018).

For adults, the effect of temperature on biomass was analysed by means of a LMM, whereas the effect of temperature on the optimum quantum yield was analysed with a GLMM with a Poisson error distribution and a logit link function. In both the models, temperature was fitted as a fixed factor and time as a crossed random factor. Additionally, a second random term, individuals' identity nested within tank, was fitted to take into account that individuals were grouped by pairs within each tank and to correct for the non-independence between measurements (repeated measurements of the same individuals over time). On the other hand, temperature effect on C:N was examined with an LMM, with treatment as a fixed factor (four levels: natural population, 21, 24 and 28°C) and tank as a random factor to deal with the individuals within tanks clustered design. A type II Wald χ^2 test was applied to each fitted model to determine the effect of the fixed factor. Finally, for each model, a Tukey post-hoc test was applied to explore the differences between temperature treatments.

For recruits, the effect of temperature on zygote settlement was examined by means of a GLMM with a quasi-Poisson error distribution where temperature was fitted as a fixed factor and culture

box was fitted as a random factor to control for the clustered design in which slides ($\times 3$) were grouped within culture boxes. Finally, the effect on survival was analysed using a GLMM with a binomial error distribution and logit link function considering temperature as a fixed factor and time as a crossed random factor. A second random effect, slides nested within cultured box, was also included to consider the clustered design and to control for the non-independence between measurements (repeated measurements of the same slides over time). Again, a type II Wald χ^2 test was applied to each model to determine the effect of the fixed factor, and Tukey's post-hoc tests were performed to look for differences within temperature treatments.

The different models were fitted using *lme4* (Bates et al., 2015) and MASS packages (Venables & Ripley, 2002) in the statistical environment R (R Core Team, 2019). *p* values were obtained by means

of a Wald χ^2 test using the 'ANOVA' function from the *CAR* package (Fox & Weisberg, 2019). Finally, the function 'glht' from the *MULTCOMP* package (Hothorn et al., 2008) was used to perform post-hoc Tukey tests.

3 | RESULTS

3.1 | Thermal anomaly

Satellite-derived SST data showed that mean temperatures recorded during summer 2015 were anomalously high at both sites, with two MHWs of 7 and 5 days duration, detected during summer at each site (Figure 2A,B). Satellite-derived SSTs recorded mean maximum temperatures of 24.3 and 25.6°C at Port de la Selva and Palamós,

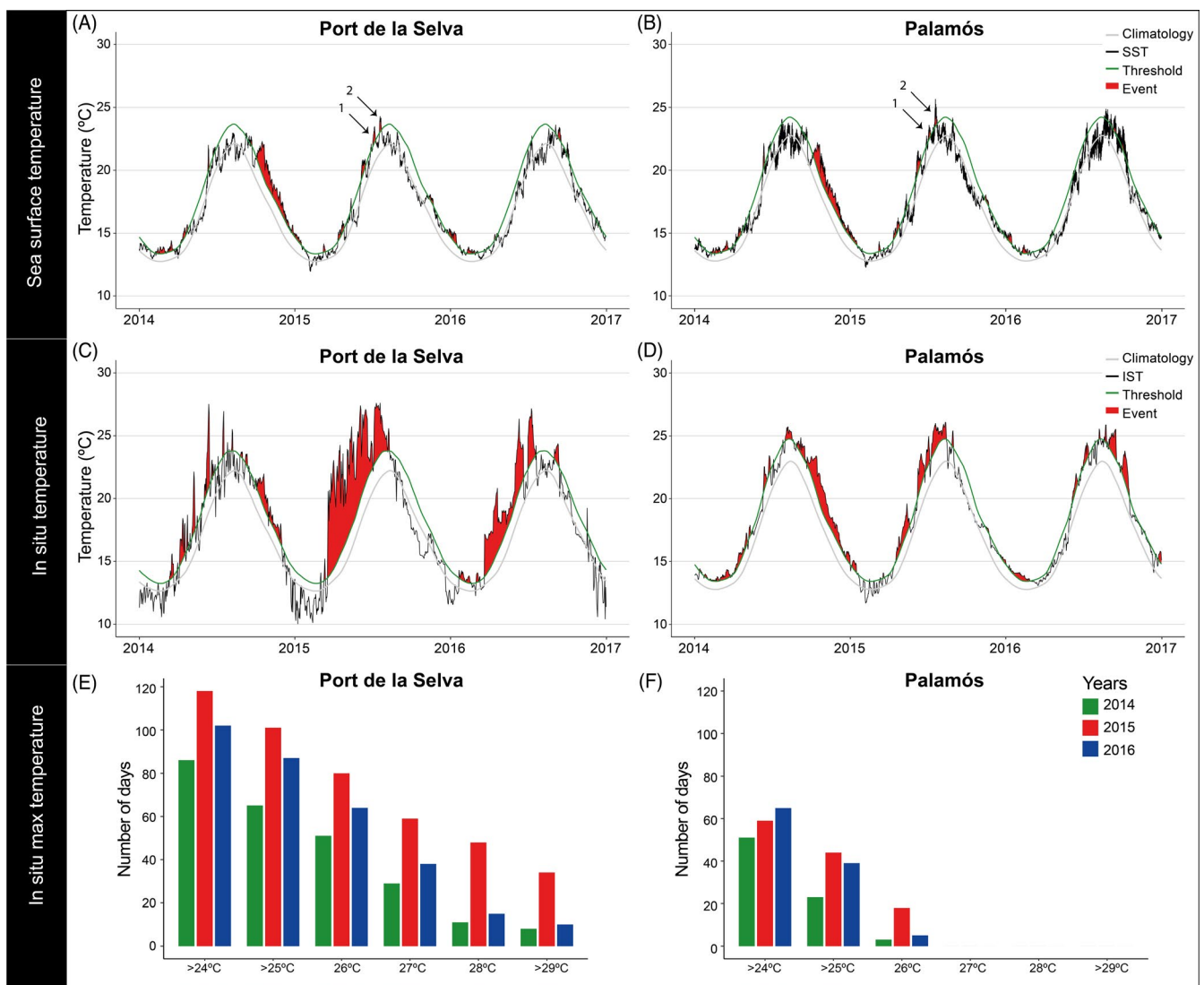


FIGURE 2 MHWs in the study sites from 2014 to 2016. (A–D) Grey line and green line indicate the seasonal climatology and the seasonally varying threshold (90th threshold) for the identification of MHWs, respectively. Black lines indicate the satellite-driven sea surface temperature (SST; A and B) and in situ seawater temperatures (IST; C and D) in Port de la Selva and Palamós populations. The arrows in (A) and (B) plots highlight the MHWs occurring during the summer of 2015 with a duration of 7 and 5 days, respectively. E and F plots show the number of days per year in which IST exceeded the different temperature thresholds (from 24 to 29°C) in Port de la Selva (E) and in Palamós (F)

respectively, representing a warming event of ~ 3.0 and $\sim 3.7^\circ\text{C}$ in magnitude, respectively (Figure 2A,B). When using high-resolution in-situ temperature data, however, maximum temperatures exceeding 29°C were recorded at Port de la Selva. Moreover, in 2015, high-resolution IST detected a prolonged MHW lasting for more than 120 days in Port de la Selva (Figure 2C) and several shorter but consecutive MHWs in Palamós (Figure 2D). During this period, temperatures exceeded 28°C on more than 40 days in Port de la Selva (Figure 2E), whereas maximum temperatures exceeded 26°C on 20 days but did not reach 28°C in Palamós (Figure 2F).

3.2 | Population monitoring

The *E. crinita* population in Port de la Selva exhibited a stable density and size-class structure over the time period from April 2014 to April 2015, with a prevalence of medium size-classes individuals (from 2 to 8 cm in length) but widely represented by individuals of each size-class, from recruits (0.1–0.5 cm) up to individuals of around 20–30 cm in length (Figures 3A and 4A). However, after summer 2015, population density decreased (Figure 3A) and all large individuals disappeared (Figure 4A); while only a few individuals remained alive as remnant basal discs or small thalli (<4 cm in length), almost totally devoid of secondary branches and, as a consequence, devoid of reproductive structures (e.g. receptacles develop in the apical part of secondary branches). Moreover, no new recruits were recorded in the survey following summer 2015 (Figure 3A). An absence of large individuals and dominance of small individuals was observed again in April and November 2016. In February 2017, the size-class distribution was a little more symmetric, with a large proportion of individuals having axis lengths between 2 and 8 cm and with a few larger individuals (from 8 to 12 cm; Figure 4A).

Density and size-class structure of the population of *E. crinita* at Palamós exhibited high stability over time (Figures 3B and 4B). A pulse of recruitment was recorded in August 2014 but the population was well represented by all size-classes, from individuals measuring 0.5 cm up to 20 cm in length. After 15 months, in November 2015, there was a dominance of medium size-classes between 4 and 14 cm but even so, larger individuals were present (up to 30 cm), a situation that was maintained in July 2016 (Figure 4B). Despite the fact that in December 2016 another recruitment pulse was detected, the size-class distribution remained stable over the following year, with a major proportion of medium size-class individuals and a lower proportion of larger individuals reaching a maximum size of 30 cm in length (Figure 4B).

3.3 | Direct effects of temperature on *Ericaria crinita*

Adult individuals were able to tolerate summer temperatures of 24°C throughout the experiment (30 days), with all of the response variables measured remaining statistically similar to individuals

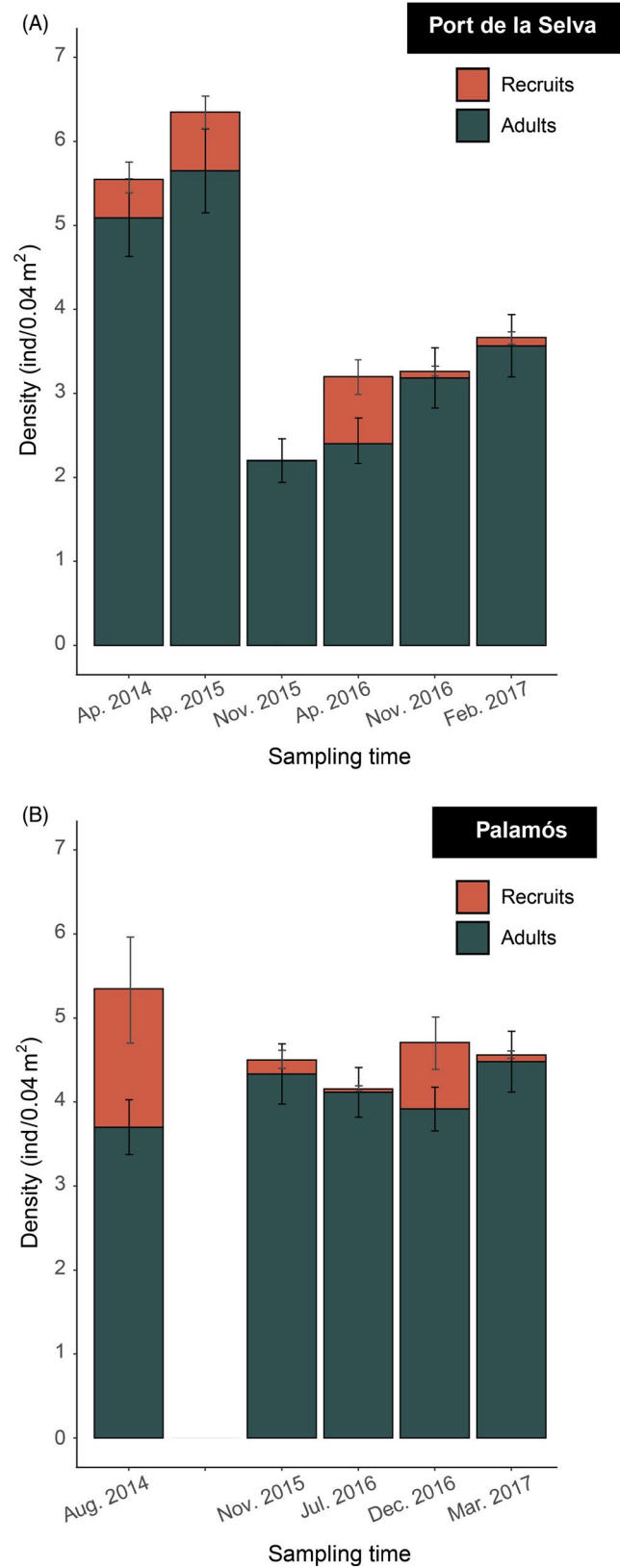


FIGURE 3 Density (mean \pm SE of the number of individuals per 0.04 m^2) of *Ericaria crinita* populations from (A) Port de la Selva and (B) Palamós, monitored from 2014 to 2017. Different colours represent the density of recruit (<0.06 cm in height) and adult individuals sampled at each time

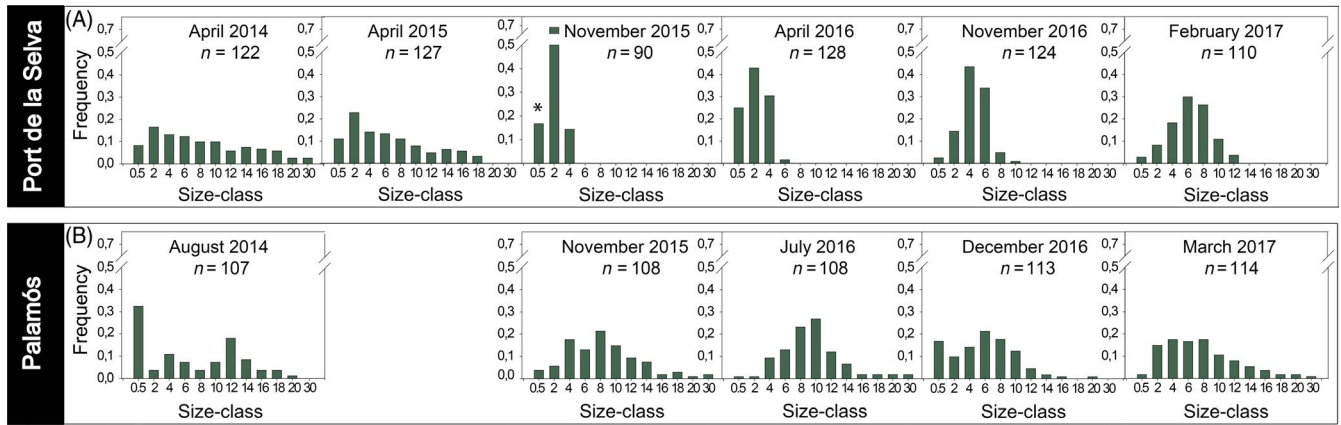


FIGURE 4 Size-class frequency distribution of the *Ericaria crinita* populations from (A) Port de la Selva and (B) Palamós, monitored from 2014 to 2017. The X-axis represents the size-classes (length of the longest axis of each individual) in 2-cm interval, except for the first size-class for which a particular size-class group (0–0.5 cm), corresponding to recruit individuals, was established. Notice that in the case of November 2015 in Port de la Selva, the individuals measuring up to 0.5 cm in length correspond to remnant bases (indicated with an asterisk * in the graph). The Y-axis represents the relative frequency of each size-class

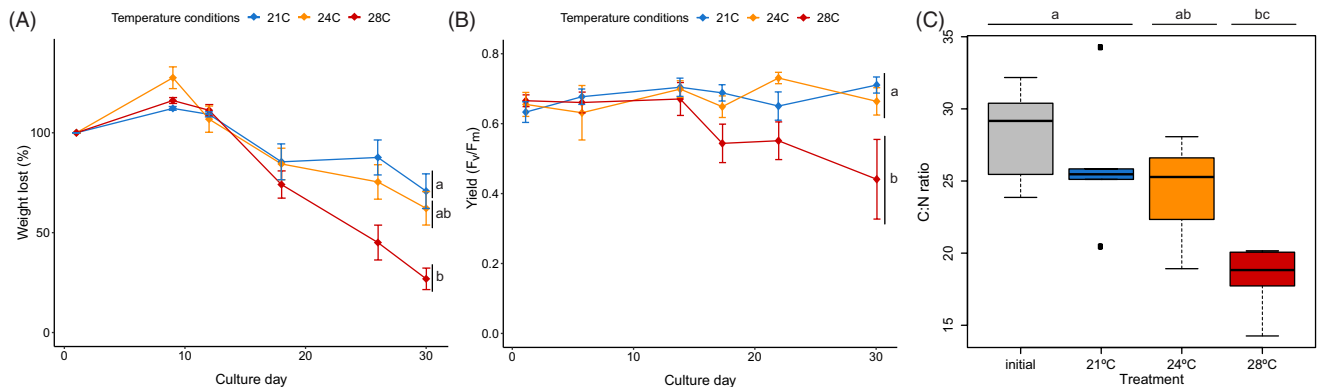


FIGURE 5 Temperature effects on the performance of *Ericaria crinita* adult individuals over 30 days of exposure at different thermal experiment conditions; (A) wet weight variation (mean \pm SE), (B) optimum quantum yield (F_v/F_m) of photosystem II (mean \pm SE) and (C) boxplot of the C:N ratio. The box plot indicates the median values (bold horizontal line), the interquartile distances (the box), the extreme values that are non-outliers (whiskers) and the outlier values (spots). Significant differences between thermal experimental conditions (p values from Tukey's test with 95% confidence intervals) are indicated with letters at each graph

maintained at 21°C (Figure 5; Online Supporting Information S2). Exposure to 28°C had a significant negative impact on biomass (Figure 5A; Online Supporting Information S2), photosynthetic efficiency (Figure 5B; Online Supporting Information S2) and carbon and nitrogen content (Figure 5C; Online Supporting Information S2). Twenty-five days of exposure to 28°C resulted in algal tissue damage, with a biomass loss of 50%, which increased to 70% after 30 days (Figure 5A). At the beginning of the experiment, all individuals exhibited F_v/F_m values of ~ 0.6 – 0.7 , which remained more or less constant until the end of the experiment for individuals held at 21 and 24°C (Figure 5B; Online Supporting Information S2). In contrast, for individuals held at 28°C, F_v/F_m values declined after only 15 days of exposure (to <0.6) and after 26 days of exposure had declined markedly, to <0.5 (Figure 5B; Online Supporting Information S2). At the end of the experiment, C:N of individuals exposed to 28°C had declined considerably compared with C:N of individuals held at 21°C

and those obtained at the beginning of the experiment (Figure 5C; Online Supporting Information S2; see absolute values of C and N in online Supporting Information S3).

The effect of temperature on early stages of *E. crinita* was pronounced, as warming strongly impacted zygote settlement and survival of early stages (Figure 6; Online Supporting Information S4). Zygote settlement declined significantly under the highest temperature treatment (Online Supporting Information S4). While no significant differences were found between 21°C (control) and 24°C, the number of settled zygotes at 28°C was on average eightfold lower than at 24°C and 14-fold lower than at 21°C (Figure 6A). Similarly, survival of recruits was severely affected by temperature over time (Online Supporting Information S4). Specifically, survival rates of recruits at 28°C were significantly lower than at 21 and 24°C, with $<50\%$ survival of individuals after 5 days of exposure to 28°C (Figure 6B).

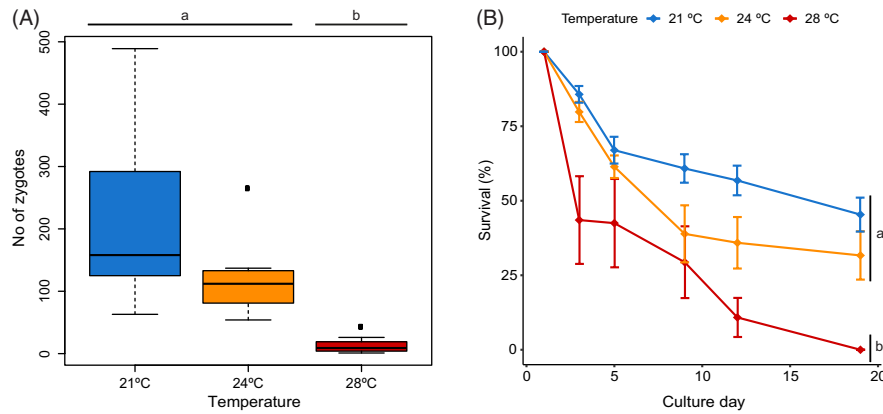


FIGURE 6 Temperature effects on *Ericaria crinita* recruitment on (A) boxplot of the number of settled zygotes for each temperature condition and on (B) recruits' survival (mean \pm SE) over 20 days of exposure at the different thermal experimental conditions. The box plot indicates the median values (bold horizontal line), the interquartile distances (the box), the extreme values that are non-outliers (whiskers) and the outlier values (spots). Significant differences between thermal experimental conditions (p values from Tukey's test with 95% confidence intervals) are indicated with letters at each graph

4 | DISCUSSION

In the summer of 2015, an anomalous warming event was caused by high rates of air-sea heat transfer and resulted in one of the most severe MHWs since 1982 in the Mediterranean Sea (Darmaraki et al., 2019; Hoy et al., 2017). Interestingly, very few mortality events of marine organisms were attributed to this MHW, whereas previous extreme warming events have led to widespread mass mortalities of cold affinity species, such as gorgonians and other benthic invertebrates that live in deeper waters (Cebrian et al., 2011; Cerrano et al., 2000; Coma et al., 2009; Garrabou et al., 2009; Perez et al., 2000). The MHW of 2015 was restricted to very shallow waters, and did not extend to deeper layers (Darmaraki et al., 2019), which may have limited the exposure to the most sensitive groups, such as deep-water cold-affinity benthic invertebrates (but see Rubio-Portillo et al., 2016).

Here, we show that the 2015 MHW coincided with high mortalities in a shallow water *E. crinita* population but it did barely affect another, suggesting that different populations can encompass different responses to warming due to small-scale variability in thermal conditions. Recent warming trends and extreme climatic events have driven abrupt changes in the structure of populations and the distribution of species in marine ecosystems (Poloczanska et al., 2013, 2016; Sunday et al., 2015). The most profound impacts have generally been observed at species' warm edges, where populations are found towards their upper thermal thresholds (Beukema et al., 2009; Jones et al., 2010; Smale, 2020). As warm edge populations of temperate kelps and fucoids have generally been most affected by warming, they are widely considered to be the most vulnerable populations to future MHWs (Coleman & Wernberg, 2017; Nicastro et al., 2013; Smale & Wernberg, 2013; Wernberg et al., 2013, 2016). However, although *E. crinita* populations can be found from the coldest to the warmest areas of the Mediterranean Sea (Sales et al., 2012), we document high mortality of a population persisting within a relatively cool portion of this species' distribution, highlighting that core range

populations may be also susceptible to MHWs (see also Bennett et al., 2015; King et al., 2019).

The magnitude of the MHW event varied between our study sites, which were characterized by different habitat features. Specifically, the MHW was markedly more intense in the enclosed 'pool' habitat of Port de la Selva when compared with the open cove of Palamós, suggesting warming as being the cause of the different responses at the population level. Thus, local-scale environmental heterogeneity seems to underlie the between-population variability in response to warming as suggested by Helmuth, Broitman, et al., 2006; Helmuth et al., 2002; Helmuth, Mieszkowska, et al., 2006.

In Port de la Selva, the reduction in the number of individuals and the biomass loss of the survivors was much more severe than in Palamós, where the population was largely unimpacted. The thermotolerance experiment pointed temperatures of 28°C as a driver of high mortality in the populations. Photosynthetic efficiency (F_v/F_m) of adult individuals was significantly reduced after only 15 days of exposure at 28°C, indicating high thermal sensitivity of photosynthetic performance, a process known to be temperature-dependent (Crafts-Brandner & Salvucci, 2002). Reductions in photosynthetic efficiency coincided with reduced C:N at 28°C, as has been previously observed in other fucoid species (Graiff et al., 2015). While temperature can have opposing effects on nitrogen content (Graba-Landry et al., 2020), in our case, the C:N reduction was mainly due to a decrease on the nitrogen content at higher temperatures, which may be related to an increment of microbial activity, an alteration of the microbial community or to processes associated with the senescence of the thalli (Campbell et al., 2011; Hanisak, 1993; Webster et al., 2011). Similarly, exposure to 28°C induced visible tissue damage after 25 days and 70% of biomass loss after 30 days. In general, biomass loss was mainly observed in branches, where reproductive structures develop, and only basal parts remained viable (as *E. crinita* is able to recover by vegetative regrowth from remnant and damaged bases it would explain the increase in medium size-classes individuals observed

in February 2017 in Port de la Selva). Early-life stages of *E. crinita* were even more vulnerable to thermal stress, since recruit's survival was drastically compromised after very short-term exposures (5 days) at 28°C. It is therefore likely that the high vulnerability of recruits combined with fertility impairment (loss of reproductive structures) will have indirect but considerable implications for the recovery and persistence of populations following extreme warming events.

Considering the severe impacts that temperature may have on *Cystoseira sensu lato* populations together with the projected future scenarios of warming and increasing severity of MHW, local management strategies to preserve *Cystoseira sensu lato* populations are urgently needed (Buonomo et al., 2018). Since the potential for natural recovery is limited and variable (Thibaut et al., 2016), one of the most promising conservation actions relies on active restoration (Verdura et al., 2018). However, we show that vulnerability to warming would have to be considered before designing and investing on a long-term and successful restoration plan (Wood et al., 2019). Another increasingly recognized strategy of local management is the identification and protection of contemporary climatic refugia (Keppel et al., 2012). Our findings may suggest that the open and connected nature of the habitat at Palamós allowed for the exchange and mixing of cooler seawater from surrounding areas, thus modulating the intensity of the 2015 MHW. As a result, Palamós provides favourable environmental conditions for *E. crinita* population persistence in a scenario of more frequent MHW events. While we primarily attribute the observed between-population variability in MHW impacts to between-site differences in thermal conditions, other factors may also promote variability in population responses. For example, limited dispersal distance in fucoids (in the order of the tens of cm to the tens of meters) could invoke site-specific

responses (Capdevila et al., 2018; Mangialajo et al., 2012; Verdura et al., 2018), while thermal divergence between populations as a result of local adaptation has been observed for other habitat-forming seaweeds (King et al., 2019; Liesner et al., 2020; Wernberg et al., 2018). Even so, given that the *E. crinita* population at Palamós is the largest population found along the Catalan coast (Mariani et al., 2019) and our results indicate that this population was less impacted by a regional-scale warming event, this location could be identified and managed as a contemporary climatic refugia, potentially safeguarding the persistence of this habitat-forming seaweed along the northwestern Mediterranean coast.

The Mediterranean Sea is a global hotspot for ocean warming (Belkin, 2009; Lejeune et al., 2009), and is highly susceptible to marine heatwaves (Hobday et al., 2016; Oliver et al., 2018), which are projected to intensify in the coming decades (Oliver et al., 2019). Given the semi-enclosed morphology of the Mediterranean basin, poleward species range shifts into more favourable climatic conditions are not possible (Burrows et al., 2014; Lejeune et al., 2009). As such, in the absence of local adaptation, and with limited potential for recovery and poleward migration, sensitive species such as *Cystoseira sensu lato*, that often present fragmented distributions, are likely to become locally extinct under projected warming scenarios (Figure 7; Clarke, 1996). Recovery may also be restricted when MHWs are spatially more extensive than species' dispersal distances, or where source populations are located 'downstream' of ocean currents, both of which limit the potential for recolonization from source populations (Straub et al., 2019; Wernberg, 2021).

Crucially, given that coarse-scale satellite-derived SST data did not adequately capture between-location variability in actual MHW profiles, and given that local-scale factors can strongly mediate ecological responses to extreme warming events, further work at finer scales and resolutions is warranted. Most predictive

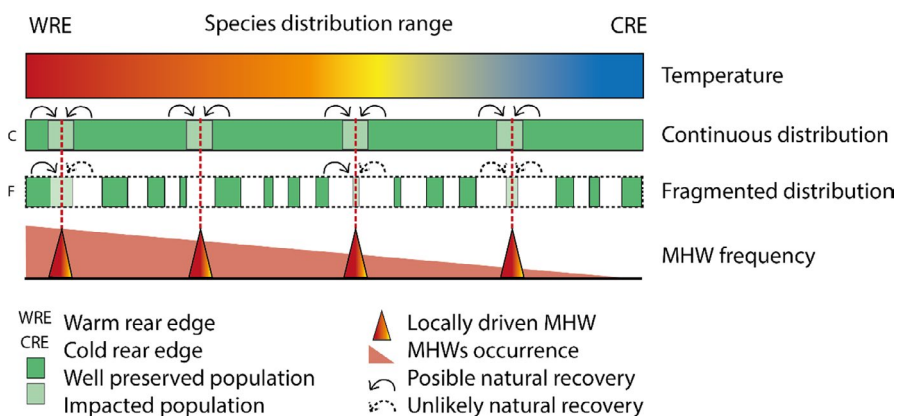


FIGURE 7 Conceptual diagram of thermal anomalies on populations throughout their climatic range, differentiating continuously distributed (C) and fragmented (F) species. Green bands represent species distribution along their geographical range. Continuous green band represents extensive and continuously distributed populations of seaweed species and the discontinuous band represents small and fragmentally distributed populations that have been historically impacted by local factors. The frequency of MHW along the latitudinal gradient is represented in red and the small red triangles represent punctual MHW. MHW impacts (modulated by local factors) lead to population declines or extinction throughout the entire species distribution range. Recovery of continuously distributed areas is ensured by neighbouring populations and prevented in small and fragmented populations (discontinuous green bars) due to the lack of connectivity where local extinctions can seriously compromise the viability of the species

studies have been conducted at regional to global scales, linking species distributions with coarse environmental data using constant critical thermal thresholds across populations or life stages, for example. However, disregarding particular conditions at local scales (such as small enclosed areas) or specific thresholds for different populations or life stages, may limit capacity to accurately predict the impacts of gradual and abrupt ocean warming in the coming decades.

ACKNOWLEDGEMENTS

We thank Simone Mariani for his help in the field. We acknowledge the Environmental Department of the Council of Palamós for providing the permits to conduct the field work. Financial support has been provided by European Union's Horizon 2020 Research and Innovation Program, MERCES Project (No. 689518), the European Union's EMFF Program, AFRIMED (No. EASME/EMFF/2017/1.2.1.12/S4/01/SI2.789059), the Spanish Ministry Project ANIMA (No. CGL2016-76341-R, MINECO/FEDER, UE) and University of Girona (MPCUdG2016/097). This output reflects only the authors' view and the European Union cannot be held responsible for any use that may be made of the information contained therein. This work was also supported by an UKRI Future Leaders Fellowship (MR/S032827/1) to D. Smale, an IF-UdG grant to J. Verdura, a 'La Caixa' Foundation Fellowship (ID 100010434) with code (LCF/BQ/DE17/11600001) to J. Santamaría and a FPI fellowship (BES-2017-079907; ANIMA Project) to R. Golo. J. Verdura, J. Santamaría, S. de Caralt, R. Golo, A. Vergés and E. Cebrian are members of the consolidated Research Group MedRecover (www.medrecover.org; 2017 SGR 1521, Generalitat de Catalunya). The authors declare no conflict of interests.

AUTHORS' CONTRIBUTIONS

E.C. and J.V. conceived the idea and designed the study; J.V., E.C., J.S., M.E.C. collected the field data; J.V., J.S., S.d.C. and A.V. performed the laboratory experiment and laboratory work; J.V., J.S. and R.G. conducted the statistical analyses and MHW characterization; E.C. supervised all the study and J.V., E.C., E.B. and D.S. discussed the results; J.V. and E.C. wrote the first draft and all authors contributed critically to writing subsequent drafts and gave their final approval for the publication.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/1365-2745.13599>.

DATA AVAILABILITY STATEMENT

Data and R codes are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.0k6djhb00> (Verdura et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Verdura J, Santamaría J, Ballesteros E, et al. Local-scale climatic refugia offer sanctuary for a habitat-forming species during a marine heatwave. *J Ecol*. 2021;00:1–16. <https://doi.org/10.1111/1365-2745.13599>