

Inferred level of calcification decreases along an increasing temperature gradient in a Mediterranean endemic coral

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Abstract

The correlation between solar radiation and sea surface temperature (SST) and growth was assessed along a latitudinal gradient. Extension rate and skeletal density were both correlated with calcification rate, indicating that calcium carbonate deposition was allocated evenly between skeletal density and linear extension. Unlike most studies on other tropical and temperate corals, in which calcification was positively correlated with solar radiation and SST, in the present study calcification was not correlated with solar radiation, whereas it was negatively correlated with SST. We hypothesize that photosynthesis of the symbiotic algae of *Balanophyllia europaea* is inhibited at high temperatures, consequently causing an inhibition of calcification. The regressions between calcification and SST predicted that the calcification of *B. europaea* would be depressed at 20.5–21.0°C mean annual SST. The scenarios of the Intergovernmental Panel on Climate Change conclude that by 2100, SST will exceed this physiological threshold for most of the populations considered in this study. This study comprises the first field investigation of the relationships between environmental parameters and calcification of a Mediterranean coral and highlights the risks of losing Mediterranean marine biodiversity over the course of future decades.

Temperature and irradiance variations associated with latitude have an important influence on global coral distribution patterns (Kleypas et al. 1999). Latitude is the main factor influencing the variation of light and temperature (Kain 1989), which are the two environmental parameters considered in this study because they have been shown to be strongly linked to coral growth, physiology, and demography (Kleypas et al. 1999; Lough and Barnes 2000). In general, coral growth decreases with increasing latitude, to a boundary beyond 30°N and 30°S, where coral reef development no longer occurs (Kinsey and Davies 1979). Coral growth is a composite of three related parameters (calcification = linear extension × skeletal density; Lough and Barnes 2000; Carricart-Ganivet 2004), and their measurement is essential when assessing the effects of environmental parameters on coral growth, because none of the three is a perfect predictor of the other two (Dodge and Brass 1984). Analyzing these variables also allows for prediction of the possible effect that climatic changes can have on coral ecosystems (Cooper et al. 2008). These three variables have been studied along a latitudinal gradient in the genera *Montastraea* (Carricart-Ganivet 2004) and *Porites* (Lough and Barnes 2000; Cooper et al. 2008), and variation of the three parameters has been linked to changes in temperature and light associated with latitude. In colonies of *Montastraea annularis* in the Gulf of Mexico and the Caribbean Sea, sea surface temperature (SST) is positively correlated with

calcification rate and skeletal density, while it is negatively correlated with linear extension rate (Carricart-Ganivet 2004). In colonies of *Porites* of the Hawaiian archipelago, Thailand, and the Great Barrier Reef (Australia), solar radiation and SST were found to be positively correlated with calcification and linear extension rates and negatively correlated with skeletal density (Lough and Barnes 2000). In contrast, a recent monitoring of 16 yr of calcification in *Porites* colonies from the Great Barrier Reef shows that calcification declined over time and indicates that the response may be due to the interactive effects of elevated seawater temperatures and pCO₂ increase (Cooper et al. 2008), as previously reported for colonies of *Stylophora pistillata* grown in aquaria (Reynaud et al. 2003).

Although there are numerous studies of the relationships between environmental parameters and coral growth in the tropics (Lough and Barnes 2000; Carricart-Ganivet 2004; Cooper et al. 2008), such studies are scarce for temperate zones. In *Astrangia danae* and *Plesiastrea versipora*, calcification rate increases with temperature, as is the trend for some tropical corals, albeit over a lower temperature range (Howe and Marshall 2002). Laboratory observations on calcification rates in *Cladocora caespitosa* and *Oculina patagonica* indicate that prolonged periods of high temperatures (corresponding to or higher than the maximum summer temperature in the field) lead to a decrease in calcification (Rodolfo-Metalpa et al. 2006b).

This study aimed to investigate the relationships between environmental parameters (solar radiation and SST) and the three growth components (calcification, skeletal density, and linear extension) in the Mediterranean coral

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Balanophyllia europaea (Risso 1826). *B. europaea* is a solitary, zooxanthellate scleractinian coral, which is endemic to the Mediterranean Sea (Zibrowius 1980). Being zooxanthellate, its distribution is limited to 0–50 m in depth (Zibrowius 1980), with abundances of more than 100 individuals m^{-2} (Goffredo et al. 2004a). It is a simultaneous hermaphrodite and brooder (Goffredo et al. 2002). Along the Italian coasts, skeletal density and population abundance are negatively correlated with SST (Goffredo et al. 2007). In addition, the population structures of this species become less stable and deviate from the steady state with increasing SST as the result of a progressive deficiency of young individuals (Goffredo et al. 2008). In the azooxanthellate coral *Leptopsammia pruvoti*, closely related to *B. europaea* and studied in the same sites sampled in this study, no significant variation was found in the skeletal and population density with solar radiation and SST (Goffredo et al. 2007). It has been hypothesized that temperature negatively influences the photosynthesis of the symbiotic algae of *B. europaea*, leading to negative effects on its growth and reproductive activity (Goffredo et al. 2007, 2008). Suggested by Goreau (1959) as the ‘light enhanced calcification’ hypothesis, in zooxanthellate corals photosynthesis stimulates calcification, as has been confirmed in several studies (Al-Horani et al. 2005; Mass et al. 2007), and both processes have an optimal temperature (Howe and Marshall 2002). Rinkevich (1989) demonstrated the energetic contribution of photosynthetic products to coral reproduction in zooxanthellate corals.

This is the first study on the variation of the three growth components in a temperate scleractinian coral, and the study aims to assess the variations in calcification rate, linear extension rate, and skeletal density in populations arranged along a temperature and solar radiation gradient. The results are also considered in light of the most recent scenarios on climate changes for the near future.

Methods

Specimens of *B. europaea* were collected from six sites along a latitudinal gradient, from 44°20'N to 36°45'N, between 09 November 2003 and 30 September 2005 (Fig. 1). With the exception of the Calafuria population, for which data were obtained from a previous study (Goffredo et al. 2004a), samples were collected at each site using transects of at least three patches of 1 m² each, arranged in a line 5 m apart along the southern side of each reef at a depth of 5–7 m. Given the random distribution pattern of *B. europaea*, this study is not affected by the problems associated with regularly spaced quadrats and transects (Goffredo et al. 2004a). All of the polyps included were collected from each patch. Sampling was performed at depths known to have high population densities and where the reproductive biology, biometry, population density, growth, population dynamics, and genetics of the species had previously been studied (Goffredo et al. 2002, 2004a,b). Sampling at the depth of maximum abundance may bias growth estimates toward a higher rate and in turn underestimate age, but by sampling in the chosen depth

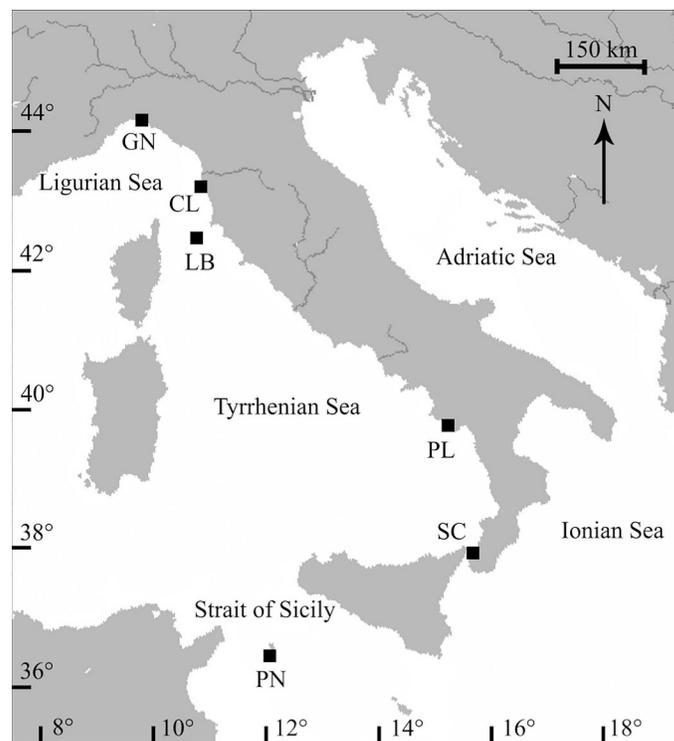


Fig. 1. Map of the Italian coastline indicating sites at which corals were collected. Abbreviations and coordinates of the sites, in decreasing order of latitude, are as follows: GN, Genova: 44°20'N, 9°08'E; CL, Calafuria: 43°27'N, 10°21'E; LB, Elba Isle: 42°45'N, 10°24'E; PL, Palinuro: 40°02'N, 15°16'E;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

range, where 62% of the biomass of this species is found (Goffredo et al. 2004a), this bias is reduced.

Corals were dried at 50°C for 4 d and were observed under a binocular microscope to remove fragments of substratum and calcareous deposits produced by other organisms. Corallite length (L : maximum axis of the oral disc), width (W : minimum axis of the oral disc), and height (h : oral–aboral axis) were measured with calipers, and the dry skeletal mass (M) was measured with a precision balance. Corallite volume (V) was determined by applying the following formula: $V = (L/2) \times (W/2) \times h\pi$ (Goffredo et al. 2007). Skeletal density (D) was calculated by dividing M by V .

The age of each sample was estimated using the von Bertalanffy length–age growth functions, previously obtained for each population based on growth bands analysis by means of computerized tomography (von Bertalanffy 1938; Goffredo et al. 2008). According to the age of the polyp, the annual linear extension rate was obtained for each sample using the von Bertalanffy length–age growth functions (von Bertalanffy 1938; Goffredo et al. 2008). The mean annual calcification rate (mass of $CaCO_3$ deposited per year per area unit) was calculated for each sample by the following formula: calcification ($mg\ mm^{-2}\ yr^{-1}$) = skeletal density ($mg\ mm^{-3}$) \times linear extension ($mm\ yr^{-1}$) (Lough and Barnes 2000; Carricart-Ganivet 2004). Thus, for each population the mean values of skeletal density, linear extension, and calcification rates of the corallites were

Table 1. Average annual solar radiation and SST values of the sample sites. The sites are arranged in order of increasing SST.*

Population	Code	Solar radiation (W m ⁻²)		SST (°C)	
		Annual mean (SE)	Annual mean (SE)	Annual mean (SE)	Annual mean (SE)
Calafuria	CL	170.07 (1.02)	18.02 (0.04)	172.74 (1.02)	18.74 (0.04)
Elba	LB	181.48 (1.01)	19.14 (0.03)	187.31 (1.02)	19.54 (0.02)
Palinuro	PL	166.95 (1.02)	19.56 (0.04)	190.95 (1.02)	19.88 (0.04)
Scilla	SC				
Genova	GN				
Pantelleria	PN				

* SE, standard error.

obtained. Samples were also divided into three age classes: immature (0–4 yr, after Goffredo et al. 2004a); mature (4–8 yr, double the age at sexual maturity); and old (>8 yr).

Correlation and regression analyses between environmental and growth parameters were performed both for the full data set and for the three age classes to check for differences due to the different mean age of the samples in the populations (Goffredo et al. 2008). Relationships between environmental and growth parameters were performed 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, in which linear functions are used (Lough and Barnes 2000; Carricart-Ganivet 2004). We used the power function model as it produced the best fit with the data and to compare the results obtained by the linear model. The power function model,

$$y = ax^b \quad (1)$$

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

$$\ln(y) = b \ln(x) + \ln(a) \quad (2)$$

SST data for 2003–2005 were obtained for each location from the National Mareographic Network of the Agency for the Protection of the Environment and Technical Services (available at <http://www.apat.gov.it>). These data are measured by mareographic stations SM3810, built by the Italian Society for Precision Apparatuses. Mean annual SST was obtained from hourly values measured from January 2001 to January 2005 (Table 1). Monthly values of solar radiation (W m⁻²) were obtained from the Interna-

tional Cloud Climatology Project (available at <http://ingrid.lidgo.columbia.edu/>). These estimates are derived from satellite measurements of cloud and atmospheric optical properties. Mean annual solar radiation was obtained for the 2.5°-latitude-by-longitude square associated with each of the six sites (Table 1).

Because of the heteroskedastic nature of the data, the nonparametric Kruskal–Wallis test was used to compare mean solar radiation, SST, skeletal density, linear extension, and calcification rates among the populations. Pearson correlation coefficients were calculated for the relationships among growth parameters and between environmental and growth parameters. Because of the low *n* value (*n* = 6) and the assumptions of the Pearson method, correlation coefficients were also estimated with bootstrapping (Efron 1981), with 100,000 resamples. All analyses were computed using SPSS 12.0, except for the bootstrapping analyses (S-PLUS 6.0 Professional).

Results

Both mean annual solar radiation and SST varied significantly among the sites (Kruskal–Wallis test, *p* < 0.001; Table 1). Mean skeletal density, linear extension, and calcification rates were significantly different among the populations (Kruskal–Wallis test, *p* < 0.001; Table 2). Mean calcification rate of the corallites in the populations was positively correlated with mean linear extension rate and mean skeletal density (Table 3). Based on the bootstrapping coefficients, calcification rate explained 66% of the variance in linear extension rate and 84% of the variance in skeletal density (Table 3).

Considering the full data set (all ages), both the linear and power function models showed that mean skeletal density of the populations was not correlated with solar radiation, whereas it was negatively correlated with SST, which explained 92–94% of its variance (Tables 4, 5). Mean linear extension rate of the populations was not significantly correlated with either solar radiation or SST (Tables 4, 5). Mean calcification rate of the populations was not correlated with solar radiation, but it was significantly negatively correlated with SST, which explained 74–75% of its variance (Tables 4, 5). The linear model indicated that a 1°C rise in SST lowered the mean skeletal density of the populations by 0.58 mg mm⁻³ and lowered the mean calcification rate of the populations by 1.00 mg mm⁻² yr⁻¹. The trends from the whole data set

Table 2. *Balanophyllia europaea*. Mean skeletal density, linear extension, and calcification rate values of the populations. The sites are arranged in order of increasing SST.*

Population	Code	<i>n</i>	Average skeletal density (mg mm ⁻³)		Average linear extension rate (mm yr ⁻¹)		Average calcification rate (mg mm ⁻² yr ⁻¹)	
			density (mg mm ⁻³)	SE	rate (mm yr ⁻¹)	SE	rate (mg mm ⁻² yr ⁻¹)	SE
Calafuria	CL	941	1.95	0.01	1.49	0.01	2.86	0.03
Elba	LB	38	1.41	0.06	1.15	0.04	1.62	0.09
Palinuro	PL	80	1.05	0.03	0.96	0.02	1.02	0.04
Scilla	SC	48	1.01	0.04	1.12	0.03	1.12	0.06
Genova	GN	55	0.93	0.02	1.17	0.04	1.09	0.04
Pantelleria	PN	171	0.91	0.02	1.08	0.01	0.97	0.02

* *n*, number of individuals; SE, standard error.

Table 3. *Balanophyllia europaea*. Linear regression and correlation analysis between mean skeletal density, linear extension rate, and calcification rate in the six sites ($n = 6$).†

Dependent variable	Independent variable	Slope (SE)	Intercept (SE)	r^2	r	r_{BS}^2	r_{BS}
Skeletal density	Linear extension	1.931 (0.612)	-1.034 (0.718)	0.713	0.845*	0.392	0.626
Calcification	Linear extension	3.805 (0.795)	-2.973 (0.932)	0.851	0.923**	0.661	0.813*
Calcification	Skeletal density	1.773 (0.163)	-0.699 (0.206)	0.967	0.984***	0.841	0.917*

† 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.

* $p < 0.050$.

** $p < 0.010$.

*** $p < 0.001$.

were confirmed by the age-stratified analyses on the subsets of immature and mature samples (Tables 4, 5). The old-samples subset showed a similar trend, except that the mean linear extension rate of the populations was positively correlated with SST and the mean calcification rate was not significantly correlated with SST when considering the bootstrapping r value (Tables 4, 5).

Based on the two significant regressions from the whole data set, the linear model predicted that calcification would have ceased at a mean annual SST of 20.5°C and the skeletal

density would fall to zero values at a mean annual SST of 21.2°C (Table 4). The power function model predicted that calcification would have approached zero values at 21.0°C and the skeletal density would have approached zero values at a mean annual SST of 21.3°C (Table 5).

Discussion

The 'stretching modulation of skeletal growth' is a mechanism that corals can adopt for preferentially

Table 4. *Balanophyllia europaea*. Linear model. Linear regression and correlation analysis between environmental and growth parameters in the six sites ($n = 6$). Regression parameters are shown only where the relationship is significant.†

Dependent variable	Independent variable	Slope (SE)	Intercept (SE)	r^2	r	r_{BS}^2	r_{BS}
All samples							
Skeletal density	Solar radiation	—	—	0.260	-0.510	0.244	-0.494
Linear extension	Solar radiation	—	—	0.304	-0.551	0.343	-0.586
Calcification	Solar radiation	—	—	0.278	-0.527	0.314	-0.560
Skeletal density	SST	-0.580 (0.077)	12.313 (1.475)	0.934	-0.967**	0.920	-0.959**
Linear extension	SST	—	—	0.527	-0.726	0.296	-0.544
Calcification	SST	-0.997 (0.209)	20.542 (4.012)	0.850	-0.922**	0.740	-0.860*
Immature samples (0-4 yr)							
Skeletal density	Solar radiation	—	—	0.372	-0.610	0.389	-0.624
Linear extension	Solar radiation	—	—	0.493	-0.702	0.530	-0.728
Calcification	Solar radiation	—	—	0.379	-0.615	0.416	-0.645
Skeletal density	SST	-0.572 (0.121)	12.049 (2.320)	0.848	-0.921**	0.674	-0.821*
Linear extension	SST	—	—	0.615	-0.784	0.415	-0.644
Calcification	SST	-1.226 (0.277)	25.192 (5.300)	0.831	-0.911*	0.667	-0.817*
Mature samples (5-8 yr)							
Skeletal density	Solar radiation	—	—	0.263	-0.513	0.329	0.574
Linear extension	Solar radiation	—	—	0.314	-0.561	0.245	-0.495
Calcification	Solar radiation	—	—	0.314	-0.561	0.318	-0.564
Skeletal density	SST	-0.643 (0.089)	13.527 (1.711)	0.928	-0.964**	0.899	-0.948**
Linear extension	SST	—	—	<0.001	-0.005	<0.001	-0.004
Calcification	SST	-0.766 (0.135)	16.109 (2.587)	0.890	-0.943**	0.792	-0.890*
Old samples (>8 yr)							
Skeletal density	Solar radiation	—	—	0.206	-0.454	0.175	-0.418
Linear extension	Solar radiation	—	—	0.255	0.505	0.233	0.483
Calcification	Solar radiation	—	—	0.166	-0.408	0.105	-0.324
Skeletal density	SST	-0.704 (0.125)	14.778 (2.396)	0.888	-0.942*	0.841	-0.917*
Linear extension	SST	0.170 (0.012)	-2.436 (0.224)	0.981	0.991***	0.974	0.987**
Calcification	SST	—	—	0.800	0.895*	0.571	-0.756

† r^2 , Pearson's coefficient of determination; r , Pearson's correlation coefficient; r_{BS}^2 and r_{BS} , Pearson's coefficients calculated with bootstrapping; SST, sea surface temperature; SE, standard error.

* $p < 0.050$.

** $p < 0.010$.

*** $p < 0.001$.

Table 5. *Balanophyllia europaea*. Power function model (Eq. 2). Linear regression and correlation analysis between environmental and growth parameters in the six sites ($n = 6$) calculated on log-transformed data. Regression parameters are shown only where the relationship is significant.†

Dependent variable	Independent variable	Slope (SE)	Intercept (SE)	r^2	r	r_{BS}^2	r_{BS}
All samples							
Skeletal density	Solar radiation	—	—	0.252	-0.502	0.230	-0.480
Linear extension	Solar radiation	—	—	0.318	-0.564	0.352	-0.593
Calcification	Solar radiation	—	—	0.316	-0.562	0.333	-0.577
Skeletal density	SST	-8.162 (0.876)	24.241 (2.586)	0.956	-0.978***	0.935	-0.967**
Linear extension	SST	—	—	0.488	-0.698	0.289	-0.538
Calcification	SST	-10.932 (1.981)	32.551 (5.848)	0.884	-0.940**	0.752	-0.867*
Immature samples (0–4 yr)							
Skeletal density	Solar radiation	—	—	0.407	-0.638	0.408	-0.639
Linear extension	Solar radiation	—	—	0.516	-0.718	0.540	-0.735
Calcification	Solar radiation	—	—	0.452	-0.672	0.460	-0.678
Skeletal density	SST	-8.829 (2.073)	26.095 (6.120)	0.819	-0.905*	0.661	-0.813*
Linear extension	SST	—	—	0.050	-0.224	0.411	-0.641
Calcification	SST	-11.503 (2.943)	34.396 (8.687)	0.792	-0.890*	0.659	-0.812*
Mature samples (5–8 yr)							
Skeletal density	Solar radiation	—	—	0.274	-0.523	0.248	-0.498
Linear extension	Solar radiation	—	—	0.314	-0.560	0.324	-0.569
Calcification	Solar radiation	—	—	0.353	-0.594	0.347	-0.589
Skeletal density	SST	-9.007 (0.918)	26.730 (2.710)	0.960	-0.980***	0.922	-0.960***
Linear extension	SST	—	—	<0.001	-0.015	<0.001	-0.016
Calcification	SST	-8.936 (1.431)	26.685 (4.224)	0.907	-0.952**	0.799	-0.894*
Old samples (>8 yr)							
Skeletal density	Solar radiation	—	—	0.191	-0.437	0.167	-0.403
Linear extension	Solar radiation	—	—	0.246	0.496	0.229	0.479
Calcification	Solar radiation	—	—	0.152	-0.390	0.097	-0.311
Skeletal density	SST	-8.980 (1.316)	26.713 (3.885)	0.921	-0.960**	0.857	-0.926**
Linear extension	SST	4.127 (0.268)	-12.382 (0.792)	0.983	0.992***	0.974	0.987***
Calcification	SST	—	—	0.798	-0.893*	0.570	-0.755

† r^2 , Pearson's coefficient of determination; r , Pearson's correlation coefficient; r_{BS}^2 and r_{BS} , Pearson's coefficients calculated with bootstrapping; SST, sea surface temperature; SE, standard error.

* $p < 0.050$.

** $p < 0.010$.

*** $p < 0.001$.

investing calcification in skeletal density or linear extension (Carricart-Ganivet and Merino 2001; Carricart-Ganivet 2004). *Porites*, for example, invests increased calcification at higher temperatures into linear extension, allowing the coral to occupy space as rapidly as possible (Lough and Barnes 2000). In contrast, *M. annularis* invests increased calcification at higher temperatures to construct more dense skeletons (Carricart-Ganivet and Merino 2001; Carricart-Ganivet 2004). In *B. europaea*, linear extension rate and skeletal density were both positively correlated with calcification rate, indicating that the capacity to colonize the substratum quickly and the mechanical strength of the skeleton are both important for this species and that calcification is allocated evenly between increasing skeletal density and linear extension, in comparison with *Porites* and *M. annularis*. For each $1 \text{ mg mm}^{-2} \text{ yr}^{-1}$ of calcification rate reduction, linear extension rate decreased by $\sim 0.3 \text{ mm yr}^{-1}$, and skeletal density decreased by $\sim 0.6 \text{ mg mm}^{-3}$.

Calculated density values were reasonable with respect to other studies on tropical species (Bucher et al. 1998; Lough and Barnes 2000; Carricart-Ganivet 2004). The

geometrically computed skeletal density used in this and previous studies (Goffredo et al. 2007) is analogous to the bulk density (Bucher et al. 1998), which is equal to the skeletal mass divided by the total volume (skeletal matrix volume + pores volume; Bucher et al. 1998). Skeletal matrix volume is further composed by the CaCO_3 and by the intracrystalline organic framework regulating the crystallization process (Cohen and McConnaughey 2003). Analyses to quantify the organic framework content and porosity in the same samples are currently underway to verify if the variation in bulk skeletal density depends on the porosity or on the specific gravity of CaCO_3 crystals or on the content of organic framework. Estimates of micro-density may be obtained by a water displacement technique, but we chose not to use this method because the procedure involves the use of acetone (Bucher et al. 1998) and could have affected the above-mentioned fine studies on organic framework quantification.

The fact that calcification rate and skeletal density were not correlated with solar radiation, while they were negatively correlated with SST, confirms previous studies on the biometry, growth, and population structure stability

of this species, in which the coral parameters show stronger and more significant relationships with temperature than with light (Goffredo et al. 2007, 2008). For both the linear and power function models, trends of the analyses performed on the full data set were confirmed by most of the analyses on the three age-based subsets, indicating that differences in the mean age of the samples in the populations (Goffredo et al. 2008) did not bias the results. The positive correlation between linear extension rate and SST in the older samples is expected, since corallite asymptotic length in the populations is positively correlated with SST. Given the reduced growth rate of this species as corallite size approaches the asymptotic one, old samples in cooler waters are close to their asymptotic length and extend their size very slowly, while old samples in warmer waters are far from the asymptote and still significantly increase their size (Goffredo et al. 2008). This is very likely the cause of the lowered r value in the negative correlation between calcification and SST for the old samples subset (i.e., linear extension in the old samples subset does not decrease with SST, as in the other subsets, and the decrease in calcification with SST is less steep).

The decrease in calcification rate with increasing temperature for *B. europaea* is in contrast with the findings of other studies on latitudinal variations of calcification in tropical and temperate corals, in which the trend was the opposite (Lough and Barnes 2000; Howe and Marshall 2002; Carricart-Ganivet 2004). In addition to being an opposite trend, the response of *B. europaea* calcification rate to temperature ($-1.00 \text{ mg mm}^{-2} \text{ yr}^{-1} \text{ }^{\circ}\text{C}^{-1}$; present work, Table 4) was three times lower than that of *Porites* ($+3.30 \text{ mg mm}^{-2} \text{ yr}^{-1} \text{ }^{\circ}\text{C}^{-1}$; Lough and Barnes 2000) and five times lower in comparison with *M. annularis* ($+5.70 \text{ mg mm}^{-2} \text{ yr}^{-1} \text{ }^{\circ}\text{C}^{-1}$; Carricart-Ganivet 2004). However, a recent study shows a decline in coral calcification in massive *Porites* from the Great Barrier Reef over a 16-yr period (Cooper et al. 2008) and indicates that this reduction is linked to the interactive effects of increasing seawater temperatures and pCO_2 -associated acidification (Reynaud et al. 2003).

The reduction of *B. europaea* calcification with increasing temperature might depend on the response of zooxanthellae photosynthesis to temperature, since in zooxanthellate corals calcification is enhanced by photosynthesis (Al-Horani et al. 2005), and both processes have temperature optima (Howe and Marshall 2002). In the closely related nonphotosynthetic coral *Leptopsammia pruvoti* the skeletal density measured in the same localities of this study is not affected by temperature (Goffredo et al. 2007). Moreover, linear extension rate and calcification are not significantly different between two populations of *L. pruvoti* situated 850 km apart, despite the different thermal regimes (S. Goffredo et al. unpubl.). Preliminary studies of various populations of *B. europaea* have found zooxanthellae belonging exclusively to clade A (M. A. Coffroth pers. comm.), as previously reported for one population in Spain (Visram et al. 2006). Under experimental conditions, zooxanthellae belonging to this clade hosted by *Cladocora caespitosa* have proved to be resistant to short-term temperature increases, even above those recorded in nature

(Rodolfo-Metalpa et al. 2006a). However, exposure to the same temperature range for prolonged periods has been lethal for 100% of the colonies of *C. caespitosa* studied (Rodolfo-Metalpa et al. 2006b). In situ, several mass mortality events have been reported for *B. europaea* and *C. caespitosa*, linked to periods of elevated temperatures and zooxanthellae bleaching (Rodolfo-Metalpa et al. 2000). The optimal temperature for the photosynthesis of the *B. europaea* symbiotic system might be equal to or lower than the lowest ever recorded in nature in the populations sampled in this study (18.0°C). Testing the hypothesis that a rise in temperature causes a significant reduction in the photosynthetic efficiency of clade A zooxanthellae in *B. europaea* requires further investigations using experimental approaches (Karako-Lampert et al. 2005; Rodolfo-Metalpa et al. 2006a,b).

Energetic constraints related to suspension feeding may provide an alternative explanation for the negative effects of increasing temperature on calcification of *B. europaea*. In the Mediterranean, the warm summer-fall season is characterized by lower nutrient levels and zooplankton availability than the cool winter-spring season (Coma et al. 2000). Corals and several benthic suspension feeding taxa have proved to be stressed by low nutrients and limited zooplankton availability (Coma et al. 2000). In *Stylophora pistillata* colonies, starved corals show significantly lower levels of calcification and photosynthesis than fed corals (Houlbrèque et al. 2004). Low availability of resources at high temperatures may slow calcification in *B. europaea*. However, if this was the case, the inhibition would also be found in the azooxanthellate, nonphotosynthetic species *L. pruvoti*. Instead, *L. pruvoti* demography seems to be unaffected by temperature (Goffredo et al. 2007). Although the hypothesis of photosynthetic inhibition at high temperatures is intriguing, other environmental parameters may influence coral growth (pH, total alkalinity, wave exposition, flow rate, etc.) and contribute to producing the observed trends. Further investigations are needed to better constrain the environmental controls on the growth of this species.

Our results encourage speculation regarding the possible effect of global climate change on this species. Global increase in sea temperature is one of the greatest threats for reef corals (Hughes et al. 2003). The linear regression between calcification rate and SST predicted that calcification of *B. europaea* would cease at a mean annual SST of 20.5°C (zero values of skeletal density would occur at 21.2°C). When considering the power function model, calcification is expected to approach zero values at 21.0°C (21.3°C for the skeletal density), values very close to the ones obtained by the linear model. Extrapolating the regressions between calcification and SST has the limitation of assuming that the linear (or power function) relationship will be maintained. This may not necessarily be true, in fact, from 18.0°C (CL) to 19.1°C (PL) calcification drops by 64% ($2.86\text{--}1.02 \text{ mg mm}^{-2} \text{ yr}^{-1}$) and from 19.1°C (PL) to 19.9°C (PN) it drops only by 5% ($1.02\text{--}0.97 \text{ mg mm}^{-2} \text{ yr}^{-1}$), indicating the existence of a possible plateau (Table 2). Using a power function model partially addresses this problem, but the limits of extrapolating beyond the warmest temperature recorded remain.

The conclusions must be taken with caution, but the concern for the possible negative fate of this endemic species with continued global warming remains. While adaptive changes such as acclimation (modifying cell metabolism to perform better at the new temperatures) or adaptation (the selection of organisms that respond better to the new temperatures; Clarke 1983) cannot be excluded as SST rises, evidence that corals and their symbionts can adapt to rapid climate change is equivocal or nonexistent (Hoegh-Guldberg et al. 2007). Global SSTs are projected to increase by 1–3°C by 2100, with a higher increase in temperate areas of the northern hemisphere than in tropical areas (Solomon et al. 2007).

Assuming an intermediate and rather conservative increase (2°C), SST is expected to approach the zero calcification point for most of the populations considered in this study (projected temperature in 2100 in the population of Calafuria = 20.0°C; Elba = 20.7°C; Palinuro = 21.1°C; Scilla = 21.5°C; Genova = 21.6°C; and Pantelleria = 21.9°C). This scenario would indicate a possible reduction in the distribution area of this species, with irrecoverable losses in terms of genetic variability, considering the fragmented genetic structure that characterizes the species (Goffredo et al. 2004b). At the same time, the fragmented genetic structure indicates that changes from one latitude to another may involve genetic differences between locally adapted corals, and corals used in our study may have had an untold number of years to adapt to the average annual temperature at their site (Kleypas et al. 2005). This may have biased our approach of using a spatial relationship to infer how populations will respond to future temperatures. Studies have shown that corals can adapt if given thousands of years, but the Intergovernmental Panel on Climate Change (IPCC) scenarios we considered are on a timescale of one order of magnitude shorter, and this could give no chances for adaptation. To produce a more accurate projection of future calcification rates in response to increased temperature, physiological experimental studies of the calcification–temperature relationship in corals from the various populations under current-seasonal and future-expected temperatures are needed. Even then, we cannot be sure that corals could not adapt if given 50–100 yr, since little is known about rates of adaptation.

This study is the first field investigation of the relationship between environmental parameters and estimated growth parameters of a Mediterranean coral. Being endemic to the Mediterranean, *B. europaea* has very limited possibilities to respond to seawater warming by moving northward toward lower temperatures, since the latitudinal range considered covers almost the entire northern distribution of this species. Even with the limits of curve extrapolation, this study highlights the risk of losing Mediterranean marine biodiversity over the course of future decades, adding a voice to the choir of scientists who for years have been asking for worldwide political intervention to slow down global warming.

Acknowledgments

We thank L. Bortolazzi, A. Comini, M. Ghelia, G. Neto, and L. Tomesani for their underwater assistance in collecting the

samples. The diving centres Centro Immersioni Pantelleria, Il Pesciolino, Polo Sub, and Sub Maldive supplied logistical assistance in the field. The Bologna Scuba Team and the Scientific Diving School collaborated in the underwater activities. The Marine Science Group (<http://www.marinesciencegroup.org>) supplied scientific, technical, and logistical support. Two anonymous reviewers gave valuable comments that improved the manuscript.

This research was financed by the Ministry of Education, University and Research, the Ministry of Tourism of the Arab Republic of Egypt, the Associazione dei Tour Operator Italiani, the Project AWARE Foundation, the Scuba Nitrox Safety International, the Scuba Schools International, the Underwater Life Project, the Marine & Freshwater Science Group Association, and the Canziani Foundation of the Department of Evolutionary and Experimental Biology of the Alma Mater Studiorum–University of Bologna. The experiments complied with current Italian law.

References

- AL-HORANI, F. A., T. FERDELMAN, S. M. AL-MOHRABI, AND D. DE BEER. 2005. Spatial distribution of calcification and photosynthesis in the scleractinian coral *Galaxea fascicularis*. *Coral Reefs* **24**: 173–180.
- BUCHER, D. J., V. J. HARRIOTT, AND L. G. ROBERTS. 1998. Skeletal micro-density, porosity and bulk density of acroporid corals. *J. Exp. Mar. Biol. Ecol.* **228**: 117–136.
- CARRICART-GANIVET, J. P. 2004. Sea surface temperature and the growth of the West Atlantic reef-building coral *Montastraea annularis*. *J. Exp. Mar. Biol. Ecol.* **302**: 249–260.
- , AND M. MERINO. 2001. Growth responses of the reef-building coral *Montastraea annularis* along a gradient of continental influence in the southern Gulf of Mexico. *Bull. Mar. Sci.* **68**: 133–146.
- CLARKE, A. 1983. Life in cold water: The physiological ecology of polar marine ectotherms. *Oceanogr. Mar. Biol. Annu. Rev.* **21**: 341–453.
- COHEN, A. L., AND T. A. MCCONNAUGHEY. 2003. Geochemical perspectives on coral mineralization. *Rev. Miner. Geochem.* **54**: 151–187.
- COMA, R., M. RIBES, J. M. GILI, AND M. ZABALA. 2000. Seasonality in coastal ecosystems. *Trends Ecol. Evol.* **12**: 448–453.
- COOPER, T. F., G. DE'ATH, K. E. FABRICIUS, AND J. M. LOUGH. 2008. Declining coral calcification in massive *Porites* in two nearshore regions of the northern Great Barrier Reef. *Glob. Change Biol.* **14**: 529–538.
- DODGE, R. E., AND G. W. BRASS. 1984. Skeletal extension, density and calcification of the reef coral, *Montastrea annularis*: St. Croix, U.S. Virgin Islands. *Bull. Mar. Sci.* **34**: 288–307.
- EFRON, B. 1981. Nonparametric estimates of standard error: The jackknife, the bootstrap and other methods. *Biometrika* **68**: 589–599.
- GOFFREDO, S., S. ARNONE, AND F. ZACCANTI. 2002. Sexual reproduction in the Mediterranean solitary coral *Balanophyllia europaea* (Scleractinia, Dendrophylliidae). *Mar. Ecol. Prog. Ser.* **229**: 83–94.
- , E. CAROSELLI, G. MATTIOLI, E. PIGNOTTI, AND F. ZACCANTI. 2008. Relationships between growth, population structure and sea surface temperature in the temperate solitary coral *Balanophyllia europaea* (Scleractinia, Dendrophylliidae). *Coral Reefs* **27**: 623–632.
- , ———, E. PIGNOTTI, G. MATTIOLI, AND F. ZACCANTI. 2007. Variation in biometry and demography of solitary corals with environmental factors in the Mediterranean Sea. *Mar. Biol.* **152**: 351–361.

- , G. MATTIOLI, AND F. ZACCANTI. 2004a. Growth and population dynamics model of the Mediterranean solitary coral *Balanophyllia europaea* (Scleractinia, Dendrophylliidae). *Coral Reefs* **23**: 433–443.
- , L. MEZZOMONACO, AND F. ZACCANTI. 2004b. Genetic differentiation among populations of the Mediterranean hermaphroditic brooding coral *Balanophyllia europaea* (Scleractinia, Dendrophylliidae). *Mar. Biol.* **145**: 1075–1083.
- GOREAU, T. F. 1959. The physiology of skeleton formation in corals. I. A method for measuring the rate of calcium deposition by corals under different conditions. *Biol. Bull.* **116**: 59–75.
- HOEGH-GULDBERG, O., AND OTHERS. 2007. Coral reefs under rapid climate change and ocean acidification. *Science* **318**: 1737–1742.
- HOULBRÈQUE, F., E. TAMBUTTÈ, D. ALLEMAND, AND C. FERRIER-PAGÈS. 2004. Interactions between zooplankton feeding, photosynthesis and skeletal growth in the scleractinian coral *Stylophora pistillata*. *J. Exp. Biol.* **207**: 1461–1469.
- HOWE, S. A., AND A. T. MARSHALL. 2002. Temperature effects on calcification rate and skeletal deposition in the temperate coral, *Plesiastrea versipora* (Lamarck). *J. Exp. Mar. Biol. Ecol.* **275**: 63–81.
- HUGHES, T. P., AND OTHERS. 2003. Climate change, human impacts, and the resilience of coral reefs. *Nature* **301**: 929–933.
- KAIN, J. M. 1989. The seasons in the subtidal. *Br. Phycol. J.* **24**: 203–215.
- KARAKO-LAMPERT, S., D. J. KATCOFF, Y. ACHITUV, Z. DUBINSKY, AND N. STAMBLER. 2005. Responses of *Symbiodinium microadriaticum* clade B to different environmental conditions. *J. Exp. Mar. Biol. Ecol.* **318**: 11–20.
- KINSEY, D. W., AND P. J. DAVIES. 1979. Carbon turnover, calcification and growth in coral reefs, p. 131–162. *In* P. A. Trudinger and D. J. Swaine [eds.], *Biogeochemical cycling of mineral forming elements*. Elsevier.
- KLEYPAS, J. A., J. W. MCMANUS, AND L. A. B. MENEZ. 1999. Environmental limits to coral reef development: Where do we draw the line? *Am. Zool.* **39**: 146–159.
- , AND OTHERS. 2005. Comment on “Coral reef calcification and climate change: The effect of ocean warming.” *Geophys. Res. Lett.* **32**: L08601, doi:10.1029/2004GL022329.
- LOUGH, J. M., AND D. J. BARNES. 2000. Environmental controls on growth of the massive coral *Porites*. *J. Exp. Mar. Biol. Ecol.* **245**: 225–243.
- MASS, T., S. EINBINDER, E. BROKOVICH, N. SHASHAR, R. VAGO, J. ÈREZ, AND Z. DUBINSKY. 2007. Photoacclimation of *Stylophora pistillata* to light extremes: Metabolism and calcification. *Mar. Ecol. Prog. Ser.* **334**: 93–102.
- REYNAUD, S., N. LECLERCQ, S. ROMAINE-LILOUD, C. FERRIER-PAGÈS, J. JAUBERT, AND J. P. GATTUSO. 2003. Interactive effects of CO₂ partial pressure and temperature on photosynthesis and calcification in a scleractinian coral. *Glob. Change Biol.* **9**: 1660–1668.
- RINKEVICH, B. 1989. The contribution of photosynthetic products to coral reproduction. *Mar. Biol.* **101**: 259–263.
- RODOLFO-METALPA, R., C. N. BIANCHI, A. PEIRANO, AND C. MORRI. 2000. Coral mortality in NW Mediterranean. *Coral Reefs* **19**: 24.
- , C. RICHARD, D. ALLEMAND, C. N. BIANCHI, C. MORRI, AND C. FERRIER-PAGÈS. 2006a. Response of zooxanthellae in symbiosis with the Mediterranean corals *Cladocora caespitosa* and *Oculina patagonica* to elevated temperatures. *Mar. Biol.* **150**: 45–55.
- , ———, ———, AND C. FERRIER-PAGÈS. 2006b. Growth and photosynthesis of two Mediterranean corals, *Cladocora caespitosa* and *Oculina patagonica*, under normal and elevated temperatures. *J. Exp. Biol.* **209**: 4546–4556.
- SOLOMON, S., AND OTHERS. 2007. *Climate change 2007: The physical science basis*. Cambridge Univ. Press.
- VISRAM, S., J. WIEDENMANN, AND A. E. DOUGLAS. 2006. Molecular diversity of symbiotic algae of the genus *Symbiodinium* (Zooxanthellae) in cnidarians of the Mediterranean Sea. *J. Mar. Biol. Assoc. UK* **86**: 1281–1283.
- VON BERTALANFFY, L. 1938. A quantitative theory of organic growth (inquiries on growth laws II). *Hum. Biol.* **10**: 181–213.
- ZIBROWIUS, H. 1980. The scleractinians of the Mediterranean and of the North-Eastern Atlantic. *Mem. Inst. Oceanogr. (Monaco)* **11**: 1–284. [In French.]

Associate editor: Anthony Larkum

Received: 04 September 2008

Accepted: 19 January 2009

Amended: 08 February 2009