

Recurrent partial mortality events in winter shape the dynamics of the zooxanthellate coral *Oculina patagonica* at high latitude in the Mediterranean

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Abstract Global warming has many biological effects on corals and plays a central role in the regression of tropical coral reefs; therefore, there is an urgent need to understand how some coral species have adapted to environmental conditions at higher latitudes. We examined the effects of temperature and light on the growth of the zooxanthellate coral *Oculina patagonica* (Scleractinia, Oculinidae) at the northern limit of its distribution in the eastern Iberian Peninsula (western Mediterranean) by transplanting colonies onto plates and excluding them from space competition over a ~4-yr period. Each year, most of the colonies (~70%) exhibited denuded skeletons with isolated polyps persisting on approximately half of the coral surface area. These recurrent episodes of partial coral mortality occurred in winter, and their severity appeared to be related to colony exposure to cold but not to light. Although *O. patagonica* exhibited high resistance to stress, coral linear extension did not resume until the coenosarc regenerated. The resumption of linear extension was related to the dissociation of the polyps from the coenosarc and the outstanding regenerative capacity of this species

(10.3 mm² d⁻¹). These biological characteristics allow the species to survive at high latitudes. However, the recurrent and severe pattern of denuded skeletons greatly affects the dynamics of the species and may constrain population growth at high latitudes in the Mediterranean.

Keywords Zooxanthellate coral · Partial mortality · Lesion regeneration · Linear extension dynamics · Cold thermal stress · Mediterranean Sea

Introduction

Latitudinal variation in environmental parameters determines coral biogeography. Temperature, solar radiation, nutrients and the saturation state of seawater aragonite are critical factors for photosynthesis and the calcification of zooxanthellate corals, and these variables co-vary with increasing latitude, thus limiting coral growth at high latitudes (e.g., Kleypas et al. 1999; Muir et al. 2015). The scarcity of zooxanthellate corals in temperate areas is related to the effects of environmental parameters, competition with macroalgae and the synergistic interactions of biotic and abiotic factors (e.g., Miller 1998; Hoegh-Guldberg 1999). However, the current decline of coral reefs in both perturbed and unperturbed areas indicates that increasing temperature is a global stressor that is playing a crucial role in the regression of reef ecosystems (e.g., Hughes et al. 2010). Temperature has long been considered to be the primary factor controlling the distribution of coral species (e.g., Hoegh-Guldberg 1999; Kleypas et al. 1999), and exposure to both high and low stressful temperatures has been documented to reduce coral growth and cause bleaching and mortality (e.g., Saxby et al. 2003; Hoegh-Guldberg et al. 2005; Colella et al. 2012; Roth et al. 2012).

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Global warming is affecting many biological aspects of coral species; even the more conservative warming projections indicate that many tropical reefs may enter a non-coral-dominant stage before the end of the century (Hoegh-Guldberg and Bruno 2010; Pandolfi et al. 2011; Frieler et al. 2013). Corals are among the organisms least expected to exhibit poleward movement because their capacity to adapt is usually outpaced by the current, rapid rate of environmental change due to human activities (Hoegh-Guldberg 2012). However, the distribution of some zooxanthellate scleractinian corals has shifted to higher latitudes in some areas, tracking the movement of suitable temperatures (e.g., Takao et al. 2015), and marginal habitats for coral reefs are predicted to expand in future climate scenarios (Freeman 2015). Understanding the ability of such coral species to adapt to environmental changes at high latitudes is crucial to predict shifts in coral communities in response to climate change.

In the shallow rocky assemblages of the temperate Mediterranean Sea, both local evidence of phase shifts from macroalgal to coral dominance and the rapid expansion of *Oculina patagonica* (Scleractinia, Oculinidae) (Serrano et al. 2012, 2013; Salomidi et al. 2013; Rodolfo-Metalpa et al. 2014) provide evidence that this zooxanthellate coral may be displaying invasive behavior that could challenge the current conceptual framework of the ecosystem (Miller 1998). Such behavior is consistent with the fact that *O. patagonica*, first documented in the Mediterranean in 1966, is currently found in many areas throughout the Mediterranean Sea (Rubio-Portillo et al. 2014a and references therein). A recent study indicated that the species is not a recent introduction, and thus its current taxonomic status is unclear because it cannot be reliably classified as either “native” or “introduced” (Leydet and Hellberg 2015). The most abundant *O. patagonica* populations have been recorded along the coast of the eastern Iberian Peninsula (Balearic Sea; Fine et al. 2001; Coma et al. 2011; Serrano et al. 2012, 2013; Rubio-Portillo et al. 2014a). However, although this coral has been expanding northward from the north Balearic Sea (40°N) toward the Gulf of Lyon (42°N) over the last two decades (Serrano et al. 2013), little is known about its growth dynamics in the expansion zone.

Similar to tropical corals, the growth rate of *O. patagonica* in the western Mediterranean is positively correlated with a certain temperature range (Rodolfo-Metalpa et al. 2008). Prolonged exposure to sublethal warm-temperature thresholds has been reported to damage *O. patagonica* colonies in short-term field studies (<2 yr) and surveys (Rodolfo-Metalpa et al. 2008, 2014; Rubio-Portillo et al. 2014b), and long-term studies in the eastern Mediterranean have shown that the species suffers severe annual bleaching and mortality events in summer (Fine et al. 2001;

Shenkar et al. 2005) that are mainly related to exposure to high temperature (Ainsworth et al. 2008). In this study, we addressed the effect of temperature and light on *O. patagonica* growth dynamics in the expansion zone at the northern limit of its population distribution along the Iberian Peninsula (Serrano et al. 2013), a critical first step toward understanding the response of this species to climate change. We assessed the seasonal variation in growth and mortality of *O. patagonica* colonies over a ~4-yr period. Although long-term monitoring studies are labor intensive, they are fundamental to acquiring a thorough understanding of the factors that influence the life cycles of long-lived species such as corals, and they enable predictions of how such species might be affected by climate change. The effects of these abiotic factors were examined by transplanting coral colonies onto plates and excluding them from space competition with other organisms. The results of this study provide new insights into the seasonal and annual growth dynamics of *O. patagonica* at the northern limit of its distribution and contribute to an understanding of the biological characteristics that allow some zooxanthellate corals to thrive in temperate systems.

Materials and methods

Sample collection

In August 2008, the encrusting colonial coral *O. patagonica* was sampled at L'Ampolla breakwater (40°49'N, 0°43'E) in the north Balearic Sea (northwest Mediterranean Sea; Fig. 1) by scuba diving at depths of 2–5 m. Coral fragments (~3 cm in diameter) were collected with a hammer and chisel from widely separated (>3 m) and healthy (<10% colony partial mortality) colonies ($n = 29$) that ranged between 25 and 40 cm in maximum diameter. The coral specimens were immediately placed in large seawater containers and transported to the Experimental Aquarium Zone at the Institute of Marine Sciences in Barcelona (<4 h). Shortly after, the coral samples were carefully cleaned of epiphytes and sediment, and each was glued onto a methacrylate plate (15 × 15 cm) with an inert mastic compound. The coral plates were placed in a 225-L acclimation tank equipped with a circulation pump and running natural seawater. The inlet and outlet pipes remained open so that the acclimation tank functioned as a flow-through open system, and the corals were maintained in aquaria under controlled conditions until the perimeter of the entire colony was growing onto the plastic plates. During the ~3-month acclimation period in the aquaria, the natural seawater temperature (ST) was gradually decreased from 25 to 18 °C, and the light conditions were adjusted to 150 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ (12:12 light:dark

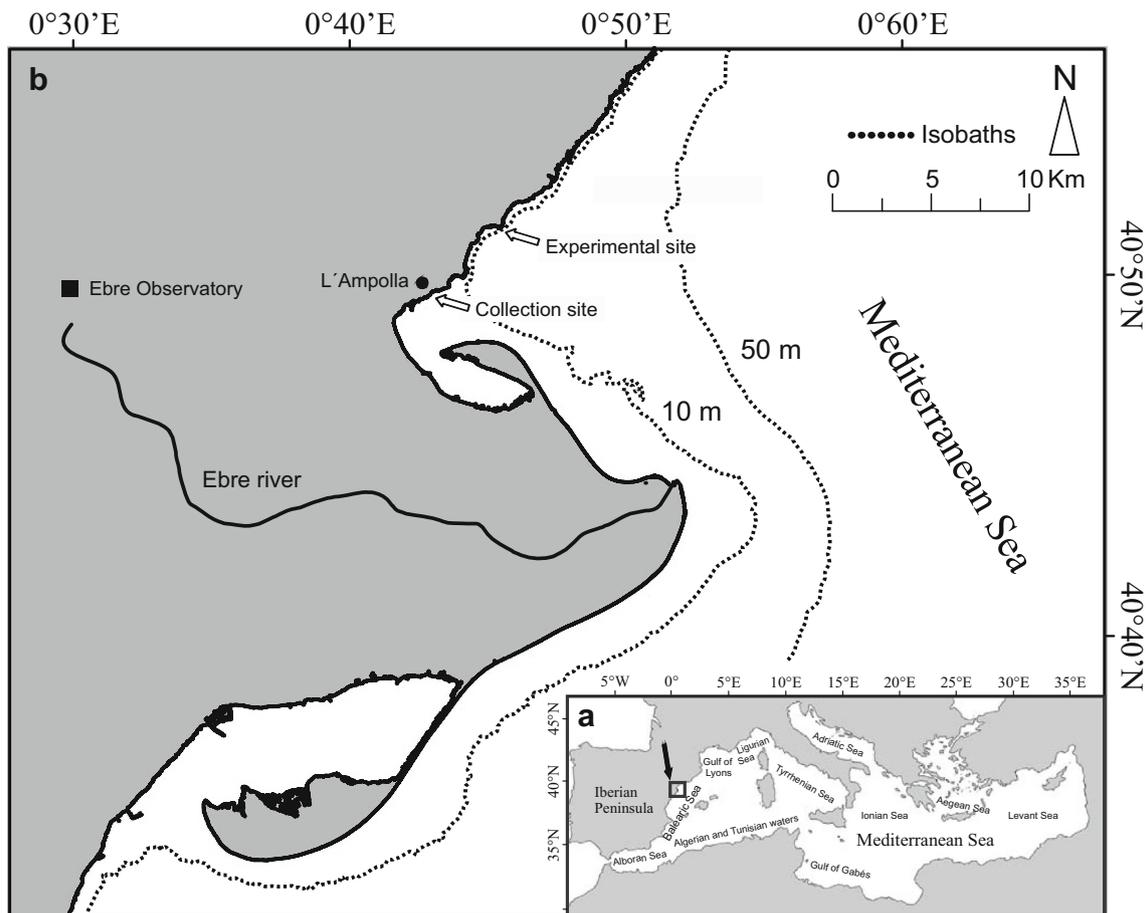


Fig. 1 **a** Map of the Mediterranean Sea showing the study area (L'Ampolla) in the north Balearic Sea. **b** Location of the collection site and the experimental site

photoperiod) to simulate late summer/early autumn conditions at the study area (Fig. 2).

Study site and experimental design

In November 2008, the 29 coral plates were transported back and randomly fixed onto a rocky reef located ~5 km north of the collection site (Fig. 1). The thermal and light regimes did not differ between the collection and experimental sites (Electronic Supplementary Material, ESM, Supplementary methods). Therefore, we will generally refer to the study area as L'Ampolla. In the study area, *O. patagonica* has a patchy distribution on shallow rocky reefs with locally abundant populations (Serrano et al. 2013). All coral plates were installed on slightly inclined surfaces (<45°) at depths of 4–5 m within a ~400-m² rocky area oriented parallel to the shore (80 × 5 m). The coral plates were monitored over a ~4-yr period (November 2008–August 2012, $n = 17$ sampling dates) at an average sampling interval of 87 ± 8 d (SE, $n = 16$). The benthic community surrounding the plates was dominated by algal

communities with a canopy height >2 cm. On each sampling date, the coral plates were cleaned of settling organisms (commonly turf algae <1 cm in height) to ensure that the corals were not exposed to algal competition, and any algae that settled on the coral skeleton were removed during the surveys.

Colony partial mortality and growth

On each sampling date, all coral plates were photographed in situ using a ruler as a size reference. Because colonies of *O. patagonica* have an encrusting morphology, the colony surface area from a planar view and the area experiencing partial mortality were measured from photographs using ImageJ software. Colony partial mortality was evaluated for each sampling date as the percentage of the colony area showing signs of mortality (i.e., denuded skeleton or coverage by sessile organisms). Partial mortality was further classified into three levels of severity: mild (<15%), moderate (15–85%) or severe (>85%). At the beginning of the study (November 2008), mean partial mortality was

$2 \pm 1\%$ (SE, $n = 29$). Colony partial mortality rates between sampling dates were calculated by dividing the change in partial mortality from one sampling date to the next by the number of days in the sampling interval expressed as a percentage of the colony area ($\% \text{ d}^{-1}$) and as $\text{mm}^2 \text{ d}^{-1}$. The rate of variation in planar area between sampling dates was calculated by dividing the accumulated colony surface area from one sampling date to the next by the number of days in the sampling interval ($\text{cm}^2 \text{ d}^{-1}$). The change in arithmetic mean diameter appears to be the most appropriate method to standardize linear growth rate data of coral colonies versus the initial size, particularly for encrusting species that tend to grow primarily in the horizontal plane and have circular areas (Pratchett et al. 2015), such as *O. patagonica* (Fig. 3). Then, to provide a size-independent measure of the linear extension rate (cm diameter d^{-1}), the planar area (A , cm^2) was translated to the arithmetic mean diameter (D , cm) using the formula $D = 2 * \sqrt{A/\pi}$. The mean annual linear extension rate was estimated for each study year by integrating the mean daily values of the different sampling intervals.

Environmental data

Global solar radiation (J m^{-2}) throughout the study period was recorded by the Ebre Observatory (located 50 m above sea level; Fig. 1). The daily photosynthetically active radiation (PAR, $\text{mol photons m}^{-2} \text{ d}^{-1}$) at a depth of 5 m was obtained from global irradiance and light attenuation coefficient data (ESM Supplementary methods). The mean annual and monthly PAR were determined based on the daily values averaged over the study period.

ST was recorded hourly throughout the study period using onset HOBO pendant temperature data loggers (UA-002–64) placed at a depth of 5 m, and the mean annual and monthly STs were determined based on the averaged daily values. We also calculated the number of days in which the mean daily ST was above and below different thresholds (≥ 20 to ≥ 28 °C and ≤ 19 to ≤ 11 °C, respectively).

Statistical analysis

The individual and combined relationships between coral performance (partial mortality and linear extension rates) and environmental parameters (PAR and ST) were assessed by multiple regression using the mean PAR and ST calculated for each sampling interval. Cross-correlation analyses were used to establish relationships between the environmental parameters (PAR and ST) over time and to determine the relationship between *O. patagonica* performance and ST. One-way repeated-measures ANOVA was used to test the inter-annual differences in mean partial

mortality and linear extension rates, combined with Tukey's test for post hoc comparison. A Chi-squared (χ^2) test was used to examine the inter-annual variability in ST thresholds. We used STATISTICA version 7.0 for the analyses, and the results are expressed as the mean \pm SE.

Results

Environmental parameters

The mean annual PAR at L'Ampolla (5 m depth) during the study period was 19.5 ± 0.7 $\text{mol photons m}^{-2} \text{ d}^{-1}$ (2009–2011, $n = 3$) and ranged between 18.3 and 20.8 $\text{mol photons m}^{-2} \text{ d}^{-1}$ (Fig. 2a). The light regime was characterized by marked seasonality, with monthly mean PARs ranging from 6.1 $\text{mol photons m}^{-2} \text{ d}^{-1}$ in December 2009 to 36.6 $\text{mol photons m}^{-2} \text{ d}^{-1}$ in July 2010 (Fig. 2a; daily

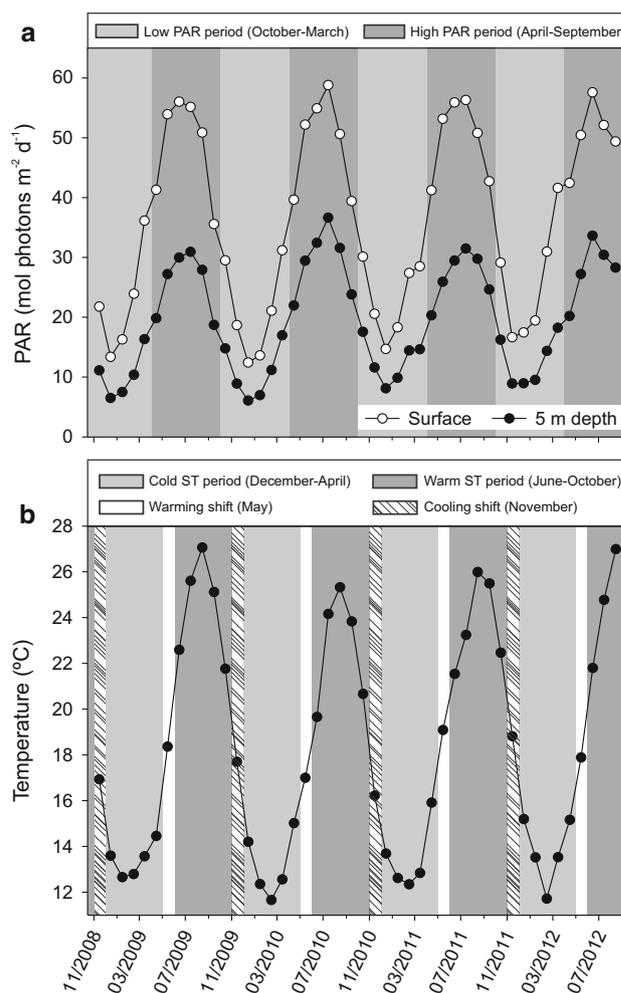


Fig. 2 **a** Monthly mean photosynthetically active radiation (PAR) at sea surface and 5 m depth at L'Ampolla. **b** Monthly mean seawater temperature (ST) at 5 m depth at L'Ampolla

mean PAR values are shown in ESM Fig. S1a). Two periods were distinguished based on the monthly mean PARs: (1) a high-radiation period from April to September (27.3 ± 1.0 mol photons $m^{-2} d^{-1}$, $n = 3$) and (2) a low-radiation period from October to March (12.1 ± 0.6 mol photons $m^{-2} d^{-1}$, $n = 3$; Fig. 2a).

The mean annual ST at L'Ampolla was 18.5 ± 0.4 °C (2009–2011, $n = 3$) and ranged between 17.7 and 18.9 °C (Fig. 2b). The thermal regime was characterized by marked seasonality with monthly mean STs ranging from 11.7 °C in February 2010 to 27.1 °C in August 2009 and a mean thermal amplitude of 13.9 ± 0.2 °C during the annual cycle. The minimum mean daily ST was observed in February 2010 (10.1 °C), and the maximum occurred in August 2009 (28.6 °C; ESM Fig. S1b). Based on the monthly mean STs, two periods were identified (each separated by a 1-month shift): (1) a cold period from December to April (13.5 ± 0.1 °C, $n = 4$) with a warming shift in May (18.1 ± 0.4 °C, $n = 4$) and (2) a warm period from June to October (23.6 ± 0.5 °C, $n = 3$) with a cooling shift in November (17.4 ± 0.6 °C, $n = 4$; Fig. 2b).

The PAR and thermal regimes exhibited similar seasonal trends but with a time delay (i.e., the maximum seasonal peaks in ST shifted to the right relative to the maximum peaks in PAR; Fig. 2). Based on the daily means, cross-correlation analysis revealed that the highest positive Pearson correlation coefficients were between the ST and the PAR measured 1–2 months earlier (the maximum correlation at -40 -d lag, $r = 0.79$; ESM Fig. S1c). The wave-like form of the cross-correlation plot, with peaks separated by ~ 6 months, reflected the seasonal nature of the changes in PAR and ST.

Annual cycle of coral partial mortality

The seasonal advent of partial mortality (i.e., tissue loss resulting in a denuded skeleton) and recovery in the *O. patagonica* colonies was the most predominant process and occurred each year throughout the four annual cycles examined at L'Ampolla (Fig. 3). The phenomenon of partial mortality began affecting small, unconnected parts of the coenosarc, exposing the denuded coenosteum in different (central and peripheral) but isolated parts of the colony (i.e., multifocal distribution; e.g., January in Fig. 3). In this first phase, partial mortality usually followed a progressive coalescence of the multifocal denuded skeleton that was conducive to the loss of nearly the entire coenosarc, but the remaining polyps remained healthy (alive and brown in color) and isolated within the calyx (e.g., April in Fig. 3). The phenomenon was rarely observed in the final phase, in which the isolated polyps disappeared from parts of the colony, leaving a completely denuded skeleton.

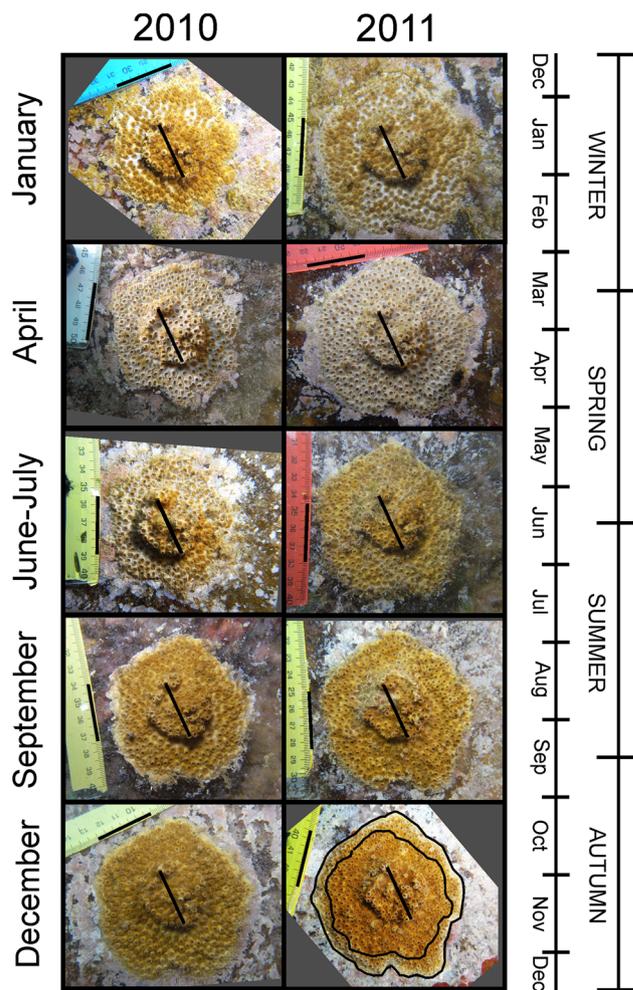


Fig. 3 Monitoring of a colony of *Oculina patagonica* from January 2010 to December 2011. Partial mortality occurred during winter and early spring, followed by recovery in late spring and linear extension during summer and autumn. The perimeter from January 2010 is superimposed on that from December 2011. Scale bars 3.40 cm

The first symptoms of denuded partial mortality were detected in December, and the symptoms increased until April of each year when the highest values were detected ($49 \pm 9\%$, 2009–2012, $n = 4$; Fig. 4a). The April peak in partial mortality resulted in the highest percentage of colonies with moderate and severe partial mortality ($>15\%$, $75 \pm 10\%$; ESM Fig. S2). The mean rate of partial mortality from December to April was $0.32 \pm 0.08\% d^{-1}$ ($n = 7$; Fig. 4b, c), which is equivalent to 10.0 ± 3.1 $mm^2 d^{-1}$. The colonies started to exhibit signs of recovery in May, when the tissue surrounding the denuded skeleton began to recover. The mean annual peak in the tissue regeneration rate from May to July was $-0.35 \pm 0.02\% d^{-1}$ (2009–2012, $n = 4$; Fig. 4b, c), which is equivalent to -10.3 ± 2.7 $mm^2 d^{-1}$. By July, the mean extent of partial mortality was reduced to $24 \pm 4\%$ of the April peak each year (2009–2012, $n = 4$; Fig. 4a).

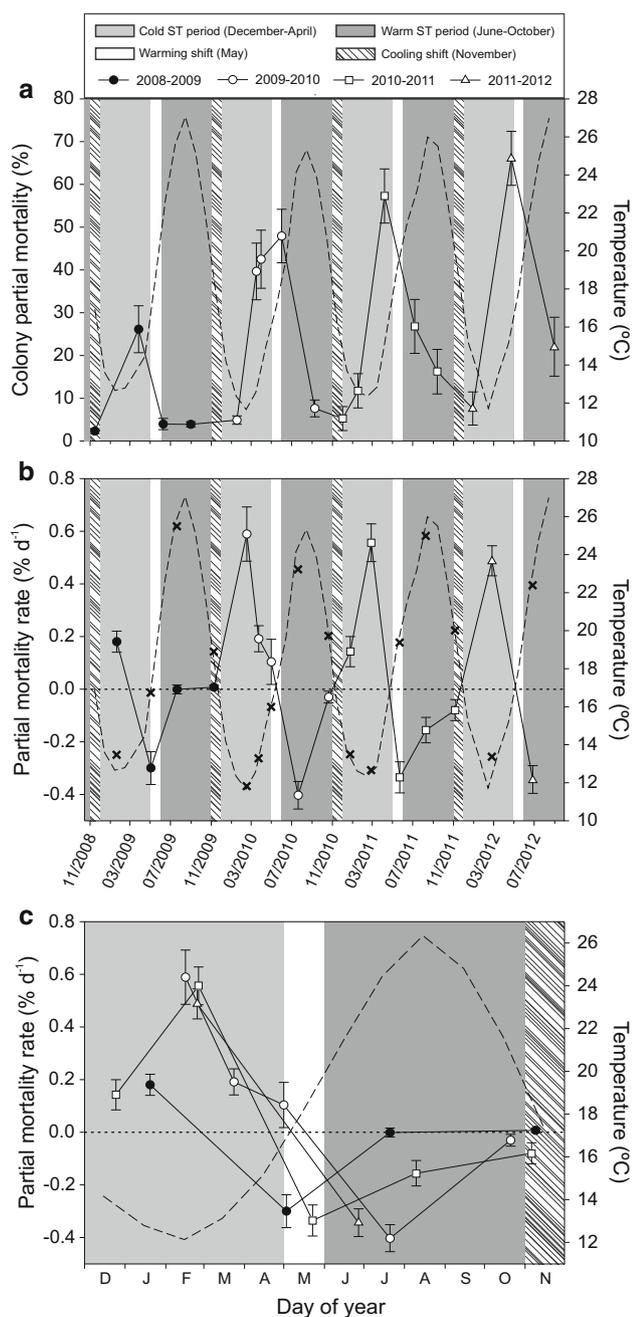


Fig. 4 Partial mortality of *Oculina patagonica* and seawater temperature (ST, dashed lines and crosses) at L'Ampolla. **a** Proportion of colony partial mortality on each sampling date ($n = 17$). Colony partial mortality rate **b** over the study period and **c** on an ordinal date for each sampling interval ($n = 16$). Values are mean \pm SE

Some overgrowth of the denuded coral skeleton by filamentous and foliose algae and deposition of sediment particles occurred during the mortality and recovery periods (Fig. 3), so after this rapid recovery phase, tissue regeneration of the remaining areas of partial mortality continued at a slower pace from August to November ($-0.05 \pm 0.03\% \text{ d}^{-1}$, $n = 5$; Fig. 4b, c). Partial mortality

rate values from this slow recovery phase were excluded in the regression analysis with environmental parameters, because lesion regeneration was already completed or affected by algae overgrowth. Overall, the regeneration process led to the lowest mean extent of partial mortality (4–8%, 2009–2011, $n = 3$) and the lowest percentage of colonies with mild partial mortality ($<15\%$, $96 \pm 2\%$) in November; these values remained low until the initiation of the subsequent partial mortality event in December (Fig. 4a; ESM Fig. S2). The occurrence of a recently denuded skeleton and/or visually apparent bleaching was not observed from May to November in any of the study years (Figs. 3, 4).

Annual cycle of coral growth

The mean size of the *O. patagonica* colonies increased from $10 \pm 1 \text{ cm}^2$ in November 2008 to $60 \pm 12 \text{ cm}^2$ in August 2012 at a mean linear extension rate of $13.27 \pm 2.95 \text{ cm}^2 \cdot \text{yr}^{-1}$ (Fig. 5a), which is equivalent to a mean increase in colony diameter of $1.27 \pm 0.19 \text{ cm yr}^{-1}$. The maximum linear extension rate of an individual colony was $2.47 \text{ cm diameter yr}^{-1}$. Coral growth exhibited a marked pattern of seasonal variation that repeatedly occurred during the ~ 4 -yr study period (Fig. 5). The mean linear extension rate reached a minimum during the 6 months from December to May ($0.0016 \pm 0.0007 \text{ cm diameter d}^{-1}$, $n = 9$; Fig. 5b, c), which coincided with a decrease in living colony size (i.e., the extent of the coral tissue, which is complementary to the proportion of partial mortality) between December and April (Fig. 5a). Despite this decline in live tissue, coral skeleton growth resumed in June following the rapid tissue regeneration that started in May (Fig. 5a). The mean linear extension rate during the ~ 6 months from June to November (growing period) was $0.0058 \pm 0.0007 \text{ cm diameter d}^{-1}$ ($n = 7$; Fig. 5b, c).

Coral mortality and growth in relation to environmental variables

The rate of *O. patagonica* partial mortality was negatively related to ST ($p = 0.0290$) but did not exhibit a significant relationship with PAR ($p = 0.64$) (multiple regression: $F_{2,8} = 15.79$, $r^2 = 0.80$, $p = 0.0017$, $n = 11$; values from the slow recovery phase were excluded). The proportion of colony partial mortality and ST displayed opposite trends but with a time delay (i.e., the maximum seasonal peaks in partial mortality shifted right relative to the minimum peaks in ST; Fig. 4a), and cross-correlation analysis indicated that ST and the proportion of partial mortality were negatively correlated and that the highest Pearson correlation coefficient was associated with a lag of -78 d ($r = -0.68$; ESM Fig. S3a). These results indicated that

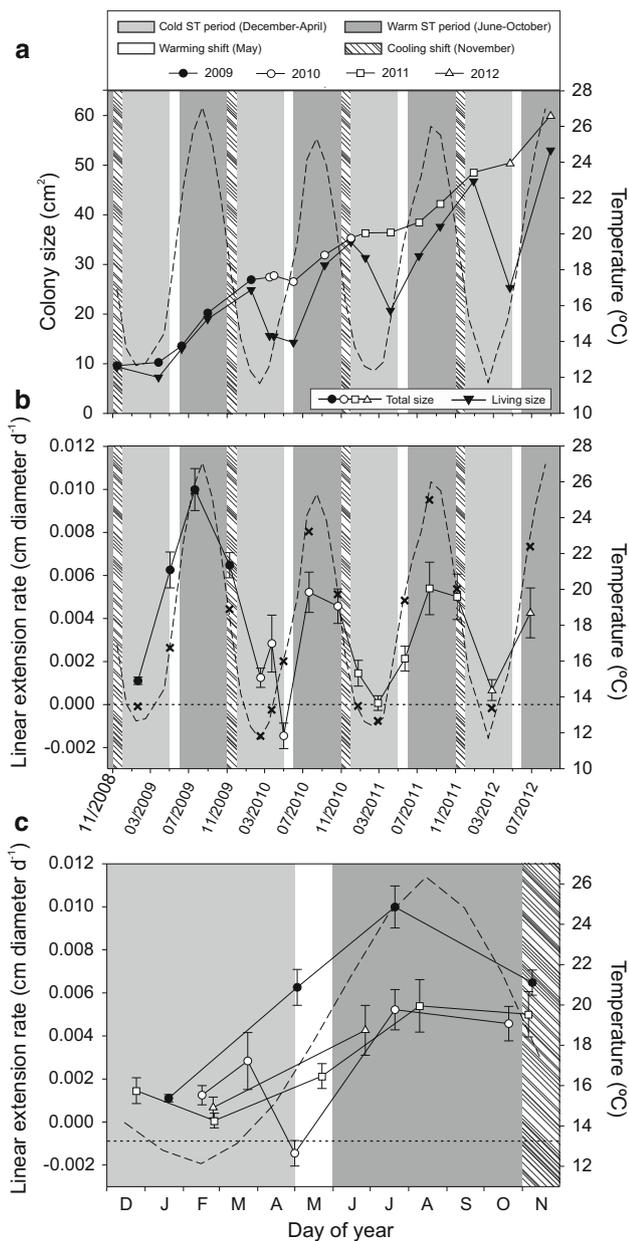


Fig. 5 Linear extension of *Oculina patagonica* and seawater temperature (ST, dashed lines and crosses) at L'Ampolla. **a** Total and living colony size on each sampling date ($n = 17$). Colony linear extension rate **b** over the study period and **c** on an ordinal date for each sampling interval ($n = 16$). Values are mean \pm SE

the pattern of increased partial mortality was preceded by the minimum ST values 2–3 months earlier (i.e., the April peak in partial mortality was related to the lowest ST in January–February; Fig. 4a). The rate of partial mortality and ST exhibited opposite trends with no time delay (i.e., the maximum seasonal peaks in partial mortality rate coincided with the minimum peaks in ST; Fig. 4b; ESM Fig. S3b), and there was a negative relationship between the two variables ($r^2 = 0.79$, $p = 0.0002$, $n = 11$),

indicating that the positive mortality rate values might be related to the <14 °C threshold that commonly occurred from December to April (Fig. 6a). These results suggest that cold STs are an important factor influencing *O. patagonica* partial mortality in the study area.

The linear extension rate of *O. patagonica* colonies was positively related to ST ($p = 0.0008$) but did not have a significant relationship with PAR ($p = 0.10$) (multiple regression: $F_{2,13} = 12.63$, $r^2 = 0.66$, $p = 0.0009$). The linear extension rate and ST exhibited similar trends with no time delay (i.e., the maximum peaks in the linear extension rate coincided with the maximum peaks in ST; Fig. 5b, ESM Fig. S3c), and there was a positive relationship between the two variables, with higher linear

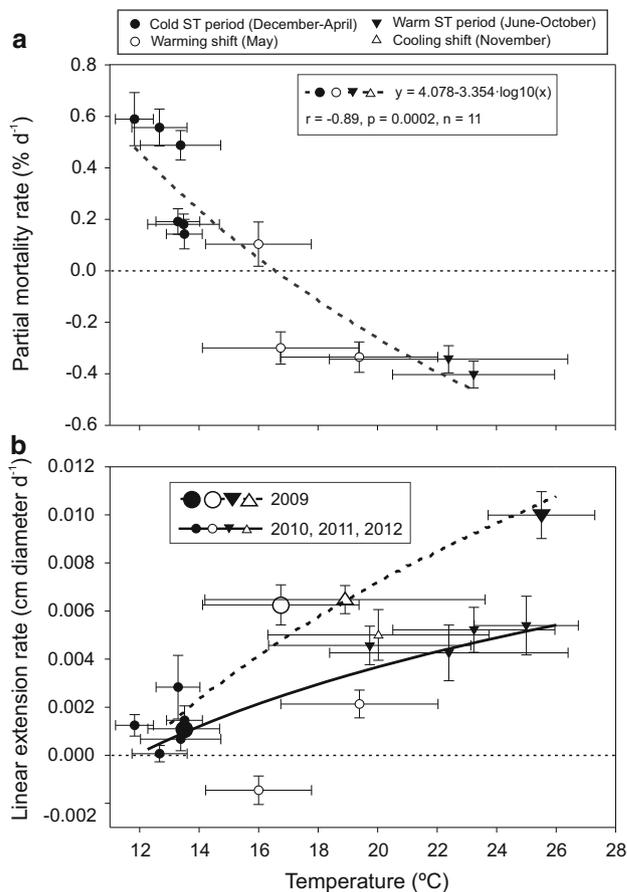


Fig. 6 Pearson product-moment correlations between *Oculina patagonica* performance and seawater temperature (ST) for each sampling interval. **a** Colony partial mortality rate. Values from the late warm ST and cooling shift periods were not included because lesion regeneration was already completed or was strongly affected by algal overgrowth. **b** Colony linear extension rate. Values are mean \pm SE for coral performance and mean \pm SD for ST. Two linear extension patterns depending on the severity of the annual event of denuded partial mortality are depicted: the pattern observed in 2009 (dashed line) and that observed in 2010, 2011 and 2012 (solid line). Data were fitted to logarithmic functions

extension rates related to the >16 °C threshold that commonly occurred from May to November (Fig. 6b). These results suggest that warm STs are an important factor increasing *O. patagonica* linear extension in the study area.

These results demonstrate that ST is related to both partial mortality and linear extension of the species. Consequently, a cross-correlation analysis was conducted to examine the potential trade-offs between the two processes. The highest negative correlation between colony partial mortality and linear extension rates occurred at a -48 -d lag (ESM Fig. S3d), indicating that the high partial mortality rate from the previous 1–2 months negatively affected linear extension of the colonies.

Inter-annual variability in coral mortality and growth in relation to ST

The yearly peak in mean denuded partial mortality observed in April was always associated with similarly low values of partial mortality due to overgrowth in November (2–8%, 2008–2011), despite the fact that the April peak in 2009 (26%) was approximately half as large as those in 2010, 2011 and 2012 (48, 57 and 66%, respectively; Fig. 4a). Similarly, the percentage of colonies suffering from moderate to severe partial mortality ($>15\%$) in April 2009 (45%) was 45–51% lower than those in 2010, 2011 and 2012 (83, 82 and 91%, respectively; ESM Fig. S2). The annual peak in the partial mortality rate was also lower in 2009 ($0.18 \pm 0.04\%$ d^{-1}) than in 2010, 2011 and 2012 ($0.54 \pm 0.03\%$ d^{-1} ; one-way repeated-measures ANOVA, $F_{3,84} = 10.62$, $p < 0.0001$). The number of days that ST was ≤ 19 to ≤ 13 °C did not vary significantly among the cold periods studied (2008–2009 to 2011–2012, $n = 4$; χ^2 , $p > 0.05$). However, the mean number of days that ST was ≤ 12 °C was 20 ± 4 d in 2009–2010, 2010–2011 and 2011–2012, a threshold that was not reached during the cold period of 2008–2009 (χ^2 , $p < 0.05$; ESM Table S1). These results indicate that the occurrence of partial mortality was lower during the less severe cold period of 2008–2009 than during the other three more severe cold periods.

Generally, colony partial mortality occurred during the cold period (December–April) and was followed by tissue regeneration and linear extension. The annual peak in the regeneration rate was similar among the studied years ($0.35 \pm 0.02\%$ d^{-1} , 2009–2012; one-way repeated-measures ANOVA, $F_{3,84} = 0.84$, $p > 0.05$). Hence, the time required for nearly complete regeneration of the tissue (i.e., when the lowest partial mortality values, of 4–8%, were first reached) appeared to be related to the severity of the annual partial mortality episodes (i.e., the time required for regeneration was longer in years showing high denuded partial mortality in April), which contributed to the inter-

annual variation of the duration of the negative effect of partial mortality on the linear extension rate. As a result, the lower incidence of partial mortality in 2009 resulted in complete regeneration by June, but as the incidence of partial mortality increased in the following years (2010 and 2011), the regeneration time was longer (September and December, respectively; Fig. 4). This pattern is consistent with the higher linear extension rate observed in May 2009 (0.0063 ± 0.0008 cm diameter d^{-1}) compared to May 2010 and 2011 (0.0003 ± 0.0018 cm diameter d^{-1} , $n = 2$) and the twofold higher peak in the linear extension rate in July–August in 2009 (0.0100 ± 0.0010 cm diameter d^{-1}) compared with 2010 and 2011 (0.0053 ± 0.0001 cm diameter d^{-1} , $n = 2$; Fig. 5b, c). The mean annual linear extension rate of *O. patagonica* was twofold higher in 2009 (1.91 ± 0.25 cm diameter yr^{-1}) than in 2010 and 2011 (0.86 ± 0.22 and 1.03 ± 0.27 cm diameter yr^{-1} , respectively; one-way repeated-measures ANOVA, $F_{2,56} = 19.36$, $p < 0.0001$). These results indicate that ST may be exerting a direct effect on the growth dynamics of the species as well as an indirect effect through partial mortality. The number of days in which the ST was ≥ 20 to ≥ 24 °C did not vary significantly among the warm periods during the study (2009–2011, $n = 3$; χ^2 , $p > 0.05$), whereas the ≥ 25 to ≥ 27 °C thresholds in the 2009 warm period were higher than those in 2010 and 2011 (χ^2 , $p < 0.05$; ESM Table S1). For instance, the number of days in which the ST was ≥ 25 °C was 25 and 60% higher in 2009 than in 2010 and 2011, respectively. However, recently denuded skeletons and/or visually apparent bleaching were not observed during the summer and fall in any of the study years.

Discussion

Pattern of partial mortality and tissue regeneration

The yearly occurrence of denuded partial mortality in the *O. patagonica* colonies in winter (December–April) was the most distinctive process observed during the study. The denuded skeleton resulted from progressive tissue loss, which caused a loss of coloniality (i.e., dissociation of polyps from their connective coenosarc). The presence of colonies with brown, isolated polyps within the calyx distributed over a white coenosteum was a sign of the observed partial mortality, which we usually refer to as a Dalmatian mortality pattern (Fig. 7). The usual persistence of isolated brown polyps on the colonies distinguished the observed pattern of mortality from the pattern of tissue loss documented at the end of summer in colonies from Albissola, Monaco and Portman; although these colonies also exhibit areas of isolated brown polyps, they commonly

Fig. 7 Dalmatian mortality pattern in *Oculina patagonica*: **a** general view and **b** close-up view



display patches of completely denuded skeleton (i.e., the coenosteum and calyx; Rodolfo-Metalpa et al. 2008, 2014) that were rarely observed in our study. The process of denuded partial mortality that affected the colonies at our study site during winter resembled that observed in February 2006 in Monaco (Rodolfo-Metalpa et al. 2008). Colonies responded a similar way to reduced pH conditions in aquaria (Kvitt et al. 2015). The process observed in February 2006 did not appear to impact the dynamics of the species because the colonies completely regenerated by May, and the process was only observed during one year (Rodolfo-Metalpa et al. 2008). The dissociation of polyps from the coenosarc at low pH appears to be an essential mechanism mediated by apoptosis by which the species withstands acidification (Kvitt et al. 2015). Although addressing the mechanisms of tissue loss was outside the scope of this study, we did not observe any evidence of tissue necrosis that might have indicated that apoptosis was involved. As observed in other zooxanthellate coral species, the symptoms of the responses to different types of stress can be similar (e.g., Gates et al. 1992; Roth et al. 2012).

Lesion recovery is fundamental to coral survival, and during this 4-yr study, the *O. patagonica* colonies began to recover shortly (a few days) after the peak of partial mortality in April and were nearly fully recovered (down to 4–8%) from the yearly, recurrent partial mortality episodes. Over the ~4-yr study, the average regeneration rate was $10.3 \text{ mm}^2 \text{ d}^{-1}$, a rate that occurred in the absence of competition with other organisms (Fine and Loya 2003). This rate was 2.5-fold faster than the recovery rate of unbleached colonies documented in the Levant Sea ($4.09 \text{ mm}^2 \text{ d}^{-1}$; Fine et al. 2002). Fine et al. (2002) observed that lesion regeneration in unbleached *O. patagonica* colonies resulted in intra-colonial translocation of resources toward recuperating lesions 4–5 cm away,

whereas bleached colonies exhibited no lesion regeneration. These observations are consistent with tissue regeneration as an energetically costly process, as has been documented in other species (Oren et al. 2001). Thus, the more rapid regeneration rate at L'Ampolla might be attributable to the timing of the recovery of the lesions during the favorable growing season, whereas in the Levant Sea, recovery was examined during the unfavorable bleaching season (Fine et al. 2001, 2002). The denuded partial mortality of *O. patagonica*, which usually left polyps alive but isolated within the calyx, represents a characteristic pattern that may favor regeneration because (1) it increases the relationship between the wound perimeter and lesion size, which has been shown to positively correlate with the regeneration rate (Meesters et al. 1997), and (2) it rids the colony of energetically costly processes, such as calcification, and tissues (Kvitt et al. 2015). Moreover, the small polyp size and encrusting morphology of *O. patagonica* colonies may help to maintain mass transfer, which also favors lesion regeneration (e.g., van Woesik et al. 2012). The immediate initiation of regeneration at the end of the partial mortality event points to the prioritization of this life-preserving process that helps to reduce the detrimental effects of the settlement of algae and other organisms on the skeleton and the disruption of the physiological integration of the colony (Oren et al. 2001).

Potential causes of the observed pattern of partial mortality and growth

The complex interaction between ST and light on zooxanthellate corals (Lesser 1996) suggests that both factors are relevant to the seasonal dynamics of colony partial mortality in *O. patagonica*. However, although the loss of tissue in the coenosarc but not in the polyps might suggest

a light effect, two sources of evidence suggest a secondary role of light in the observed pattern of partial mortality. First, the process of partial mortality started in December, the period with the lowest PAR levels. Second, the annual pattern of partial mortality exhibited a negative relationship with ST but not PAR.

The linear extension of *O. patagonica* colonies was positively related to ST but not to PAR, which also indicates that light might play a secondary role in the growth pattern of *O. patagonica*, in accordance with the results of previous studies (Shenkar et al. 2005; Rodolfo-Metalpa et al. 2008; Rubio-Portillo et al. 2014b). This finding is also consistent with the lack of a negative effect of turbidity on colony growth observed by Rubio-Portillo et al. (2014b), who observed that growth of the colonies did not differ between a harbor and a marine protected area, despite the much greater sedimentation in the harbor and the consequent reduction in light due to turbidity. This observation supports the hypothesis that *O. patagonica* may have a high capacity for photoacclimation to distinct and variable light regimes that may allow it to function as a facultative zooxanthellate and thrive in a wide range of light conditions, as has been observed (Fine et al. 2001; Rodolfo-Metalpa et al. 2014). Such characteristics would be consistent with the secondary role that light usually plays in promoting coral growth at high latitudes (Miller 1998; Rodolfo-Metalpa et al. 2008; Dimond et al. 2013). The absence of bleaching and/or mortality in the study area in summer might be related to the relatively low PAR levels caused by river runoff, which has also been suggested to contribute to the lack of partial mortality in response to warming in the laboratory (Rodolfo-Metalpa et al. 2014).

During the four annual cycles that were examined, the partial mortality episodes at L'Ampolla occurred during the cold periods, and thus we estimated the extent of exposure of this coral species to low ST based on data from this study and previous field studies to examine whether the intensity of the partial mortality episodes was related to the severity of the cold ST period. During the warmest winter at L'Ampolla, 2008–2009 (63 d \leq 13 °C, 0 d \leq 12 °C; ESM Table S1), the peak in partial mortality (26%) was similar to that reported during the winter of 2005–2006 in Monaco (5–20%) under similarly cold ST conditions (66 d \leq 13 °C, 0 d \leq 12 °C; Rodolfo-Metalpa et al. 2008). By contrast, the higher incidence of partial mortality (48–66%) during the more severe cold ST periods (2009–2010 to 2011–2012) at L'Ampolla could be related to exposure to the \leq 12 °C threshold (15–29 d; ESM Table S1), suggesting that years with severely cold ST periods increased partial mortality in *O. patagonica*. The analysis of published data is consistent with this hypothesis because coral populations in the mid-Balearic Sea did not suffer from partial mortality and/or visually apparent

bleaching during the winter of 2010–2011 (0 d \leq 13 °C; Rubio-Portillo et al. 2014b) nor during the examined winters since 1993 in the Levant Sea (0 d \leq 16 °C; e.g., Fine et al. 2001; Shenkar et al. 2005, 2006). Thus, the degree of exposure to cold ST appears to be related to the occurrence and severity of partial mortality events. However, although the cold thermal regimes at L'Ampolla were similar between 2010 and 2012, our results showed that the yearly peak in *O. patagonica* partial mortality gradually increased during this time period (Fig. 4a; ESM Table S1). As observed during consecutive extreme summers in *Porites astreoides* (Schoepf et al. 2015), we hypothesize that the cumulative impact of consecutive winter events of partial mortality may have affected the physiological status (energy budget) of the colonies, thus diminishing their recovery capacity.

The recurrent and severe partial mortality of the colonies in winter indicates that cold ST may be exerting both a direct effect on the linear extension dynamics of the species and an indirect effect via partial mortality, as the growth of the colonies did not resume until the colonies recovered from their lesions. Such direct and indirect effects are consistent with (1) the lower incidence of partial mortality during the warmest first winter period at L'Ampolla (2008–2009), which reduced the time needed for complete tissue regeneration, and (2) the twofold higher linear extension detected in 2009 compared to 2010 and 2011. Our interpretation is that the high linear extension observed in summer 2009 was not an isolated estimate that could be considered an outlier because compared to the other years, linear extension in that year was also higher in spring and fall. Although the colonies in 2009 were exposed to 27 °C during summer, the linear extension in fall suggested no detrimental effect on the colonies (probably due to the low PAR levels, see above). The lack of a detrimental effect may be related to the lower impact of partial mortality in winter 2008–2009, which permitted rapid recovery and an earlier onset of the linear extension period (Figs. 4, 5). These results suggest the occurrence of two linear extension patterns depending on the severity of the annual event of denuded partial mortality: the pattern observed in 2009, i.e., an increase with ST up to \sim 26 °C, and that observed in the other years, i.e., an increase with ST up to \sim 20 °C and then a plateau, which may be related to the cost of the regeneration process (Fig. 6b). Thus, cold STs may be playing an important role in constraining the growth dynamics of *O. patagonica* at the northern limit of its distribution, in contrast to the dynamics documented in the Levant Sea, where growth occurs during the cold period (16–26 °C, November–May) and bleaching recurrently affects the colonies in summer ($>$ 26–32 °C, June–October; Fine et al. 2002; Shenkar et al. 2005). The *O. patagonica* linear extension rate at L'Ampolla during the study period

(1.27 cm in diameter yr^{-1}) was 69–112% higher than those in natural populations from the Levant Sea (0.60–0.75 cm in diameter yr^{-1} ; Fine et al. 2001), suggesting that the negative effects of high ST stress occurring at the Levant Sea are more harmful than the cold ST stress occurring at the north Balearic Sea. This conclusion is consistent with previous studies documenting the effect of cold STs on corals (Gates et al. 1992; Saxby et al. 2003; Hoegh-Guldberg et al. 2005; Colella et al. 2012) and the differential effect of low- and high-ST stress on *Acropora yongei* (Roth et al. 2012). However, the detrimental effect of competition on scleractinian corals (e.g., Fine and Loya 2003), which may diminish coral linear extension in natural populations, was excluded in our study.

Our results also indicate a trade-off between regeneration and linear extension that is consistent with the priority of energy allocation to recovery rather than to other biological processes. This trade-off is in agreement with previous studies from the Levant Sea, where bleaching and mortality events in *O. patagonica* during summer result in a low-energy state of the colonies that is responsible for the cessation of resource translocation and a reduction in gametogenesis and colony growth (Fine et al. 2001, 2002; Armoza-Zvuloni et al. 2011). The recurrent mortality events at L'Ampolla peaked in April and overlapped temporally with the gametogenesis of *O. patagonica* (March–September; Fine et al. 2001), suggesting that this energy shortage might also impair species reproduction and population growth.

The results of this study have demonstrated that *O. patagonica* at this northern limit of its distribution can survive and grow under wide seasonal variation in ST (monthly mean ranging from 11.7 to 27.1 °C). The coral exhibits a strong seasonal cycle that includes partial mortality and cessation of linear extension during winter (December to April), tissue regeneration starting in late spring (May) and linear extension during summer and fall (June to November), a cycle that appears to be primarily driven by ST. However, our data provide only correlational evidence, and causation of the observed pattern of denuded skeleton cannot be determined without additional experimental work. Partial mortality affected approximately half of the surface area and most of the colonies (~70%) and occurred repeatedly in all four years studied, indicating that partial mortality is a crucial process affecting the dynamics of the species, the relevance of which is comparable to that of the recurrence of summer bleaching in the Levant Sea (e.g., Fine et al. 2001).

Due to concerns regarding the threat of global warming to tropical coral reefs, understanding the resilience of zooxanthellate corals at high latitudes is crucial for predicting shifts in coral communities and their responses to climate change. The results of our experimental exclusion

from competition indicate that the recurrent and severe pattern of denuded skeletons results from unfavorable environmental conditions that may constrain the population dynamics of the coral and affect the poleward expansion of the species. However, *O. patagonica* can withstand harsh environments because of its high regeneration capacity, which is among the highest reported for a coral species, particularly at high latitudes (Henry and Hart 2005). The stress response of polyp dissociation from the coenosarc appears to be a crucial pattern favoring the rapid regeneration of the species. The combination of the dissociation stress response and the rapid regeneration of the species appears to be a decisive biological characteristic that enables the species to withstand unfavorable environmental conditions affecting zooxanthellate coral species at high latitudes.

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References

- Ainsworth TD, Fine M, Roff G, Hoegh-Guldberg O (2008) Bacteria are not the primary cause of bleaching in the Mediterranean coral *Oculina patagonica*. *ISME J* 2:67–73
- Armoza-Zvuloni R, Segal R, Kramarsky-Winter E, Loya Y (2011) Repeated bleaching events may result in high tolerance and notable gametogenesis in stony corals: *Oculina patagonica* as a model. *Mar Ecol Prog Ser* 426:149–159
- Colella MA, Ruzicka RR, Kidney JA, Morrison JM, Brinkhuis VB (2012) Cold-water event of January 2010 results in catastrophic benthic mortality on patch reefs in the Florida Keys. *Coral Reefs* 31:621–632
- Coma R, Serrano E, Linares C, Ribes M, Díaz D, Ballesteros E (2011) Sea urchins predation facilitates coral invasion in a marine reserve. *PLoS One* 6:e22017
- Dimond JL, Kerwin AH, Rotjan R, Sharp K, Stewart FJ, Thornhill DJ (2013) A simple temperature-based model predicts the upper latitudinal limit of the temperate coral *Astrangia poculata*. *Coral Reefs* 32:401–409
- Fine M, Loya Y (2003) Alternate coral–bryozoan competitive superiority during coral bleaching. *Mar Biol* 142:989–996
- Fine M, Zibrowius H, Loya Y (2001) *Oculina patagonica*: a non-lessepsian scleractinian coral invading the Mediterranean Sea. *Mar Biol* 138:1195–1203
- Fine M, Oren U, Loya Y (2002) Bleaching effect on regeneration and resource translocation in the coral *Oculina patagonica*. *Mar Ecol Prog Ser* 234:119–125
- Freeman LA (2015) Robust performance of marginal Pacific coral reef habitats in future climate scenarios. *PLoS One* 10:e0128875
- Frieler K, Meinshausen M, Golly A, Mengel M, Lebek K, Donner SD, Hoegh-Guldberg O (2013) Limiting global warming to 2 °C is unlikely to save most coral reefs. *Nat Clim Chang* 3:165–170

- Gates RD, Baghdasarian G, Muscatine L (1992) Temperature stress causes host cell detachment in symbiotic cnidarians: implications for coral bleaching. *Biol Bull* 182:324–332
- Henry LA, Hart M (2005) Regeneration from injury and resource allocation in sponges and corals—a review. *Int Rev Hydrobiol* 90:125–158
- Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. *Mar Freshw Res* 50:839–866
- Hoegh-Guldberg O (2012) The adaptation of coral reefs to climate change: is the Red Queen being outpaced? *Sci Mar* 76:403–408
- Hoegh-Guldberg O, Bruno JF (2010) The impact of climate change on the world's marine ecosystems. *Science* 328:1523–1528
- Hoegh-Guldberg O, Fine M, Skirving W, Johnstone R, Dove S, Strong A (2005) Coral bleaching following wintry weather. *Limnol Oceanogr* 50:265–271
- Hughes TP, Graham NAJ, Jackson JBC, Mumby PJ, Steneck RS (2010) Rising to the challenge of sustaining coral reef resilience. *Trends Ecol Evol* 25:633–642
- Kleypas JA, McManus JW, Meñez LAB (1999) Environmental limits to coral reef development: where do we draw the line? *Am Zool* 39:146–159
- Kvitt H, Kramarsky-Winter E, Maor-Landaw K, Zandbank K, Kushmaro A, Rosenfeld H, Fine M, Tchernov D (2015) Breakdown of coral colonial form under reduced pH conditions is initiated in polyps and mediated through apoptosis. *Proc Natl Acad Sci USA* 112:2082–2086
- Lesser MP (1996) Elevated temperatures and ultraviolet radiation cause oxidative stress and inhibit photosynthesis in symbiotic dinoflagellates. *Limnol Oceanogr* 41:271–283
- Leydet KP, Hellberg ME (2015) The invasive coral *Oculina patagonica* has not been recently introduced to the Mediterranean from the western Atlantic. *BMC Evol Biol* 15:79
- Meesters EH, Pauchli W, Bak RPM (1997) Predicting regeneration of physical damage on a reef-building coral by regeneration capacity and lesion shape. *Mar Ecol Prog Ser* 146:91–99
- Miller MW (1998) Coral/seaweed competition and the control of reef community structure within and between latitudes. *Oceanogr Mar Biol Annu Rev* 36:65–96
- Muir PR, Wallace CC, Done T, Aguirre JD (2015) Limited scope for latitudinal extension of reef corals. *Science* 348:1135–1138
- Oren U, Benayahu Y, Lubinevsky H, Loya Y (2001) Colony integration during regeneration in the stony coral *Favia fava*. *Ecology* 82:802–813
- Pandolfi JM, Connolly SR, Marshall DJ, Cohen AL (2011) Projecting coral reef futures under global warming and ocean acidification. *Science* 333:418–422
- Pratchett MS, Anderson KD, Hoogenboom MO, Widman E, Baird AH, Pandolfi JM, Edmunds PJ, Lough JM (2015) Spatial, temporal and taxonomic variation in coral growth—implications for the structure and function of coral reef ecosystems. *Oceanogr Mar Biol Annu Rev* 53:215–295
- Rodolfo-Metalpa R, Reynaud S, Allemand D, Ferrier-Pagès C (2008) Temporal and depth responses of two temperate corals, *Cladocora caespitosa* and *Oculina patagonica*, from the north Mediterranean Sea. *Mar Ecol Prog Ser* 369:103–114
- Rodolfo-Metalpa R, Hoogenboom MO, Rottier C, Ramos-Esplá A, Baker AC, Fine M, Ferrier-Pagès C (2014) Thermally tolerant corals have limited capacity to acclimatize to future warming. *Glob Chang Biol* 20:3036–3049
- Roth MS, Goericke R, Deheyn DD (2012) Cold induces acute stress but heat is ultimately more deleterious for the reef-building coral *Acropora yongei*. *Sci Rep* 2:240
- Rubio-Portillo E, Vázquez-Luis M, Izquierdo-Muñoz A, Ramos-Esplá AA (2014a) Distribution patterns of alien coral *Oculina patagonica* De Angelis D'Ossat, 1908 in western Mediterranean Sea. *J Sea Res* 85:372–378
- Rubio-Portillo E, Vázquez-Luis M, Valle C, Izquierdo-Muñoz A, Ramos-Esplá AA (2014b) Growth and bleaching of the coral *Oculina patagonica* under different environmental conditions in the western Mediterranean Sea. *Mar Biol* 161:2333–2343
- Salomidi M, Katsanevakis S, Issaris Y, Tsiamis K, Katsiaras N (2013) Anthropogenic disturbance of coastal habitats promotes the spread of the introduced scleractinian coral *Oculina patagonica* in the Mediterranean Sea. *Biol Invasions* 15:1961–1971
- Saxby T, Dennison WC, Hoegh-Guldberg O (2003) Photosynthetic responses of the coral *Montipora digitata* to cold temperature stress. *Mar Ecol Prog Ser* 248:85–97
- Schoepf V, Grotoli AG, Levas SJ, Aschaffenburg MD, Baumann JH, Matsui Y, Warner ME (2015) Annual coral bleaching and the long-term recovery capacity of coral. *Proc R Soc Lond B Biol Sci* 282:20151887
- Serrano E, Coma R, Ribes M (2012) A phase shift from macroalgal to coral dominance in the Mediterranean. *Coral Reefs* 31:1199
- Serrano E, Coma R, Ribes M, Weitzmann B, García M, Ballesteros E (2013) Rapid northward spread of a zooxanthellate coral enhanced by artificial structures and sea warming in the western Mediterranean. *PLoS One* 8:e52739
- Shenkar N, Fine M, Loya Y (2005) Size matters: bleaching dynamics of the coral *Oculina patagonica*. *Mar Ecol Prog Ser* 294:181–188
- Shenkar N, Fine M, Kramarsky-Winter E, Loya Y (2006) Population dynamics of zooxanthellae during a bacterial bleaching event. *Coral Reefs* 25:223–227
- Takao S, Yamano H, Sugihara K, Kumagai NH, Fujii M, Yamanaka Y (2015) An improved estimation of the poleward expansion of coral habitats based on the inter-annual variation of sea surface temperatures. *Coral Reefs* 34:1125–1137
- van Woesik R, Irikawa A, Anzai R, Nakamura T (2012) Effects of coral colony morphologies on mass transfer and susceptibility to thermal stress. *Coral Reefs* 31:633–639