

Inferred calcification rate of a temperate azooxanthellate caryophylliid coral along a wide latitudinal gradient

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Abstract Correlations between environmental parameters (depth temperature and solar radiation) and growth parameters (bulk skeletal density, linear extension rate and net calcification rate) of the solitary azooxanthellate coral, *Caryophyllia inornata*, were investigated along an 8° latitudinal gradient on the western Italian coasts. Net calcification rate correlated positively with both bulk skeletal density and linear extension rate, showing that *C. inornata* allocates calcification resources evenly to thickening the skeleton and increasing linear growth. Overall, the three growth parameters did not follow gradients in the two environmental parameters, showing a different trend compared to most studies on zooxanthellate corals. However, the results are in agreement with the only previous analysis of an azooxanthellate coral, *Leptopsammia pruvoti*, studied along the same latitudinal gradient. In a comparison of the response to temperature of all Mediterranean species whose growth has been investigated to date, azooxanthellate corals were more tolerant to temperature increases than zooxanthellate corals.

Keywords Global warming · Net calcification · Linear extension · Skeletal density · *Caryophyllia inornata* · Scleractinia

Introduction

Temperature and solar radiation (SR), both strongly influenced by latitude, are fundamental in determining the global distribution of scleractinians (Kleypas et al. 1999). Additionally, these same parameters have a wide number of implications for coral physiology, demography, reproduction and distribution patterns (Kleypas et al. 1999; Coma et al. 2000; Reynaud et al. 2003; Goffredo and Lasker 2008; Goffredo et al. 2008; Airi et al. 2014). Ongoing climate change, through global warming and ocean acidification, poses serious threats to coral reef ecosystems and causes increased mass coral bleaching and alterations in some ecological processes (Hoegh-Guldberg 2011). For example, recruitment is a key process strongly influenced by climate variability, as are primary and secondary production, causing repercussions in food chains, migrations and spatial distributions of organisms (Walther et al. 2002). Coral growth is another mechanism that is threatened by climate change. For example, the net calcification rate of *Porites* sp. on the Great Barrier Reef (Cooper et al. 2008) and in Thailand (Tanzil et al. 2009) has decreased with increasing sea surface temperature (SST) in the last 16–21 yr. In the Red Sea, ocean warming is slowing the net calcification rate of *Diploastrea heliophora* (Cantin et al. 2010). Even though SST variations in space (e.g., along a latitudinal gradient) are not equivalent to ocean warming through time (Kleypas et al. 2005; Lough and Cantin 2014), spatial temperature gradients have been used to infer the response of species to rising

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temperatures. In *Porites* sp. living in the Hawaiian archipelago, in Thailand and on the Great Barrier Reef, net calcification rate increases with SST (Lough and Barnes 2000). In the Mediterranean Sea, the colonial zooxanthellate coral *Cladocora caespitosa* increases its net calcification rate with SST along a natural temperature gradient (Kružić et al. 2012), but laboratory observations showed that long-term exposure to high temperature led to a decrease in net calcification (Rodolfo-Metalpa et al. 2006). The net calcification rate of another zooxanthellate but solitary Mediterranean coral, *Balanophyllia europaea*, correlated negatively with increasing SST along a natural temperature gradient on the western Italian coast (Goffredo et al. 2009), while the net calcification rate of the solitary azooxanthellate coral *Leptopsammia pruvoti* did not vary along the same gradient (Caroselli et al. 2012). Interest in the repercussions of SR on coral biology, physiology and ecology is increasing (Shick et al. 1996; Brown et al. 2000; Anthony and Kerswell 2007). This parameter is a possible regulator of the growth of *Porites* sp., even if SST is the primary control (Lough and Barnes 2000).

Calcification is an energy-consuming physiological process in which the maximum rate can be reached when environment conditions are optimal (Marshall and Clode 2004). Optimal conditions vary with species (Carricart-Ganivet et al. 2012). As a consequence, correlations between temperature (or SR) and calcification can show whether environmental variation influences the growth of a particular species positively or negatively, thus moving environmental conditions toward or away from the calcification optimum. It is then possible to project the likely effects of global climate change on scleractinian growth and calcification (Cooper et al. 2008; Tanzil et al. 2009; Cantin et al. 2010).

Coral growth is described by three parameters: linear extension rate (mm yr^{-1}), bulk skeletal density (mg mm^{-3}) and net calcification rate ($\text{mg mm}^{-2} \text{yr}^{-1}$), obtained by multiplying the former two (Dodge and Brass 1984; Lough and Barnes 2000; Carricart-Ganivet 2004; Goffredo et al. 2009; Tanzil et al. 2009; Cantin et al. 2010; Caroselli et al. 2012). The measurement of all three growth components is fundamental when assessing the effect of the environment on coral growth, since none of the three is a perfect predictor of the other two (Dodge and Brass 1984) and each one can respond differently to environmental conditions (Lough and Barnes 2000; Carricart-Ganivet 2004; Goffredo et al. 2009; Tanzil et al. 2009; Caroselli et al. 2012). Each scleractinian may adopt a different growth strategy, for example, by preferentially investing calcification resources in bulk skeletal density while sacrificing linear extension, as done by *Orbicella annularis* (formerly *Montastraea annularis*, Budd et al. 2012) in the southern Gulf of Mexico with the ‘stretching modulation of skeletal growth’ (Carricart-

Ganivet and Merino 2001; Carricart-Ganivet 2007). In contrast, *Porites* invests calcification resources in linear extension (Lough and Barnes 2000). Investing in thicker skeletons may imply a greater resistance to mechanical stresses, while increasing the linear extension rate may be advantageous in the competition for space (Goffredo et al. 2009; Caroselli et al. 2012) and for the achievement of sexual maturity, which in solitary corals is reached at a certain size, depending on the species (Goffredo et al. 2008; Airi et al. 2014). As a result, environmental variations can have a wide range of implications on coral growth patterns, depending on the species.

While studies on the relationship between coral growth and environmental parameters in the tropics are numerous, such studies are scarce for temperate zones (Howe and Marshall 2002; Caroselli et al. 2012). The species involved in the present study is the temperate–subtropical azooxanthellate coral *Caryophyllia inornata* (Duncan, 1878). All species of the genus *Caryophyllia* are solitary, including *C. inornata*, which is present in the Mediterranean basin and in the eastern Atlantic Ocean from the Canary Islands to the southern coasts of Great Britain (Zibrowius 1980). *Caryophyllia inornata* colonizes vaults of caves and crevices, walls and wrecks from the surface to 100 m depth, and it can be a very common species in some overhangs (Zibrowius 1980). It is a gonochoric brooding species and has unusual embryogenesis with possible agamic production of embryos (Goffredo et al. 2012a). Sexual maturity is reached at a size of ~ 6.1 mm (Marchini et al. 2015), corresponding to ~ 7 -yr-old polyps. Its abundance and age–length relationship are homogenous along the western Italian coast, while demographic parameters indicate less stable populations and juvenile deficits with increasing SR (i.e., going southward; Caroselli et al. 2016).

This study aimed to understand the growth strategy of *C. inornata* by investigating the relationships between the three growth parameters (bulk skeletal density, linear extension rate and net calcification rate) and depth temperature (DT) and SR.

Materials and methods

Specimens of *C. inornata* were collected at six sites along a latitudinal gradient on the western Italian coasts, from $44^{\circ}20'N$ to $36^{\circ}45'N$ (Fig. 1), between 14 May 2009 and 14 April 2011. At each site, samples were collected using transects that consisted of 4–8 square patches of 0.1 m^2 each, 3 m apart (site and number of patches: Genova: $n = 4$; Calafuria: $n = 8$; Elba: $n = 4$; Palinuro: $n = 6$; Scilla: $n = 6$; and Pantelleria: $n = 7$). The sampling was performed within a depth range (11–16 m) known to have high population density and where the reproductive

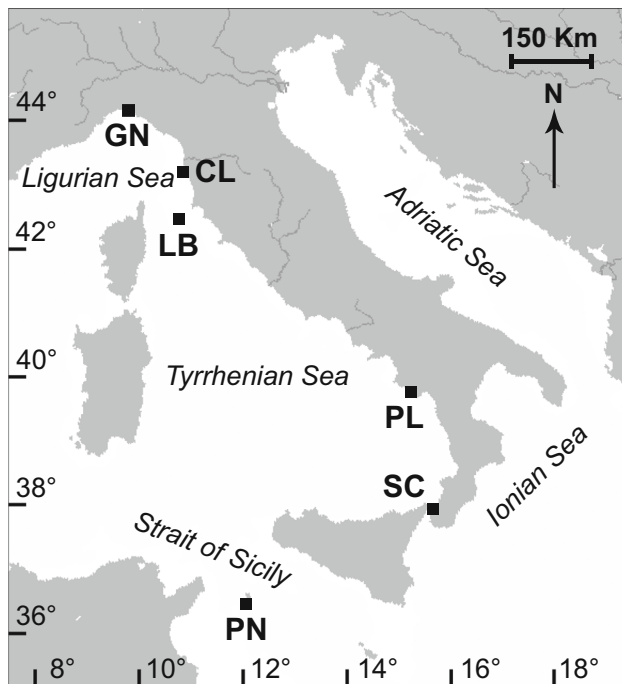


Fig. 1 Map of the Italian coastline indicating the sites where the corals were collected. Abbreviations and coordinates of the site in decreasing order of latitude: GN Genova, 44°20'N, 9°08'E; CL Calafuria, 43°27'N, 10°21'E; LB Elba Isle, 42°45'N, 10°24'E; PL Palinuro, 40°02'N, 15°16'E; SC Scilla, 38°01'N, 15°38'E; PN Pantelleria Isle, 36°45'N, 11°57'E

biology (Goffredo et al. 2012a), biometry and abundance (Caroselli et al. 2015), and growth and population demography have been studied (Caroselli et al. 2016). Patches were sampled on the vault of crevices, except at the Elba site, where samples were collected under the wings of a sunken plane wreck. All of the polyps found within each patch were collected.

Collected corals were dried at 50 °C for 4 d, then fragments of substratum and calcareous deposits produced by other organisms were removed after observation under binocular microscope. A low drying temperature was chosen to avoid phase transitions in the skeletal aragonite/calcite composition (Vongsavat et al. 2006; Goffredo et al. 2012b). Corallite length (L : maximum axis of the oral disk), width (W : minimum axis of the oral disk) and height (h : oral–aboral axis) were measured using calipers, and dry skeletal mass (M) was measured using a precision balance (Goffredo and Chadwick-Furman 2003). Corallite volume (V) was determined by applying the formula (Goffredo et al. 2007, 2008)

$$V = \frac{L}{2} \times \frac{W}{2} \times h\pi \quad (1)$$

The bulk skeletal density (Bucher et al. 1998) of each individual was obtained by dividing M by V . The age of each sample was estimated using the von Bertalanffy

length–age growth function, previously obtained and based on growth band analysis by means of computerized tomography (von Bertalanffy 1938; Sparre et al. 1989; Caroselli et al. 2012, 2016). Using the von Bertalanffy length–age growth function to estimate the age of the polyp, the annual linear extension rate was obtained for each sample (von Bertalanffy 1938; Caroselli et al. 2012). The mean annual net calcification rate (mass of CaCO_3 deposited per year per area unit) was calculated for each sample by the formula: net calcification rate ($\text{mg mm}^{-2} \text{yr}^{-1}$) = bulk skeletal density (mg mm^{-3}) \times linear extension rate (mm yr^{-1}) (Lough and Barnes 2000; Carricart-Ganivet 2004; Goffredo et al. 2009; Caroselli et al. 2012). Thus, for each population the mean bulk skeletal density, linear extension rate and net calcification rate of each coral were calculated. Samples were divided into three age classes: immature (0–7 yr, after Marchini et al. 2015), mature (7–14 yr, double the age at sexual maturity) and old (>14 yr). Correlation and regression analyses between environmental and growth parameters were performed for the three age classes (Goffredo et al. 2009; Caroselli et al. 2012). Relationships between environmental and growth parameters were investigated using two models: a linear model and a power function model. The linear model was used to compare the results with other studies on environmental controls of coral growth that used linear functions (Lough and Barnes 2000; Carricart-Ganivet 2004; Goffredo et al. 2009; Caroselli et al. 2012). The power function model was used because it produced the best fit with the data, as occurred for other Mediterranean species (see Goffredo et al. 2009; Caroselli et al. 2012). The power function model:

$$y = ax^b \quad (2)$$

was linearized with a log transformation of both the independent and dependent variables, producing the equation:

$$\ln(y) = b \ln(x) + \ln(a) \quad (3)$$

In this study, the environmental parameters (DT and SR) for each site were obtained by averaging monthly values that covered the mean turnover time of the populations, found to be 6 yr (Caroselli et al. 2016). Thus, 72 monthly values were considered for each site, starting from the sampling month backward. With this method, the mean environmental parameter values considered were those experienced by the polyps for most of their lifespan. Physical measurement data were obtained from data banks, as commonly done by several authors to study the influence of the environmental parameters on coral growth (e.g., Lough and Barnes 2000; Carricart-Ganivet 2004; Cantin et al. 2010; Harriott 1999; Peirano et al. 1999, 2005a, b).

Temperature data (°C) were recorded by three digital thermometers (i-Button, DS1921G-F5#, Maxim Integrated

Products, Dallas Semiconductors) that were placed at the experimental sites and recorded seawater temperature every 2–3 h during time intervals depending on the site. Thermometers were replaced every 3 months to avoid problems of encrustation and overgrowth by marine organisms. SST historical data (°C) were obtained for each site from the National Mareographic Network of the Superior Institute for the Environmental Protection and Research (ISPRA; <http://isprambiente.gov.it>). These data are measured by SM3810 mareographic stations placed close to the sampling sites and produced by the Society for Environmental and Industrial Monitoring (SIAP + MICROS). Site-by-site, historical at-depth temperatures were estimated by linear regression produced between DT and SST. In this study, the average DT of the 6 yr preceding the sampling ($n = 72$ monthly temperatures) was considered.

Monthly values of SR ($W m^{-2}$) were obtained from the databank of the Satellite Application Facility on Climate Monitoring (CM-SAF/EUMETSAT; <http://www.cmsaf.eu>). These are estimates derived from real-time satellite measurements and data sets registered with intersensor-calibrated radiances. Mean annual SR was calculated for the 15-km square associated with each study site by averaging 72 monthly values.

When assumptions for parametric statistics were met, analysis of variance (ANOVA) was used to compare groups of means. Otherwise, the Kruskal–Wallis test (Potvin and Roff 1993) was used to compare mean age, bulk skeletal density, linear extension rate and net calcification rate among populations. Pearson's correlation coefficients were calculated to test the relationship within mean growth parameters and between environmental and mean growth parameters. Given the low sample size ($n = 6$) and the assumptions of the Pearson method, correlation coefficients were also estimated with a bootstrapping procedure (Efron 1981), with 1000 resamples. A multiple regression was run to predict the net calcification rate from linear extension rate and bulk skeletal density. All analyses were computed using IBM SPSS Statistic 22.0.

Results

Linear regressions between SST and DT were significant at each site (Pearson's correlation, $p < 0.001$) allowing the calculation of the mean DT along the turnover time period for each site. In the investigated latitudinal range, DT and SR varied by 2.41 °C and 52.47 $W m^{-2}$, respectively (Table 1). DT and SR both varied among sites (ANOVA, $p < 0.01$). While SR was negatively correlated with latitude (Pearson's correlation, $p < 0.001$), DT was not correlated with latitude (Pearson's correlation, $p > 0.05$).

Mean age, net calcification rate, linear extension rate and bulk skeletal density (Table 2) were significantly different among populations (Kruskal–Wallis test, $p < 0.001$). While mean linear extension rate and mean bulk skeletal density were not correlated with each other, they were both significantly correlated with the mean net calcification rate (Table 3). These variables predicted the net calcification rate (F test, $p < 0.001$) explaining 99 % of variance in net calcification rate. The result of the multiple regression was:

$$\begin{aligned} \text{Net calcification rate} = & 0.852 \times \text{Bulk skeletal density} \\ & + 1.201 \times \text{Linear extension rate} - 0.996 \end{aligned} \quad (4)$$

The age stratification analysis (Tables 4, 5) found no relationship between growth and environmental parameters in mature and old individuals (no old individuals were found at Genova and Calafuria, so sample size for the correlations of old individuals was 4; Tables 4 and 5). For immature individuals and based on bootstrapping coefficients, SR correlated negatively with linear extension rate in both the linear and power function models (Pearson's correlation, $p < 0.05$), and DT correlated negatively with net calcification rate (Pearson's correlation, $p < 0.05$). Excluding the Calafuria dataset from the analysis, the correlation between DT and immature net calcification rate was not significant ($n = 5$, Pearson's correlation, $p > 0.05$).

Discussion

The mean growth parameter values found in this study were similar to previous studies. In fact, calculated bulk skeletal densities were comparable with the values found for other tropical and temperate species (Lough and Barnes 2000; Carricart-Ganivet 2004; Goffredo et al. 2009; Tanzil et al. 2009; Caroselli et al. 2012). Moreover, the average linear extension rate for French and Spanish *C. inornata* populations (0.68 $mm yr^{-1}$; Teixido et al. 2011) falls within the range found in this study (0.63–0.90 $mm yr^{-1}$; Table 2).

A coral's growth strategy is the mechanism through which it can preferentially invest calcification resources between thickening the skeleton (increasing skeletal density) and accelerating linear extension. For example, two tropical zooxanthellate corals show different growth patterns: while *Porites* sp. allocates enhanced calcification into linear extension (Lough and Barnes 2000), *Orbicella annularis* allocates calcification resources into denser skeletons (Carricart-Ganivet 2004). In the Mediterranean Sea, the zooxanthellate colonial coral *C. caespitosa* shows a similar strategy to massive *Porites* (Kružić et al. 2012).

Table 1 Values of sampling depth temperature (DT) and solar radiation (SR) at each site

Site	Code	Latitude	Depth temperature (°C), annual mean (SE)	Solar radiation (W m ⁻²), annual mean (SE)
Calafuria	CL	43°27'N	16.74 (0.38)	174.88 (10.59)
Elba	LB	42°45'N	17.63 (0.38)	183.45 (10.64)
Scilla	SC	38°01'N	18.20 (0.41)	203.22 (10.44)
Genova	GN	44°20'N	18.24 (0.45)	161.77 (9.35)
Palinuro	PL	40°02'N	18.94 (0.44)	194.94 (10.78)
Pantelleria	PN	36°45'N	19.15 (0.41)	214.23 (10.17)

DT and SR both varied among the sites (Kruskal–Wallis test, $p < 0.001$). Sites are arranged in increasing order of DT. SE standard error

Table 2 Mean age, bulk skeletal density, linear extension rate and net calcification rate of populations *Caryophyllia inornata* at six sites in Italy

Site	Code	n	Age (yr), mean (SE)	Bulk skeletal density (mg mm ⁻³), mean (SE)	Linear extension rate (mm yr ⁻¹), mean (SE)	Net calcification rate (mg mm ⁻² yr ⁻¹), mean (SE)
Calafuria	CL	62	3.29 (0.19)	1.64 (0.11)	0.90 (0.01)	1.50 (0.11)
Elba	LB	241	6.52 (0.26)	1.24 (0.04)	0.74 (0.01)	0.92 (0.04)
Scilla	SC	47	8.28 (0.56)	1.16 (0.04)	0.65 (0.02)	0.76 (0.04)
Genova	GN	86	4.58 (0.29)	0.99 (0.03)	0.83 (0.02)	0.84 (0.04)
Palinuro	PL	93	8.45 (0.41)	0.97 (0.02)	0.64 (0.02)	0.63 (0.03)
Pantelleria	PN	39	8.81 (0.67)	1.11 (0.05)	0.63 (0.03)	0.70 (0.05)

Sites are arranged in order of increasing depth temperature. n number of individuals, SE standard error

Table 3 Linear regression and correlation analysis between mean bulk skeletal density, linear extension rate and net calcification rate of *Caryophyllia inornata* at six sites ($n = 6$)

Dependent variable	Independent variable	Slope (SE)	Intercept (SE)	r^2	r	r_{BS}^2	r_{BS}
Bulk skeletal density	Linear extension rate	–	–	0.401	0.633	0.211	0.459
Net calcification rate	Linear extension rate	2.344 (0.706)	–0.821 (0.521)	0.734	0.857*	0.727	0.853*
Net calcification rate	Bulk skeletal density	1.211 (0.225)	–0.544 (0.271)	0.879	0.938**	0.665	0.816*

r^2 = Pearson's coefficient of determination, r = Pearson's correlation coefficient, r_{BS}^2 and r_{BS} = Pearson's coefficients calculated with bootstrapping, SE standard error

* $p < 0.05$; ** $p < 0.01$

The three growth parameters have been investigated in only two solitary corals, the azooxanthellate *L. pruvoti* (Caroselli et al. 2012) and the zooxanthellate *B. europaea* (Goffredo et al. 2009). The net calcification rate of *L. pruvoti* responds in a similar way to the tropical *M. annularis*, with calcification resources preferentially allocated to increasing bulk skeletal density (Caroselli et al. 2012). The endemic *B. europaea* allocates calcification evenly between linear extension and skeletal density, as the mechanical strength of the skeleton and the ability to colonize new substratum quickly are equally important for this species (Goffredo et al. 2009). *Caryophyllia inornata* behaved in a similar way to *B. europaea*, with a balanced modulation of skeletal growth. Net calcification rate correlated positively with both linear extension rate and bulk skeletal density, which did not correlate with each other. Multiple regression showed that the net calcification rate of

this species was significantly described by both linear extension rate and bulk skeletal density (Eq. 4). Thus, the pattern suggests that fast colonization of new substratum and the strength of the corallite against mechanical stress are also both important for *C. inornata*, as illustrated by the Elba population. In fact, the habitat normally occupied by *C. inornata* is also colonized by *L. pruvoti* (Teixido et al. 2011), which is normally present in higher densities in the crevices of the study sites (Caroselli et al. 2012, 2015). However, *C. inornata* is the only coral present at the Elba sampling site under the wings of the sunken plane wreck and it is present with unusually high abundance (Caroselli et al. 2015). A possible explanation could be that *C. inornata* may invest more calcification resources in linear extension than *L. pruvoti*, which deploys most calcification resources in increasing skeletal thickness. This could result in better performance when colonizing unoccupied space

Table 4 Linear regression and correlation analysis between mean environmental (SR solar radiation, DT depth temperature) and growth parameters of *Caryophyllia inornata* at six sites using a linear model

Dependent variable	Independent variable	Slope (SE)	Intercept (SE)	r^2	r	r_{BS}^2	r_{BS}
Immature individuals (0–6 yr, $n = 6$)							
Skeletal density	SR	–	–	0.099	–0.315	0.067	–0.259
Linear extension	SR	–0.002 (0.001)	1.196 (0.123)	0.664	–0.815*	0.684	–0.827*
Calcification	SR	–	–	0.133	–0.365	0.130	–0.360
Skeletal density	DT	–	–	0.707	–0.841*	0.513	–0.716
Linear extension	DT	–	–	0.654	–0.809	0.581	–0.762
Calcification	DT	–0.252 (0.059)	5.633 (1.065)	0.823	–0.907*	0.796	–0.892*
Mature individuals (7–13 yr, $n = 6$)							
Skeletal density	SR	–	–	0.002	0.041	0.000	0.021
Linear extension	SR	–	–	0.518	–0.720	0.557	–0.746
Calcification	SR	–	–	0.033	–0.183	0.011	–0.104
Skeletal density	DT	–	–	0.533	–0.730	0.397	–0.630
Linear extension	DT	–	–	0.596	–0.772	0.461	–0.679
Calcification	DT	–	–	0.689	–0.830*	0.493	–0.702
Old individuals (>13 yr, $n = 4$)							
Skeletal density	SR	–	–	0.077	–0.278	0.086	–0.293
Linear extension	SR	–	–	0.008	0.089	0.000	–0.018
Calcification	SR	–	–	0.046	–0.215	0.012	–0.109
Skeletal density	DT	–	–	0.656	–0.810	0.635	–0.797
Linear extension	DT	–	–	0.085	0.292	0.076	0.275
Calcification	DT	–	–	0.299	–0.547	0.200	–0.447

r^2 = Pearson's coefficient of determination, r = Pearson's correlation coefficient, r_{BS}^2 and r_{BS} = Pearson's coefficients calculated with bootstrapping, SE standard error

* $p < 0.05$

such as a recently sunk wreck. Besides that, reproduction in *C. inornata* could also benefit from this kind of modulation, as the size at sexual maturity can be achieved quickly. Moreover, the possible asexual reproduction that characterizes this species (Goffredo et al. 2012a, b) could be another factor favoring *C. inornata* in comparison with *L. pruvoti*, which does not reproduce asexually. However, this interpretation should be treated with caution because this caryophylliid may possibly tolerate the non-natural metallic substratum better than *L. pruvoti*, which could be linked to aspects other than calcification. In fact, even though *C. inornata* was the only coral found under the wings, *L. pruvoti* was dominant in the nearby crevices (E. Caroselli, personal observation).

The age stratification analyses did not reveal any correlation between growth of mature and old individuals and environmental parameters. The negative correlation between SR and linear extension rate for immature individuals, confirmed both by the linear and the power function model based on bootstrapped coefficients, may be due to the increasing mean age of immature individuals in the southernmost populations, i.e., the populations with the lowest SR. In fact, the linear extension rate of this species

decreases with increasing age (Caroselli et al. 2016), and the mean immature age is higher at lower latitudes (Pearson's correlation test, $p < 0.05$). Consequently, this result is likely to be biased by the slightly higher age of immature individuals in populations characterized by higher SR.

The negative correlation between DT and net calcification rate based on bootstrapped coefficients suggests that calcification of immature individuals decreased with increasing temperature. However, if the Calafuria data were excluded from the analysis, the correlation became insignificant. The Calafuria site is characterized by a high abundance of zooplankton (Santangelo et al. 2009; Saiz et al. 2014) that is likely to enhance the calcification rate (Ferrier-Pagès et al. 2003; Naumann et al. 2011), explaining the higher level of net calcification rate at this site compared to all the others. However, the trend was observed only for immature individuals, which could be explained by a different energy allocation strategy during the lifespan of the individuals. An immature polyp at Calafuria could benefit from the additional energy coming from zooplankton by allocating it to the calcification process, thus increasing linear extension (to achieve the size at sexual maturity) and skeletal density (to strengthen the first

Table 5 Linear regression and correlations analysis between mean environmental (*SR* solar radiation, *DT* depth temperature) and growth parameters of *Caryophyllia inornata* at six sites using a linearized power function model (Eq. 3)

Dependent variable	Independent variable	Slope (SE)	Intercept (SE)	r^2	r	r_{BS}^2	r_{BS}
Immature individuals (0–6 yr, $n = 6$)							
Skeletal density	SR	–	–	0.081	–0.284	0.044	–0.209
Linear extension	SR	–0.396 (0.141)	1.914 (0.741)	0.663	–0.814*	0.667	–0.817*
Calcification	SR	–	–	0.120	–0.346	0.095	–0.309
Skeletal density	DT	–	–	0.726	–0.852*	0.524	–0.724
Linear extension	DT	–	–	0.648	–0.805	0.530	–0.728
Calcification	DT	–3.953 (0.786)	11.481 (2.278)	0.863	–0.929**	0.815	–0.903*
Mature individuals (7–13 yr, $n = 6$)							
Skeletal density	SR	–	–	0.024	0.154	0.009	0.096
Linear extension	SR	–	–	0.537	–0.733	0.516	–0.718
Calcification	SR	–	–	0.010	–0.100	0.002	–0.042
Skeletal density	DT	–	–	0.465	–0.682	0.364	–0.603
Linear extension	DT	–	–	0.599	–0.774	0.479	–0.692
Calcification	DT	–	–	0.672	–0.820*	0.479	–0.692
Old individuals (>13 yr, $n = 6$)							
Skeletal density	SR	–	–	0.028	–0.167	0.040	–0.201
Linear extension	SR	–	–	0.003	0.059	0.004	0.060
Calcification	SR	–	–	0.009	–0.097	0.000	0.005
Skeletal density	DT	–	–	0.588	–0.767	0.570	–0.755
Linear extension	DT	–	–	0.078	0.279	0.094	0.307
Calcification	DT	–	–	0.279	–0.528	0.173	–0.416

n = number of populations, r^2 = Pearson's coefficient of determination, r = Pearson's correlation coefficient, r_{BS}^2 and r_{BS} = Pearson's coefficients calculated with bootstrapping, *SE* standard error

* $p < 0.05$; ** $p < 0.01$

skeletal elements). As they age, these individuals could alter their investment of surplus energy to the costly reproductive process that characterizes this species (Marchini et al. 2015). Consequently, the statistically significant correlation between calcification and SR for immature individuals is not likely to describe a true dependence on temperature variation along the gradient, but is probably due to the local trophic conditions characterizing Calafuria.

These responses to temperature variations have also been observed for the only other azooxanthellate coral studied in the Mediterranean (*L. pruvoti*; Caroselli et al. 2012) and contrast with zooxanthellate species in both the tropics (*Porites* sp.: Lough and Barnes 2000; *O. annularis*: Carricart-Ganivet 2004; and *Diploastrea heliophora*: Cantin et al. 2010) and in the Mediterranean Sea (*B. europaea*: Goffredo et al. 2009; and *C. caespitosa*: Kružić et al. 2012). In zooxanthellate corals, the relationship between calcification and temperature is thought to be linked to the response of photosynthesis by zooxanthellae to temperature (Goffredo et al. 2009; Cantin et al. 2010). In fact, calcification is enhanced by photosynthesis in tropical systems (Al-Horani et al. 2005),

where calcification is positively correlated with SST, for example, for *Porites* sp. in the Great Barrier Reef and *O. annularis* in the Caribbean (Lough and Barnes 2000; Carricart-Ganivet 2004). In contrast, in the Red Sea, *D. heliophora* shows a decrease in net calcification and linear extension rates with increased SST, assuming constant inferred bulk density (Cantin et al. 2010). However, a recent study demonstrated that coral net calcification rate increased to a maximum and declined afterward, with different sensitivity among species (Carricart-Ganivet et al. 2012). For example, in *Orbicella* sp. net calcification decreased more moderately than in *Porites* sp., leading to the hypothesis that changes in reef-building community composition—where the majority of species are zooxanthellate—are likely to happen under predicted global warming scenarios (Carricart-Ganivet et al. 2012). Furthermore, in zooxanthellate corals calcification also decreases in suboptimal thermal conditions (Hoegh-Guldberg et al. 2007) and under high temperature stress (Rodolfo-Metalpa et al. 2006; Cooper et al. 2008; Tanzil et al. 2009; Cantin et al. 2010), emphasizing concern for these species. In temperate seas, particularly the Mediterranean Sea, net calcification rate variations with

environmental parameters have been investigated in only a few species (Caroselli and Goffredo 2014). Net calcification of the endemic *B. europaea* and *C. caespitosa* is temperature dependent, while in the azooxanthellate *L. pruvoti* and *C. inornata* net calcification is unaffected by temperature. In particular, while net calcification rate of *C. caespitosa* is positively correlated with SST (Kružić et al. 2012), net calcification of *B. europaea* has the opposite trend (Goffredo et al. 2009).

The previously formulated hypothesis that azooxanthellate Mediterranean scleractinians have a higher tolerance to high temperature than zooxanthellate corals (Caroselli and Goffredo 2014) is supported by the present findings and by previous studies on other biological parameters of *C. inornata* (such as population abundance, mortality and population structure stability) which are not related to temperature variations (Caroselli et al. 2015, 2016). It can be argued that an adaptive shift in the symbiont community may promote higher resilience (Baker et al. 2004; Fitt et al. 2009), and thus, zooxanthellate scleractinians could enhance their temperature tolerance. Nevertheless, there have been no studies in temperate environments on symbiont community shifts; in addition, the clades of *Symbiodinium* sp. reported in Mediterranean corals do not include the clades demonstrated to be more high-temperature-tolerant (Baker et al. 2004; Visram et al. 2006; Fitt et al. 2009).

This study adds knowledge about the response of poorly studied azooxanthellate corals in the Mediterranean Sea and supports concerns for zooxanthellate species in the face of global warming. However, these results should not be generalized broadly since this is the first investigation of the relationship between two major environmental parameters and growth parameters of a caryophylliid coral, and other species may show different tolerance to temperature increases.

In conclusion, it was observed that (1) net calcification rate correlated positively both with bulk skeletal density and linear extension rate, and (2) *C. inornata* appears to be tolerant to the natural range of DT and SR experienced in the field.

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