

Latitudinal variations in biometry and population density of a Mediterranean solitary coral

Erik Caroselli,¹ Valentina Nanni,¹ Oren Levy,² Giuseppe Falini,³ Zvy Dubinsky,² Stefano Goffredo*¹

¹Department of Biological, Marine Science Group, Geological and Environmental Sciences, Section of Biology, University of Bologna, Bologna, Italy

²The Mina and Everard Goodman Faculty of Life Science, Bar-Ilan University, Ramat-Gan, Israel

³Department of Chemistry <<Giacomo Ciamician>>, University of Bologna, Bologna, Italy

Abstract

Correlations between solar radiation, sea surface temperature (SST), biometry, and population density were assessed along a wide latitudinal gradient in the non-zooxanthellate solitary coral *Caryophyllia inornata*. Biometric parameters were more strongly correlated with temperature than with solar radiation as in previous studies on Mediterranean solitary corals. With increasing SST, populations were characterized by bigger polyps, and consequently by a higher percent area coverage and mass per square meter. Population abundance was not correlated with SST, similarly to the non-zooxanthellate solitary *Leptopsammia pruvoti*. Instead, the population density of the zooxanthellate solitary *Balanophyllia europaea* decreases with increasing SST. When extrapolating the relationships between biological parameters of the three species and SST, according to the projected seawater temperature increase, a higher tolerance to temperature for non-zooxanthellate species seems to be confirmed.

Global warming and ocean acidification caused by human activities since the industrial revolution of the 19th century (such as deforestation, burning of fossil fuels, and land use change) represent a serious threat for tropical coral reef ecosystems (Hoegh-Guldberg 2011). Climate change projections estimate that the Earth's average surface air temperature is likely to increase of 1.1–6.4°C by 2100 (Solomon et al. 2007). Marine organisms are likely to be more sensitive to climate changes than their terrestrial counterparts, because temperature influences water column stability, nutrient enrichment, and the degree of new production (Richardson 2008). In particular, during the last 2–3 decades an increase with at least 0.3–0.4°C has been recorded in mean annual sea surface temperatures (SST) across much of the global tropics and subtropics (Kleypas et al. 2008). Increasing temperature is considered the major cause of many large-scale coral bleaching events (Guest et al. 2012; Furby et al. 2013), which are becoming ever more frequent (Wilkinson 2004). In temperate areas, the effect of increasing temperature is expected to be even greater. For instance, the Mediterranean Sea seems to show warming rates three times higher than the global ocean (Solomon et al. 2007), and simulations for the Mediterranean region project an increase in air surface temperature of 3.1–4.6°C by 2081–2100 under a moderate (A1B)

scenario (Giorgi and Lionello 2008). Similar increase rates in Mediterranean SSTs (+ 1.8°C) are projected for 2050 (Gualdi et al. 2013). This makes the Mediterranean Sea, whose monthly mean SSTs range between 12°C and 28°C during the year (Nykjaer 2009), a perfect field for research on the effects of temperature on corals.

Coral growth, physiology, demography, and distribution patterns are strongly linked to the variation of light and temperature, which strictly depend on latitude (Kleypas et al. 1999; Lough and Barnes 2000; Carricart-Ganivet 2004). The development of coral reefs generally decreases from the equator to 30°N and 30°S latitude (Kinsey and Davies 1979; Grigg 1982). Three related parameters are the main factors influencing coral growth: net calcification rate, skeletal bulk density (Bucher et al. 1998), and linear extension rate (net calcification = skeletal bulk density × linear extension; Lough and Barnes 2000; Carricart-Ganivet 2004). Analyzing these variables also allows to predict the possible effect of climatic changes on coral ecosystems (Cooper et al. 2008; Cantin et al. 2010; Caroselli et al. 2012a). The three growth components have been studied along a latitudinal gradient in the tropical genera *Diploastrea* (Cantin et al. 2010), *Montastraea* (Carricart-Ganivet 2004) and *Porites* (Lough and Barnes 2000; Tanzil et al. 2009; Cooper et al. 2012) and their variation has been related to changes in temperature and light associated with time and latitude. While studies on the

*Correspondence: s.goffredo@unibo.it

relationship between coral growth and environmental parameters in the tropics are numerous, such studies are scarce for temperate zones. In colonies of the Mediterranean endemic zooxanthellate coral *Cladocora caespitosa* from the Adriatic Sea, SST is positively correlated to calcification and linear extension rates (Kružić et al. 2012). However, laboratory observations on calcification rates in *C. caespitosa* and *Oculina patagonica*, showed that long periods of elevated temperatures corresponding to, or higher than, the maximum summer temperature in the field lead to a decrease of calcification (Rodolfo-Metalpa et al. 2006a). The studies along a wide latitudinal gradient in the Mediterranean Sea on two solitary dendrophylliid corals observed a different sensitivity to SST in the zooxanthellate *Balanophyllia europaea* and in the non-zooxanthellate *Leptopsammia pruvoti*. In *B. europaea*, SST is negatively correlated with a broad range of biological parameters such as population abundance (Goffredo et al. 2007), skeletal bulk density, due to an increase in porosity (Caroselli et al. 2011), population structure stability (Goffredo et al. 2008), and calcification rate (Goffredo et al. 2009). In *L. pruvoti* all these biometric (Goffredo et al. 2007), growth, and demographic parameters (Caroselli et al. 2011, 2012a,b) are unrelated to SST. The greater sensitivity of *B. europaea* to increasing SST has been hypothesized to depend on the inhibition of the zooxanthellar photosynthetic process at excessively high temperatures (Goffredo et al. 2008; Caroselli et al. 2012, 2012). The sensitivity to high temperature may depend on the zooxanthellae clade host by *B. europaea* (clade A-temperate; Visram et al. 2006), even if also clade B2 has been found in specimens maintained in aquaria and transplanted at CO₂ vents (Meron et al. 2012). In fact, clade A-temperate is sensitive to long term temperature increases (Rodolfo-Metalpa et al. 2006b), while clade B2 is resistant to cold temperatures and wide annual temperature fluctuations (Thornhill et al. 2008). Investigating the different response between symbiotic and nonsymbiotic corals may highlight different sensitivity related to the presence of the symbionts, and shed light on the possible species assemblage shifts that may occur because of climate change (van Woesik et al. 2011). Since very few data are available on non-zooxanthellate species (Caroselli and Goffredo 2014), it is strongly needed to target also this group of corals for studies related to the effects of climate change.

This study investigated the relationship of the latitudinal variation of SST and solar radiation with biometry and population density in the temperate-subtropical coral *Caryophyllia inornata* (Duncan 1878). The Caryophylliidae family is ubiquitous through all oceans of the world, and is composed both by solitary and colonial forms divided into 51 genera that include 296 living species (Cairns 1999; Kitahara et al. 2010). In the Mediterranean Sea, five genera are reported consisting of nine species (Minelli et al. 1995). The exclusively non-zooxanthellate genus *Caryophyllia* is the most diverse within the non-zooxanthellate scleractinian genera,

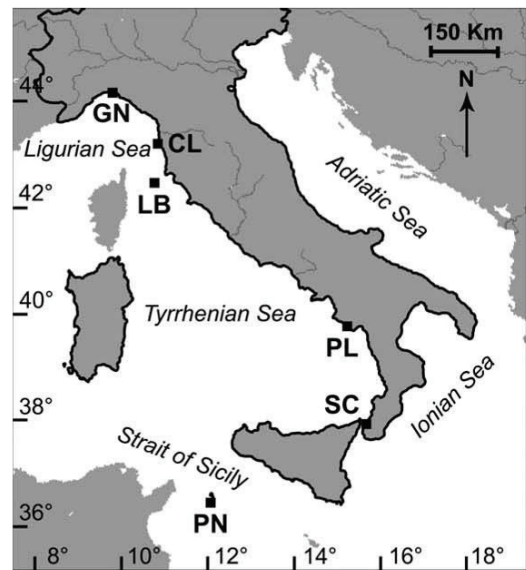


Fig. 1. Map of the Italian coastline indicating the sites where corals were collected. Abbreviations and coordinates of the site in decreasing order of latitude: GN Genova, 44°20'N and 9°08'E; CL Calafuria, 43°27'N and 10°21'E; LB Elba, 42°45'N and 10°24'E; PL Palinuro, 40°02'N and 15°16'E; SC Scilla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

comprising 66 exclusively solitary species, including *C. inornata* (Cairns 1999; Kitahara et al. 2010). *C. inornata* is distributed from the Mediterranean basin up to the Northeastern Atlantic coast from the Canary Islands to the North Sea (Zibrowius 1980; Cairns 1999). It is one of the main species colonizing dimly lit environments of vertical or overhanging walls, caves and wrecks from the surface down to 100 m depth (Zibrowius 1980), and in some cases it is the dominant species (Zibrowius 1978). It is a gonochoric and brooder species, for which a possible asexual production of embryos is proposed (Goffredo et al. 2012b).

The aim of this documentary study was to assess for the first time the variation in biometric parameters (corallite length, width, height, volume, mass, and skeletal bulk density), and population density of *C. inornata* in sites along a latitudinal gradient spanning 850 km along the Western Italian coast, and spanning 2.5°C of average SST. Since the species is non-zooxanthellate, it was expected to be tolerant to increasing SST such as the non-zooxanthellate *L. pruvoti*.

Methods

From 14 May 2009 to 14 April 2011, specimens of *C. inornata* were collected from six sites along a latitudinal gradient on the Italian coasts, from 44°20'N to 36°45'N (Fig. 1; Table 1). Latitude is the main factor influencing the variation of temperature and light (Kain 1989), which are the two environmental parameters considered in this study since they are

Table 1. Values of solar radiation and SST indicated for six Mediterranean sites. Solar radiation and SST both varied among the sites (Kruskal–Wallis test, $p < 0.001$). Sites are arranged in decreasing order of latitude. SE standard error.

| Code | Mean annual solar radiation (W m^{-2}), mean (SE) | Mean annual sea surface temperature ($^{\circ}\text{C}$), mean (SE) |
|------|--|---|
| GN | 163.3 (6.7) | 18.93 (0.39) |
| CL | 177.0 (7.7) | 18.88 (0.39) |
| LB | 183.3 (7.5) | 18.45 (0.43) |
| PL | 193.5 (7.4) | 19.72 (0.36) |
| SC | 202.4 (7.3) | 19.04 (0.27) |
| PN | 210.7 (7.1) | 20.65 (0.38) |

strongly linked to coral biometry, physiology and demography (Kleypas et al. 1999; Lough and Barnes 2000; Harriott and Banks 2002; Al-Horani 2005). Samples were collected at each site using transects that consisted of 4–8 square patches of 1 dm^2 each, situated on the vault of crevices, 3 m apart and at a depth of 11–16 m (site, number of patches, and sampling depth: Genova: $n = 6$, at 11 m; Calafuria: $n = 8$, at 16 m; Elba: $n = 4$, at 13 m; Palinuro: $n = 6$, at 11 m; Scilla: $n = 6$, at 16 m; and Pantelleria: $n = 7$, at 15 m). At the Elba site, samples were collected from underneath the wings of a sunken plane wreck. Regular spacing of quadrats and transects may be biased if laid over a population with a natural regular spacing. However, this should not have occurred in this case since the distributional pattern of the species is disaggregated (random; personal observation). All polyps found in each patch were collected. The sampling was performed at depths known to have high population densities and where the reproductive biology of *C. inornata* had been previously studied (Goffredo et al. 2012b). Addition of quadrats to have a higher number of replicates would have resulted in a stronger population abundance dataset which would not have required the Monte Carlo correction for low sample size (see statistical analyses below). However, sampling effort and data trends were comparable to previous studies on other Mediterranean corals, for which the same statistical analysis was performed (Goffredo et al. 2007).

Collected corals were dried at 50°C for 4 days, and then observed under a binocular microscope to remove fragments of substratum and calcareous deposits produced by other organisms. A low drying temperature was chosen to avoid phase transitions in the skeletal aragonite/calcite composition (Vongsavat et al. 2006), as this problem is being investigated using these samples in diffractometric analyses (see Goffredo et al. 2012a). Polyp length (L : maximum axis of the oral disc), width (W : minimum axis of the oral disc), and height (h : oral-aboral axis) were measured using a pair of calipers, and dry skeletal mass (M) was measured using a precision balance (Goffredo et al. 2002, 2007; Goffredo

and Chadwick-Furman 2003). Polyp volume (V) was determined by applying the formula $V = L/2 \times W/2 \times h\pi$ (Goffredo et al. 2002, 2006, 2007). Surface/volume (S/V) ratio was obtained by dividing S by V , where S is the surface of the entire upper area of the coral, obtained as a sum of the surface of the oral disc $\pi \times L/2 \times W/2$ and the lateral surface of the coral obtained with the formula $\pi \times [3 \times (L/2 + W/2) - \sqrt{(3 \times L/2 + W/2) \times (L/2 + 3 \times W/2)}] \times h$ (Ram-anujan 1914), excluding the base in contact with the reef. Skeletal bulk density (D) was calculated by dividing M by V . The population density was obtained as: (1) NI, numbers of individuals per area unit (N m^{-2}), (2) MA, mass per area unit (g m^{-2}) and (3) P, percent coverage.

As done by a number of authors (e.g., Lough and Barnes 2000; Carricart-Ganivet 2004; Cantin et al. 2010) in their studies on the influence of the environmental parameters on coral growth, the physical measurement data in this study (SST and solar radiation) also have been obtained from data banks. SST data of the period January 1999–December 2010 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 mareographic stations, SM3810 manufactured by the Society for the Environmental and Industrial monitoring (SIAP+MICROS), placed closed to the sampling sites (1–15 km from the actual sampling site). Mean annual SST was obtained from hourly values (number of hourly values = 105,120 for each site). Three digital thermometers (i-Button, DS1921G-F5#, Maxim Integrated Products, Dallas Semiconductors) were placed at the experimental sites, to record seawater temperature every 2–3 h during a time interval depending on the site (Fig. 2). Thermometers were replaced every 3 months to avoid encrustation and overgrowth by marine organisms. Thermometer data were used to check if SST data are representative of the temperature at the depth of coral sampling.

Monthly values of solar radiation (W m^{-2}) were obtained from the archives of the Satellite Application Facility on Climate Monitoring (CM-SAF/EUMETSAT; <http://www.cmsaf.eu>). These estimates are derived from real time satellite measurements and data sets based on intersensor calibrated radiances. Mean annual solar radiation of each site was obtained for the 15 km square associated with each of the six sites (number of monthly values = 144 for each site).

When data were nonnormally distributed, the Spearman's rank correlation coefficient was used to calculate the significance of the correlations between biometric parameters, population density and environmental variables. Spearman's coefficient is a powerful nonparametric alternative to Pearson's correlation coefficient (Altman 1991) and was calculated with SPSS 12.0 (Apache Computer Software Foundation, Forest Hill, Maryland).

SST, polyp length, and population density did not meet the assumptions of normality and homoscedasticity, thus

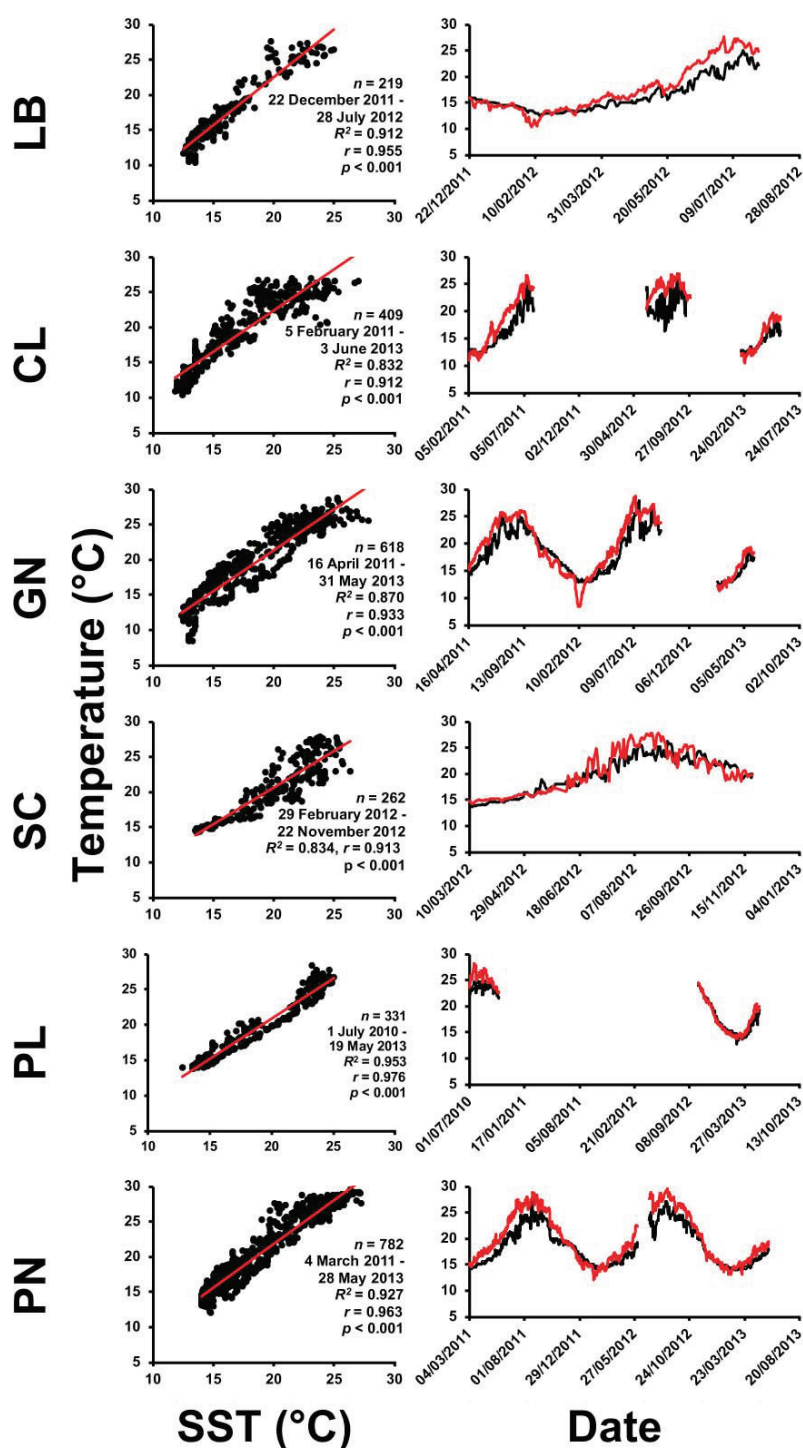


Fig. 2. Comparison between SST and temperature at sampling depth (Genova: 11 m; Calafuria: 16 m; Elba: 13 m; Palinuro: 11 m; Scilla: 16 m; and Pantelleria: 15 m) during the indicated time interval. The left column shows correlation analyses between average daily SST and temperature at sampling depth in each site for the indicated time interval. The right column shows SST (red line) and temperature at depth (black line) trends. n number of samples (days).

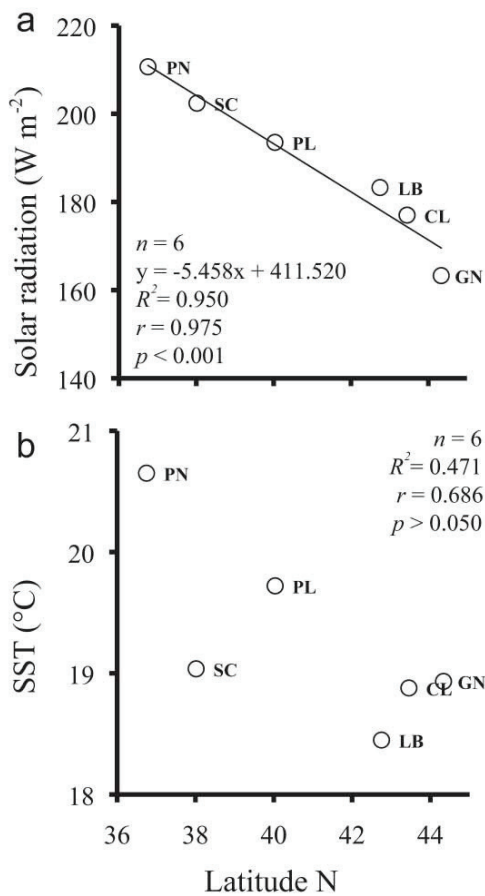


Fig. 3. Scatterplot of latitude and solar radiation of study sites (a). Scatterplot of latitude and SST of study sites (b). n number of sites; r Pearson's correlation coefficient.

their homogeneity among sites was analyzed using a permutational multivariate analysis of variance (Permanova), which has no assumptions on data distribution and shape (Anderson et al. 2008). Tests were run using euclidean distances among samples and 999 permutations in the software

Primer®. To estimate the significance of the Permanova test when comparing the mean population densities among study sites, the nonparametric Monte Carlo method was used (Gabriel and Lachenbruch 1969). This method solves problems in the nonparametric test for small samples, in fact it estimates the p -value by taking a random sample from the reference set and studies its permutations (Senchaudhuri et al. 1995).

Results

The correlation between average daily SST data from data banks and average daily temperature data collected by the digital thermometers at the sampling sites produced R^2 values ranging from 0.832 to 0.953, indicating that 83-95% of the variance of seawater temperature at the sampling depth is explained by SST variations (Fig. 2). At Pantelleria, the mean difference between SST and temperature at sampling depth on an annual basis was 1.48°C ($\text{SD} = 1.56^{\circ}\text{C}$; $\text{SE} = 0.06^{\circ}\text{C}$). Solar radiation and SST both varied among the sites (Permanova, $\text{df} = 5$, $p < 0.001$; Table 1). While solar radiation was negatively correlated with latitude, SST was not correlated with latitude (Fig. 3).

Polyp length (Fig. 4) was selected as the main biometric parameter since it is a good indicator of skeletal mass and has been used as the measure of size in biometric and reproductive biology analyses of *C. inornata* and other solitary corals (Bell and Turner 2000; Goffredo and Chadwick-Furman 2003; Goffredo et al. 2012b). Polyp width, height, volume and skeletal mass all correlated positively with polyp length, while S/V Ratio was negatively correlated with polyp length in all sites (Fig. 5). Skeletal bulk density was negatively correlated with polyp length in three sites (Calafuria, Genova, and Palinuro) and not correlated with polyp length in the other three (Elba, Scilla, and Pantelleria; Fig. 5).

The increase of polyp width with respect to polyp length exhibited either an isometric growth (Genova and Calafuria, the 95% confidence interval CI of the regression equation exponent contained 1.0, 0.961-1.059, $\text{df} = 61-85$) or an allometric growth, with polyp length increasing more rapidly

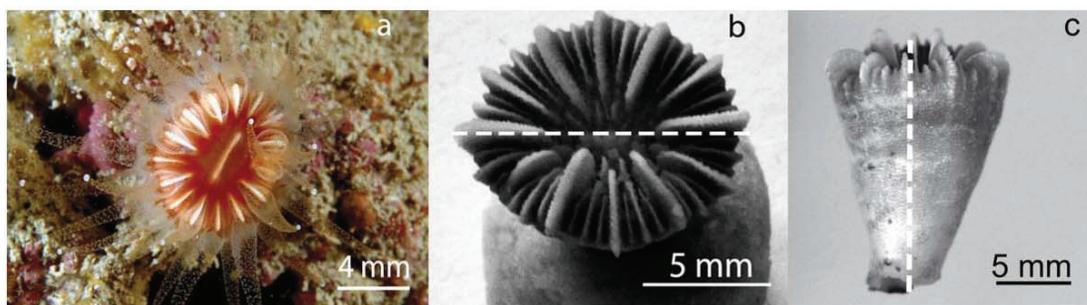


Fig. 4. *Caryophyllia inornata* a: living polyp; b: top view of the corallite with the dotted line indicating polyp length (L : maximum axis of the oral disc); c: side view of the corallite with the dotted line indicating polyp height (h : oral-aboral axis).

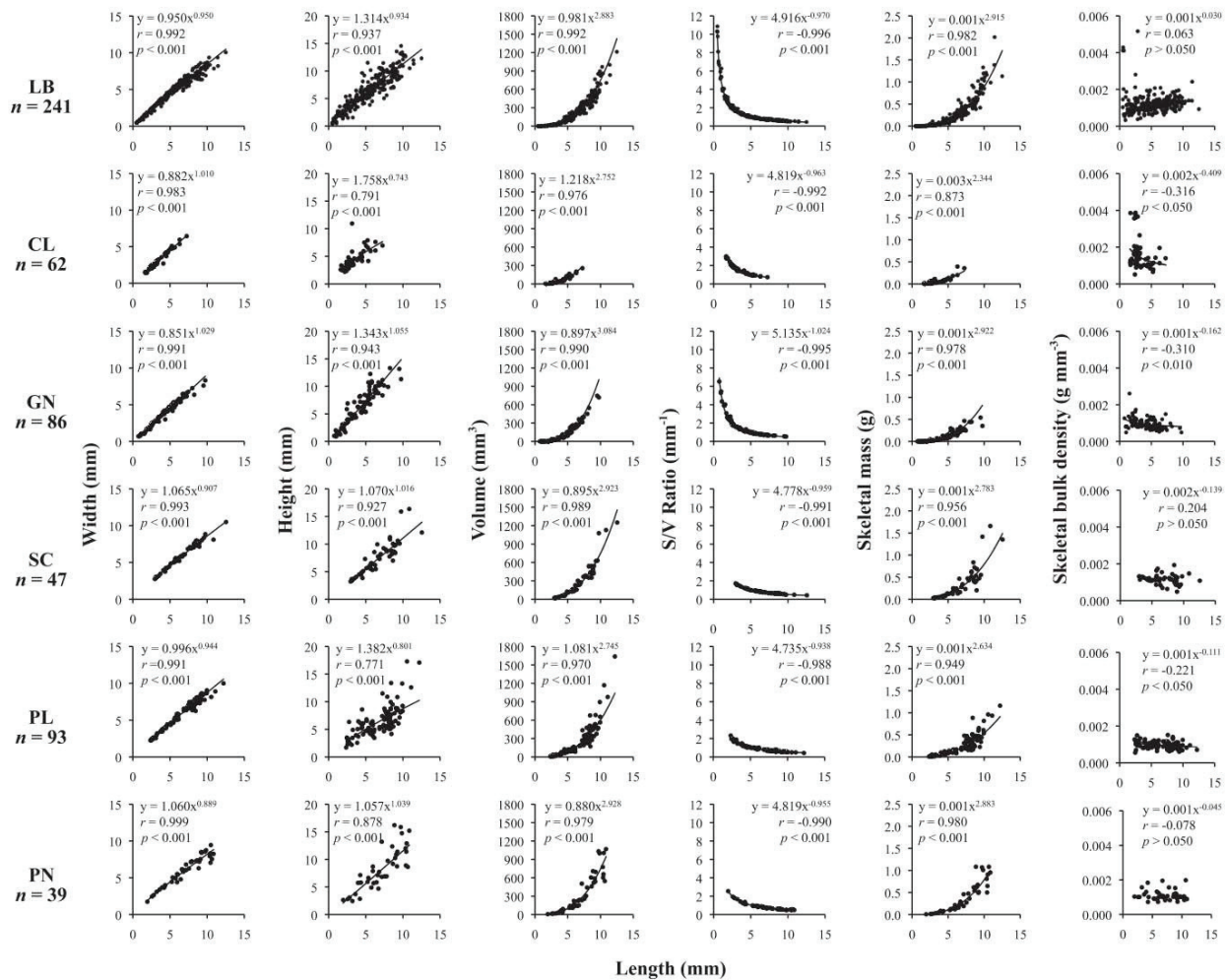


Fig. 5. *Caryophyllia inornata*. Dependence of biometric parameters on polyp length (including regression fit exponents) in the six sites (GN Genova, CL Calafuria, LB Elba, PL Palinuro, SC Scilla and PN Pantelleria). n number of individuals; r Pearson's correlation coefficient. The sites are arranged in order of increasing SST.

than width, (Elba, Palinuro, Scilla, and Pantelleria, the 95% CI of the regression equation exponent was <1.0 , $0.829\text{--}0.970$, $df = 38\text{--}240$; Fig. 5), which resulted in a progressively oval oral disc as polyp size increased.

Each relationship between biometric parameters and polyp length was linearized by log-transforming both the dependent and independent variable and the obtained slopes (equal to the exponents of the power function equations reported in Fig. 5) were compared among study sites. None of the exponents was homogeneous among study sites (the 95% CIs of the exponents were never overlapped among all sites; Table 2). The exponents of the relationships between polyp length and width correlated negatively with solar radiation (Fig. 6) while they were not correlated with SST, indicating a trend of "ovalization" of the oral disc with decreasing latitude. For all the other parameters, the

exponents were not correlated with environmental parameters.

The length of sampled individuals differed significantly among sites (Permanova, $df = 5$, $p < 0.001$). For this reason, analyses of correlation between the other biometric parameters (W , h , V , S/V , M , D) and environmental variables were performed after applying to the data the method of the adjusted values in relation to length (Steel 1980; Goffredo et al. 2007). Polyp length and width showed a positive correlation with both solar radiation and SST, while S/V ratio showed a positive correlation only with solar radiation. Polyp height and skeletal mass were negatively correlated with both solar radiation and SST. Negative correlations were also found between polyp volume and solar radiation and between skeletal bulk density and SST (Fig. 7). The same analyses were repeated after exclusion of the Elba site to

Table 2. Exponents of the relationships between biometric parameters and polyp length for six sites where corals were collected. None of the exponents was homogeneous among study sites. Sites are arranged in decreasing order of latitude.

| Parameter | Code | Exponent (mean) | 95% Confidence interval |
|---|------|-----------------|-------------------------|
| Width (mm) | GN | 1.029 | 0.999-1.059 |
| | CL | 1.010 | 0.961-1.059 |
| | LB | 0.950 | 0.935-0.965 |
| | PL | 0.944 | 0.918-0.970 |
| | SC | 0.907 | 0.874-0.940 |
| | PN | 0.889 | 0.829-0.949 |
| Height (mm) | GN | 1.055 | 0.974-1.135 |
| | CL | 0.743 | 0.594-0.891 |
| | LB | 0.934 | 0.889-0.978 |
| | PL | 0.801 | 0.663-0.939 |
| | SC | 1.016 | 0.892-1.139 |
| | PN | 1.039 | 0.850-1.227 |
| Volume (mm ³) | GN | 3.084 | 2.988-3.180 |
| | CL | 2.752 | 2.595-2.910 |
| | LB | 2.883 | 2.835-2.931 |
| | PL | 2.745 | 2.603-2.888 |
| | SC | 2.923 | 2.791-3.054 |
| | PN | 2.928 | 2.725-3.130 |
| S/V ratio (mm ⁻¹) | GN | -1.024 | -(1.046-1.002) |
| | CL | -0.963 | -(0.995-0.931) |
| | LB | -0.970 | -(0.982-0.959) |
| | PL | -0.938 | -(0.969-0.908) |
| | SC | -0.959 | -(0.987-0.932) |
| | PN | -0.955 | -(1.001-0.910) |
| Skeletal mass (g) | GN | 2.921 | 2.787-3.056 |
| | CL | 2.344 | 2.006-2.681 |
| | LB | 2.915 | 2.844-2.987 |
| | PL | 2.634 | 2.451-2.817 |
| | SC | 2.783 | 2.527-3.039 |
| | PN | 2.883 | 2.689-3.076 |
| Skeletal bulk density (g mm ⁻³) | GN | -0.162 | -(0.270-0.054) |
| | CL | -0.409 | -(0.725-0.092) |
| | LB | 0.032 | -0.033-0.097 |
| | PL | -0.111 | -(0.214-0.009) |
| | SC | -0.139 | -0.340-0.062 |
| | PN | -0.045 | -0.236-0.147 |

consider only the sites characterized by a natural substratum. Also after exclusion of the Elba site, the length of sampled individuals differed significantly among sites (Permanova, $df = 4$, $p < 0.001$). In the majority of cases (71%), both SST and solar radiation explained 1.3-555.6 times more of the biometric parameter variance after exclusion of the Elba site (Fig. 7). Without considering the Elba site, polyp length and S/V ratio showed a positive correlation with both solar radiation and SST, while width and skeletal bulk density were positively

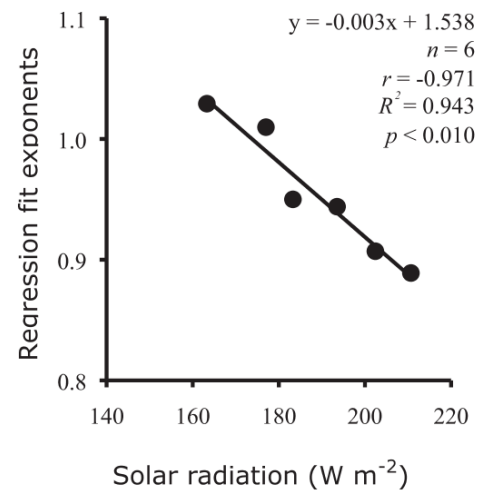


Fig. 6. *Caryophyllia inornata*. Correlation and linear regression analysis between the regression fit exponents of the width-length relationships (y axis) and solar radiation (x axis) of the six sites. n number of sites; r Pearson's correlation coefficient; R^2 Pearson's determination coefficient.

correlated only with solar radiation (Fig. 7). Polyp height, volume, and skeletal mass showed a negative correlation both with solar radiation and SST (Fig. 7). Summarizing these results, polyp width, height, volume and skeletal bulk density resulted more correlated with solar radiation, while length and skeletal mass were more correlated with SST (Fig. 7).

The analyses on population density were also carried out after exclusion of the Elba site, since the plane wreck where corals were collected displayed a population abundance that was 10 times higher than the mean of all other natural sites analyzed. All the three measures of population density varied significantly among the sites (Permanova, Monte Carlo correction for small sample size, $df = 4$, $p < 0.01$; Fig. 8). While population abundance (NI) was not correlated with environmental parameters, mass per square meter (MA) showed a positive correlation both with solar radiation and SST, with SST variation explaining a higher percentage of MA variance than solar radiation (41.0% for SST, 19.1% for solar radiation; Fig. 8). Percent cover (P) showed a positive correlation only with SST, whose variation explained 33.3% of percent cover variance (Fig. 8).

Two plots were produced (Figs. 9, 10) by projecting the relationships between skeletal bulk density, NI and SST for the three species *C. inornata* (present study), *B. europaea*, and *L. pruvoti* (from Goffredo et al. 2007) to compare their sensitivity to the projected increase of seawater temperature according to different Intergovernmental Panel on Climate Change (IPCC) scenarios.

Discussion

The 82-95% of seawater temperature variance at coral sampling depth (11-16 m) was explained by variations in

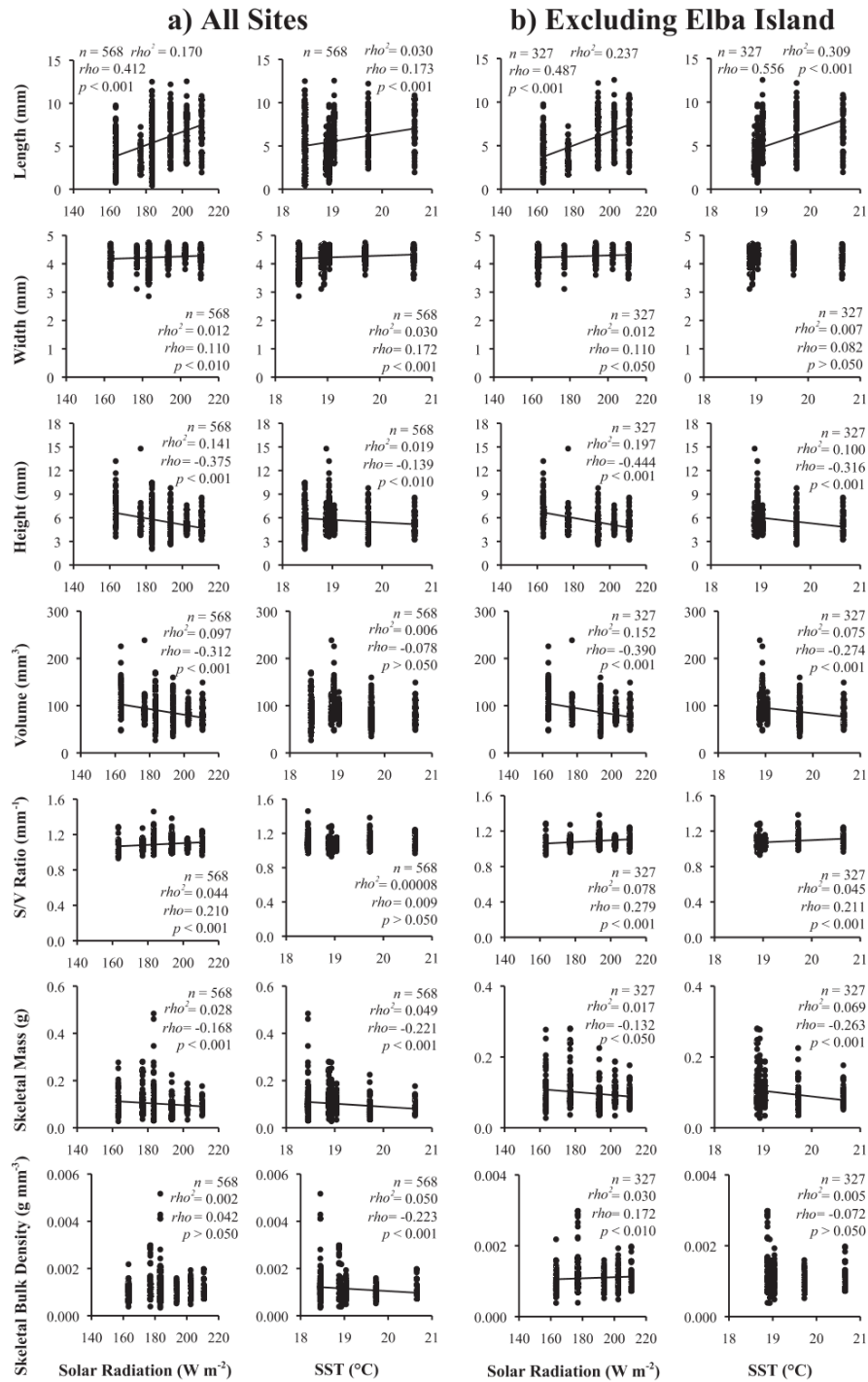


Fig. 7. *Caryophyllia inornata*. Variation in biometric parameters with solar radiation and SST, including all sites (a) and after exclusion of the Elba site (b). Since the length of sampled individuals differed significantly among sites, the values of width, height, volume, S/V ratio, skeletal mass, and skeletal bulk density were corrected by applying the method of the adjusted values in relation to length. ρ^2 Spearman's determination coefficient; ρ Spearman's correlation coefficient; n number of individuals.

SST, indicating that SST generally follows the actual temperature trend at the sampling depth, as shown by the temperature trends at both depths (Fig. 2). At the Calafuria and Pantelleria sites, where more temperature data were collected (some populations display periods of missing data because the thermometers were damaged or lost), 87–93% of SST variance was explained by variations of temperature at sampling depth (Fig. 2). This trend was maintained across all populations, indicating that SST is a good proxy for actual temperature at the sampling depth of this study. Even if, in the Mediterranean Sea, temperature ranges, seasonal variations and anomalies appear highly important in affecting organism metabolism, growth rates, diseases and mortality (Crisci et al. 2011), we prefer the use of annual mean temperature to discriminate thermal differences among sites, to allow comparisons with previous studies on other Mediterranean scleractinians for which mean annual SSTs have been used (Goffredo et al. 2009; Caroselli et al. 2012; Fantazzini et al. 2013). Since the present study focused on the influence of SR and SST, we selected sites with similar environmental traits other than SR and SST, but we did not thoroughly analyze all the site characteristics such as zooplankton availability, geographic orientation, pollution, exposure to streams and waves, and water turbidity, which could all contribute to the observed differences in some population traits. However, these local differences, while contributing to the variability of population parameters, are not strong enough to determine variations in population abundance (NI). For example, in the Mediterranean Sea zooplankton abundance decreases southwards, while NI did not decrease southward in this study.

The relationship between skeletal bulk density and polyp size can be interpreted in terms of relationship between calcification and linear extension. In *C. inornata*, as known for several other solitary corals (Bablet 1985; Yamashiro and Nishihira 1998; Goffredo et al. 2009), the linear extension rate is expected to decrease with increasing polyp size (age). Since $\text{calcification} = \text{skeletal density} \times \text{linear extension}$ (Lough and Barnes 2000; Carricart-Ganivet 2004), a parallel decrease of linear extension and calcification rates could explain the stable skeletal bulk density around values of 0.001 g mm^{-3} regardless of polyp size, at three of the six sites studied (Elba, Scilla, and Pantelleria). At the Calafuria, Genova, and Palinuro sites, the decrease of skeletal bulk density with increasing polyp size may have been due to a greater decrease in calcification than in linear extension, as already suggested for *L. pruvoti* (Goffredo et al. 2007). The sclerochronological analyses underway on *C. inornata* will further explore the relationships between calcification and linear extension rates in this species.

In the majority of sites (four out of six), an allometric relationship was found between polyp width and length, with larger (older) polyps characterized by a progressively oval oral disc. Moreover, the negative correlation between

solar radiation and the exponents of the relation between length and width, outlined a trend of increasing ovalization of the oral disc with increasing solar radiation (decreasing latitude). The shape of polyp oral discs has been put in relation to sedimentation stress. To prevent the negative effects of sedimentation, corals can adopt different strategies, as sediment rejection behavior or resistant growth forms (Goffredo et al. 2010; Bongaerts et al. 2012; Erftemeijer et al. 2012), such as an oval oral disc (Hoeksema 1991). The progressive ovalization of the oral disc with increasing length in the Mediterranean zooxanthellate *B. europaea* is hypothesized to prevent damage from sedimentation, which might occur as polyps become larger (Goffredo et al. 2004, 2007). However, in corals living on vertical walls, such as *C. inornata*, sediment removal should be easily carried out by gravity, rather than by active mechanisms (Stafford-Smith and Ormond 1992). For example, the non-zooxanthellate *L. pruvoti*, colonizing the vaults of Mediterranean caves and crevices with the oral pole facing downward, has more circular oral discs (Goffredo et al. 2007). Thus, the progressively oval shape of the oral discs in *C. inornata* polyps, who colonizes vertical walls and overhangs, is hardly explained as a direct response to sedimentation stress. As an alternative hypothesis, morphology has been put in relation with zooplankton capture ability (Houlbrèque and Ferrier-Pagès 2009). Having a greater feeding surface area has shown to be advantageous for zooplankton capture (Sebens 1979; Hoeksema and Waheed 2012). In the presence of high flow speed, a high surface area or S/V ratio could increase zooplankton capture by providing greater contact area (Sebens and Johnson 1991; Helmuth and Sebens 1993), as suggested by field observation in the Caribbean Sea (Sebens et al. 1996, 1998), in the Gulf of Panama (Palardy et al. 2005) and laboratory observation (Ferrier-Pagès et al. 2010). In this study, S/V increased with solar radiation. Since in the Mediterranean zooplankton abundance generally decreases with increasing solar radiation (Saiz et al. 2014), the morphological variation registered could represent an adaptation to improve the prey capture under conditions of decreased prey abundance and high flow, typical of the shallow waters where the samples of *C. inornata* were collected.

All of *C. inornata* biometric parameters showed a higher correlation with the environmental variables after the exclusion of the Elba site, where corals were collected under the wings of a sunken plane wreck lying on a sandy substrate. In this site, all of the population density parameters for *C. inornata* resulted in a 10 times higher mean value than at the other five sites, and this is the only scleractinian present on the shaded parts of the wreck, even if other scleractinian species (such as *L. pruvoti*) colonize natural rocky environments close to the wreck (Goffredo et al. 2007). These higher values of population density may be the result of (1) higher competitive strategies making *C. inornata* a pioneer species that colonizes available substratum quicker than other organisms;

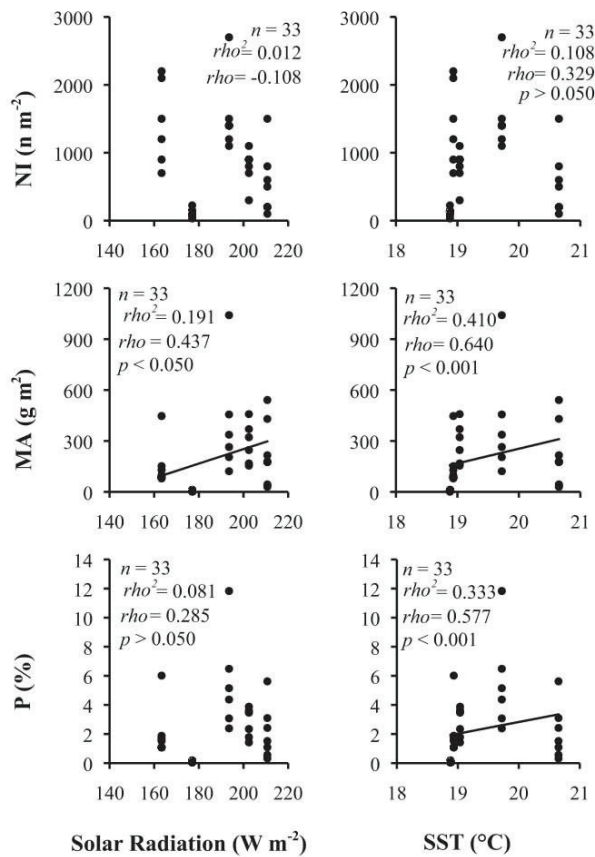


Fig. 8. *Caryophyllia inornata*. Variation in population density parameters with solar radiation and SST after the exclusion of the Elba site. NI number of individuals per square meter, MA mass per square meter, P percent cover. ρ^2 Spearman's determination coefficient; ρ Spearman's correlation coefficient; n number of quadrats.

(2) higher tolerance/resistance to artificial substrata such as a wreck; (3) a combination of the two; and (4) other unknown factors. Indeed, *C. inornata* is thought to asexually produce embryos throughout the year (Goffredo et al. 2012), while other potentially competitive corals such as *L. pruvoti* exhibit only a single sexual reproductive event per year. This trait, coupled with a possible higher tolerance to artificial substrata, may explain the exceptionally high population abundance on the plane wreck of the Elba site. Due to these particular conditions, the Elba site was excluded from all analyses between biometric and population density parameters and environmental variables. This choice was also supported by the increase of all correlation parameters between environmental and biometric parameters after exclusion of the Elba site.

Both solar radiation and SST were negatively correlated with polyp height in *C. inornata*. Calyx height is one of the factors influenced by the depth of surrounding sediment. For

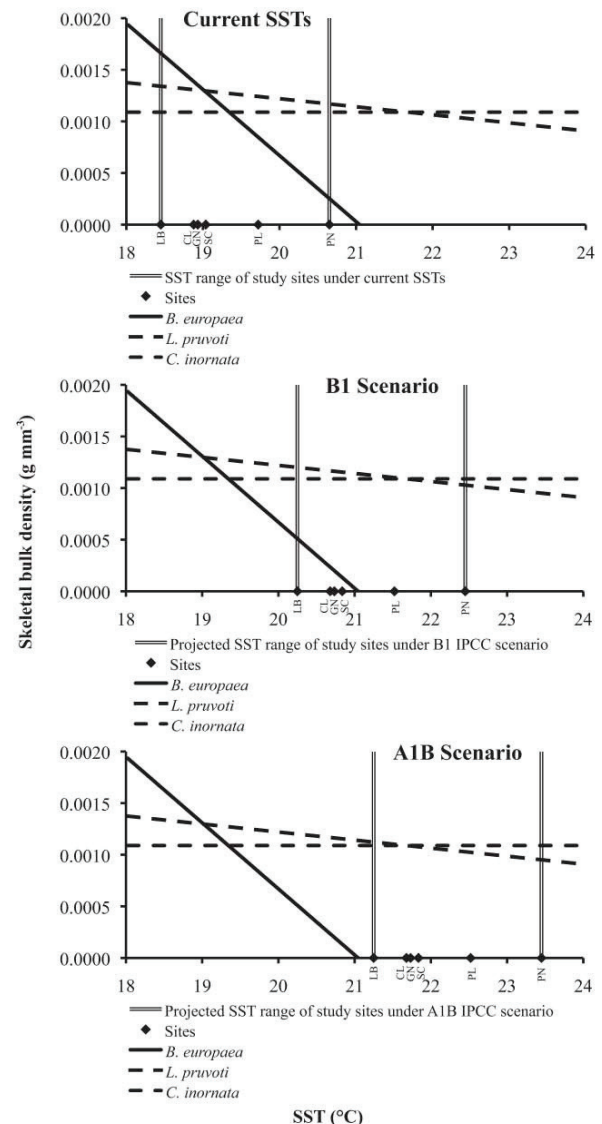


Fig. 9. *Caryophyllia inornata*, *B. europaea*, and *L. pruvoti*. Projected relationships between skeletal bulk density and SST in relation to current temperatures and two IPCC scenarios of SST increase: scenario B1 (average warming of $1.8^{\circ}C$), and A1B (average warming of $2.8^{\circ}C$).

example, polyps of the congeneric species *Caryophyllia smithii* living in horizontal and vertical walls characterized by high sedimentation have been found to grow with a taller calyx than those living in low sediment areas (Bell and Turner 2000). The decrease in height with increasing solar radiation is in agreement with the decreasing sedimentation stress with decreasing latitude along Italian coasts, as shown by a sea water quality survey conducted along the Italian coast by the Italian Ministry of the Environment and Land and Sea Protection during the period of this study (Si.Di.Mar. available at <http://www.sidimar.tutelamare.it/index.jsp>).

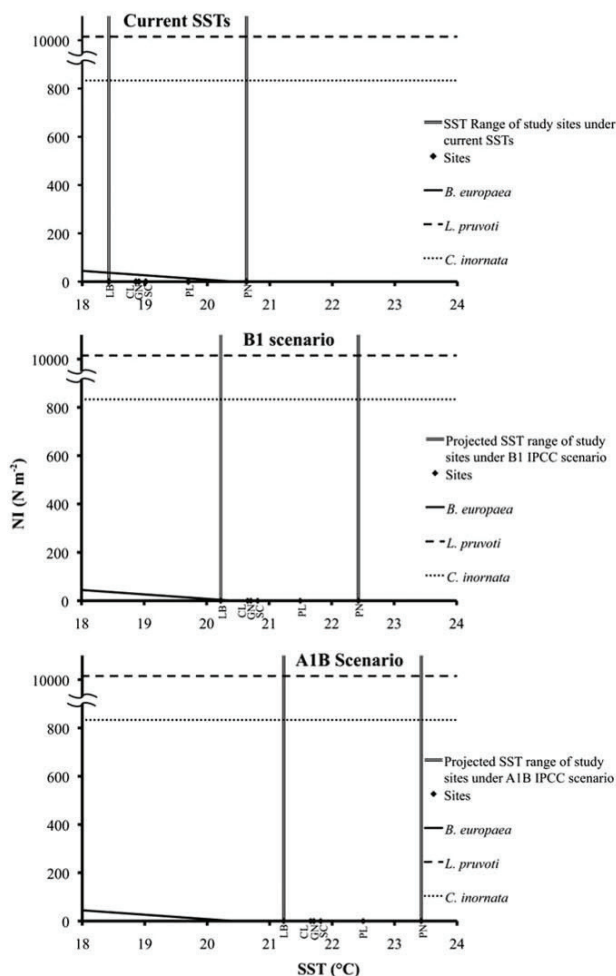


Fig. 10. *Caryophyllia inornata*, *B. europaea* and *L. pruvoti*. Projected relationships between NI, number of individuals per square meter, and SST in relation to current temperatures and two IPCC scenarios of SST increase: scenario B1 (average warming of 1.8°C), and A1B (average warming of 2.8°C).

Skeletal bulk density of *C. inornata* was unrelated to SST (Fig. 7). This confirmed the expectations of this study, and it is consistent with recent analyses proposing a higher tolerance to temperature increase of non-zooxanthellate Mediterranean corals than their symbiotic counterparts (Caroselli et al. 2011, 2012a,b). In fact, the zooxanthellate *B. europaea*, studied in the same sites and with the same methods as the present study, strongly decreases its skeletal bulk density with increasing temperature (Goffredo et al. 2007), due to an increase in porosity (Caroselli et al. 2011). Instead, the non-zooxanthellate *L. pruvoti* studied in the same sites has an homogeneous skeletal bulk density with SST, and may even benefit from increasing temperature, since corals living in sites with higher SSTs have a higher density of the crystals of

calcium carbonate (micro-density; sensu Bucher et al. 1998) composing their skeleton (Caroselli et al. 2011).

Percent cover and mass per square meter of *C. inornata* were positively correlated to SST. This increase was likely due to the increase in polyp length with SST (Fig. 7). In fact, it must be noted that correlations in Fig. 7 are based on the corrected values in relation to length. Thus, the lack of correlation between width and SST must be interpreted as if there is no correlation after eliminating the contribution due to polyp length (i.e., as if all polyps had the same length). However, since width is dependent on length (Fig. 5), with increasing SST populations are characterized by polyps that are more long (and consequently wide), then they have a larger surface area and this explains the increase of percent cover with SST. The same applies to mass per square meter, since also polyp mass is strictly dependent on polyp length (Fig. 5). The number of polyps per square meter was not related to environmental variables, similarly to what reported for the non-zooxanthellate *L. pruvoti* and again differently from the zooxanthellate *B. europaea*, whose abundance decreases with SST (Goffredo et al. 2007). The absence of symbionts in *C. inornata* and *L. pruvoti* is proposed as the cause of their higher tolerance to the effects of temperature than *B. europaea* (Caroselli et al. 2011, 2012a,b). The non-zooxanthellate coral *C. inornata* seems to be quite tolerant to the temperature range considered in this study, without strong variations of its skeletal bulk density and population abundance. When comparing this coral to the other species previously studied along the same latitudinal gradient, it appears that also the non-zooxanthellate *L. pruvoti* is tolerant to the temperature range experienced in the field, since its biometry, growth, demography, and skeletal characteristics are not negatively correlated with SST (Caroselli et al. 2011, 2012a,b). Conversely, increasing seawater temperature seems to strongly and negatively affect both polyp growth and colonization process of the zooxanthellate *B. europaea* (Goffredo et al. 2007, 2008, 2009). In this latter species, warmer populations are less stable and show a progressive deficiency of young individuals, so that there is concern for the future of this species (Goffredo et al. 2008).

The IPCC projects an increase of global SSTs of 1-3°C by 2100 (Solomon et al. 2007). The speed of many negative changes in the oceans are near or are tracking the worst-case scenario from the IPCC and other predictions (Rogers and Laffoley 2011). For instance, many recent mass mortality events in the Mediterranean Sea are put in relation to temperature increase (Rodolfo-Metalpa et al. 2000; Coma et al. 2009; Garrabou et al. 2009). A plot was produced by projecting the relationships between skeletal bulk density and SST for the three species *C. inornata* (present study), *B. europaea*, and *L. pruvoti* (data from Goffredo et al. 2007) to compare their sensitivity to the projected increase of seawater temperature according to different IPCC scenarios (Fig. 9). Extrapolating the regression between skeletal bulk density and SST

has the limitation of assuming that the linear relationship will be maintained, which may not necessarily be true (Goffredo et al. 2009). *C. inornata* was represented as a straight line as a result of the mean value of skeletal bulk density registered among the sites considered in this study, since it did not show correlations with SST (Fig. 9). Assuming a quite slow and conservative increase (1.8°C, B1 scenario), SST is expected to exceed the zero skeletal bulk density point for *B. europaea* (21.0°C) in a wide part of its areal extent, while the skeletal bulk density of *L. pruvoti* will drop only by 10% with respect to current values (Fig. 9). When assuming a moderate case scenario (A1B) with a 2.8°C increase, *B. europaea* is expected to exceed the zero skeletal bulk density point in all of its areal extent, while *L. pruvoti* will drop only by 16% in skeletal bulk density (Fig. 9). In a subsequent plot the relationships between population abundance (NI) and SST were projected for the three species according to the IPCC scenarios already considered (Fig. 10). *C. inornata* and *L. pruvoti* were both represented as straight lines in correspondence to their mean value of NI, which was not related to SST (Fig. 10). Assuming the more conservative increase (1.8°C, B1 scenario), SST would exceed the zero population density point for *B. europaea* in all sites except the coldest one (LB), while assuming the moderate case scenario (A1B) with a 2.8°C increase, *B. europaea* is expected to disappear from all of its areal extent (Fig. 10).

Even with the limitations of extrapolating relationships beyond the actually measured temperatures, these projections confirm that these three species, sharing a wide part of their distribution area, may have very different temperature tolerance and consequent response to seawater warming. These findings also support the hypothesis that non-zooxanthellate scleractinians may be more tolerant to temperature increase than symbiotic ones. However, the limit of temperature increase that will still be tolerable by these non-zooxanthellate species is unknown. Concern for the future of Mediterranean zooxanthellate corals and the need for further studies on non-zooxanthellate species is confirmed by the present findings.

References

- Al-Horani, F. A. 2005. Effects of changing seawater temperature on photosynthesis and calcification in the scleractinian coral *Galaxea fascicularis*, measured with O₂, Ca²⁺ and pH microensors. *Sci. Mar.* **69**: 347-354.
- Altman, D. G. 1991. Practical statistics for medical research. Chapman & Hall.
- Anderson, M. J., R. N. Gorley, and K. R. Clarke. 2008. PERMANOVA+ for PRIMER: Guide to software and statistical methods. PRIMER-E.
- Bablet, J. P. 1985. Report on the growth of a scleractinia (*Fungia paumotensis*), v. **4**, p. 361-365. In Proceedings of the Fifth International Coral Reef Symposium.
- Bell, J. J., and J. R. Turner. 2000. Factors influencing the density and morphometrics of the cup coral *Caryophyllia smithii* in Lough Hyne. *J. Mar. Biol. Assoc. U.K.* **80**: 437-441. doi:10.1017/S0025315400002137
- Bongaerts, P., B. W. Hoeksema, K. B. Hay, and O. Hoegh-Guldberg. 2012. Mushroom corals overcome live burial through pulsed inflation. *Coral Reefs* **31**: 399. doi:10.1007/s00338-011-0862-z
- 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. doi:10.1016/S0022-0981(98)00020-3
- Cairns, S. D. 1999. Species richness of recent Scleractinia. *Atoll Res. Bull.* **459**: 1-46. doi:10.5479/si.00775630.459.1
- Cantin, N. E., A. L. Cohen, K. B. Karnauskas, A. M. Tarrant, and D. C. McCorkle. 2010. Ocean warming slows coral growth in the central red sea. *Science* **329**: 322-325. doi:10.1126/science.1190182
- Caroselli, E., and S. Goffredo. 2014. Mediterranean coral population dynamics: A tale of 20 years of field studies, p. 275-284. In S. Goffredo and Z. Dubinsky [eds.], *The Mediterranean Sea: Its history and present challenges*. Springer.
- Caroselli, E., G. Mattioli, O. Levy, G. Falini, Z. Dubinsky, and S. Goffredo. 2012a. Inferred calcification rate of a Mediterranean azooxanthellate coral is uncoupled with sea surface temperature along an 8° latitudinal gradient. *Front. Zool.* **9**: 32. doi:10.1186/1742-9994-9-32
- Caroselli, E., F. Zaccanti, G. Mattioli, G. Falini, O. Levy, Z. Dubinsky, and S. Goffredo. 2012b. Growth and demography of the solitary scleractinian coral *Leptopsammia pruvoti* along a sea surface temperature gradient in the Mediterranean Sea. *PLoS ONE* **7**: e37848. doi:10.1371/journal.pone.0037848
- Caroselli, E., and others. 2011. Environmental implications of skeletal micro-density and porosity variation in two scleractinian corals. *Zoology* **114**: 255-264. doi:10.1016/j.zool.2011.04.003
- 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. doi:10.1016/j.jembe.2003.10.015
- Coma, R., M. Ribes, E. Serrano, E. Jimenez, J. Salat, and J. Pasqual. 2009. Global warming enhanced stratification and mass mortality events in the Mediterranean. *Proc. Natl. Acad. Sci. USA* **106**: 6176-6181. doi:10.1073/pnas.0805801106
- 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. Chang. Biol.* **14**: 529-538. doi:10.1111/j.1365-2486.2007.01520.x
- Cooper, T. F., R. A. O'Leary, and J. M. Lough. 2012. Growth of Western Australian corals in the Anthropocene. *Science* **335**: 593-596. doi:10.1126/science.1214570

- Crisci, C., N. Bensoussan, J.-C. Romano, and J. Garrahou. 2011. Temperature anomalies and mortality events in marine communities: Insights on factors behind differential mortality impacts in the NW Mediterranean. *PLoS ONE* **6**: e23814. doi:10.1371/journal.pone.0023814
- Erfteimeijer, P. L. A., B. Riegl, B. W. Hoeksema, and P. A. Todd. 2012. Environmental impacts of dredging and other sediment disturbances on corals: A review. *Mar. Pollut. Bull.* **64**: 1737-1765. doi:10.1016/j.marpolbul.2012.05.008
- Fantazzini, P., and others. 2013. Time-domain NMR study of Mediterranean scleractinian corals reveals skeletal-porosity sensitivity to environmental changes. *Environ. Sci. Technol.* **47**: 12679-12686. doi:10.1021/es402521b
- Ferrier-Pagès, C., C. Rottier, E. Beraud, and O. Levy. 2010. Experimental assessment of the feeding effort of three scleractinian coral species during a thermal stress: Effect on the rates of photosynthesis. *J. Exp. Mar. Biol. Ecol.* **390**: 118-124. doi:10.1016/j.jembe.2010.05.007
- Furby, K. A., J. Bouwmeester, and M. L. Berumen. 2013. Susceptibility of central Red Sea corals during a major bleaching event. *Coral Reefs* **32**: 505-513. doi:10.1007/s00338-012-0998-5
- Gabriel, K. R., and P. A. Lachenbruch. 1969. Non-parametric ANOVA in small samples: A Monte Carlo study of the adequacy of the asymptotic approximation. *Biometrics* **25**: 593-596. doi:10.2307/2528915
- Garrahou, J., and others. 2009. Mass mortality in the NW Mediterranean rocky benthic communities: Effects of the 2003 heat wave. *Glob. Chang. Biol.* **15**: 1090-1103. doi:10.1111/j.1365-2486.2008.01823.x
- Giorgi, F., and P. Lionello. 2008. Climate change projections for the Mediterranean region. *Glob. Planet. Chang.* **63**: 90-104. doi:10.1016/j.gloplacha.2007.09.005
- Goffredo, S., V. Airi, J. Radetić, and F. Zaccanti. 2006. Sexual reproduction of the solitary sunset cup coral *Leptopsammia pruvoti* (Scleractinia: Dendrophylliidae) in the Mediterranean. 2. Quantitative aspects of the annual reproductive cycle. *Mar. Biol.* **148**: 923-932. doi:10.1007/s00227-005-0137-8
- 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. doi:10.3354/meps229083
- Goffredo, S., 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. doi:10.1007/s00338-008-0362-y
- Goffredo, S., E. Caroselli, G. Mattioli, E. Pignotti, Z. Dubinsky, and F. Zaccanti. 2009. Inferred level of calcification decreases along an increasing temperature gradient in a Mediterranean endemic coral. *Limnol. Oceanogr.* **54**: 930-937. doi:10.4319/lo.2009.54.3.0930
- Goffredo, S., E. Caroselli, G. Mattioli, and F. Zaccanti. 2010. Growth and population dynamic model for the non-zooxanthellate temperate solitary coral *Leptopsammia pruvoti* (Scleractinia, Dendrophylliidae). *Mar. Biol.* **157**: 2603-2612. doi:10.1007/s00227-010-1522-5
- Goffredo, S., E. Caroselli, E. Pignotti, G. Mattioli, and F. Zaccanti. 2007. Variation in biometry and population density of solitary corals with solar radiation and sea surface temperature in the Mediterranean Sea. *Mar. Biol.* **152**: 351-361. doi:10.1007/s00227-007-0695-z
- Goffredo, S., and N. E. Chadwick-Furman. 2003. Comparative demography of mushroom corals (Scleractinia, Fungiidae) at Eilat, northern Red Sea. *Mar. Biol.* **142**: 411-418. doi:10.1007/s00227-002-0980-9
- Goffredo, S., G. Mattioli, and F. Zaccanti. 2004. Growth and population dynamics model of the Mediterranean solitary coral *Balanophyllia europaea* (Scleractinia, Dendrophylliidae). *Coral Reefs* **23**: 433-443. doi:10.1007/s00338-004-0395-9
- Goffredo, S., and others. 2012a. The puzzling presence of calcite in skeletons of modern solitary corals from the Mediterranean Sea. *Geochim. Cosmochim. Acta* **85**: 187-199. doi:10.1016/j.gca.2012.02.014
- Goffredo, S., and others. 2012b. Unusual pattern of embryogenesis of *Caryophyllia inornata* (Scleractinia, Caryophylliidae) in the Mediterranean Sea. Maybe agamic reproduction? *J. Morphol.* **273**: 943-956. doi:10.1002/jmor.20039
- Grigg, R. W. 1982. Darwin Point: A threshold for atoll formation. *Coral Reefs* **1**: 29-34. doi:10.1007/BF00286537
- Gualdi, S., and others. 2013. The CIRCE simulations: Regional climate change projections with realistic representation of the Mediterranean Sea. *Bull. Am. Meteorol. Soc.* **94**: 65-81. doi:10.1175/BAMS-D-11-00136.1
- Guest, J. R., and others. 2012. Contrasting patterns of coral bleaching susceptibility in 2010 suggest an adaptive response to thermal stress. *PLoS ONE* **7**: e33353. doi:10.1371/journal.pone.0033353
- Harriott, V. J., and S. A. Banks. 2002. Latitudinal variation in coral communities in eastern Australia: A qualitative biophysical model of factors regulating coral reefs. *Coral Reefs* **21**: 83-94. doi:10.1007/s00338-001-0201-x
- Helmuth, B., and K. P. Sebens. 1993. The influence of colony morphology and orientation to flow on particle capture by the scleractinian coral *Agaricia agaricites* (Linnaeus). *J. Exp. Mar. Biol. Ecol.* **165**: 251-278. doi:10.1016/0022-0981(93)90109-2
- Hoegh-Guldberg, O. 2011. The impact of climate change on coral reef ecosystems, p. 391-403. In Z. Dubinsky and N. Stambler [eds.], *Coral reefs: An ecosystem in transition*. Springer.
- Hoeksema, B. W. 1991. Evolution of body size in mushroom corals (Scleractinia: Fungiidae) and its ecomorphological consequences. *Neth. J. Zool.* **41**: 112-129. doi:10.1163/156854291X00072
- Hoeksema, B. W., and Z. Waheed. 2012. It pays to have a big mouth: Mushroom corals ingesting salps at Sabah,

- Malaysia. Mar. Biodivers. **42**: 297-302. doi:10.1007/s12526-012-0110-y
- Houlbrèque, F., and C. Ferrier-Pagès. 2009. Heterotrophy in tropical scleractinian corals. Biol. Rev. **84**: 1-17. doi:10.1111/j.1469-185X.2008.00058.x
- Kain, J. M. 1989. The seasons in the subtidal. Br. Phycol. J. **24**: 203-215. doi:10.1080/00071618900650221
- 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.
- Kitahara, M. V., S. D. Cairns, and D. J. Miller. 2010. Monophyletic origin of *Caryophyllia* (Scleractinia, Caryophylliidae), with descriptions of six new species. Syst. Biodivers. **8**: 91-118. doi:10.1080/14772000903571088
- Kleypas, J. A., G. Danabasoglu, and J. M. Lough. 2008. Potential role of the ocean thermostat in determining regional differences in coral reef bleaching events. Geophys. Res. Lett. **35**: L03613. doi:10.1029/2007GL032257
- 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. doi:10.1093/icb/39.1.146
- Kružić, P., P. Sršen, and L. Benković. 2012. The impact of seawater temperature on coral growth parameters of the colonial coral *Cladocora caespitosa* (Anthozoa, Scleractinia) in the eastern Adriatic Sea. Facies **58**: 477-491. doi:10.1007/s10347-012-0306-4
- 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. doi:10.1016/S0022-0981(99)00168-9
- Meron, D., R. Rodolfo-Metalpa, R. Cuning, A. C. Baker, M. Fine, and E. Banin. 2012. Changes in coral microbial communities in response to a natural pH gradient. ISME J. **6**: 1775-1785. doi:10.1038/ismej.2012.19
- Minelli, A., S. Ruffo, and S. La Posta. 1995. Checklist delle specie della fauna italiana. Cnidaria, Ctenophora. III. Edizioni Calderini.
- Nykjaer, L. 2009. Mediterranean Sea surface warming 1985-2006. Clim. Res. **39**: 11-17. doi:10.3354/cr00794
- Palardy, J. E., A. G. Grottoli, and K. A. Matthews. 2005. Effects of upwelling, depth, morphology and polyp size on feeding in three species of Panamanian corals. Mar. Ecol. Prog. Ser. **300**: 79-89. doi:10.3354/meps300079
- Ramanujan, S. 1914. Modular equations and approximations to π . Q. J. Math. **45**: 350-372.
- Richardson, A. J. 2008. In hot water: Zooplankton and climate change. ICES J. Mar. Sci. **65**: 279-295. doi:10.1093/icesjms/fsn028
- Rodolfo-Metalpa, R., C. N. Bianchi, A. Peirano, and C. Morri. 2000. Coral mortality in NW Mediterranean. Coral Reefs **19**: 24. doi:10.1007/s003380050221
- Rodolfo-Metalpa, R., C. Richard, D. Allemand, C. N. Bianchi, C. Morri, and C. Ferrier-Pages. 2006a. Response of zooxanthellae in symbiosis with the Mediterranean corals *Cladocora caespitosa* and *Oculina patagonica* to elevated temperatures. Mar. Biol. **150**: 45-55. doi:10.1007/s00227-006-0329-x
- Rodolfo-Metalpa, R., C. Richard, D. Allemand, 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. doi:10.1242/jeb.02550
- Rogers, A. D., and D. d'A. Laffoley. 2011. International Earth system expert workshop on ocean stresses and impacts. Summary report. IPSO.
- Saiz, E., A. Sabatés, and J. M. Gili. 2014. The zooplankton, p. 183-211. In S. Goffredo and Z. Dubinsky [eds.] The Mediterranean Sea: Its history and present challenges. Springer.
- Sebens, K. P. 1979. The energetics of asexual reproduction and colony formation in benthic marine invertebrates. Am. Zool. **19**: 683-699. doi:10.1093/icb/19.3.683
- Sebens, K. P., and A. S. Johnson. 1991. Effects of water movement on prey capture and distribution of reef corals. Hydrobiologia **226**: 91-101. doi:10.1007/BF00006810
- Sebens, K. P., S. Grace, B. Helmuth, E. Maney, and J. Miles. 1998. Water flow and prey capture by three scleractinian corals, *Madracis mirabilis*, *Montastrea cavernosa*, and *Porites porites* in a field enclosure. Mar. Biol. **131**: 347-360. doi:10.1007/s002270050328
- Sebens, K. P., K. S. Vandersall, L. A. Savina, and K. R. Graham. 1996. Zooplankton capture by two scleractinian corals *Madracis mirabilis* and *Montastrea cavernosa* in a field enclosure. Mar. Biol. **127**: 303-317. doi:10.1007/BF00942116
- Senchaudhuri, P., C. R. Mehta, and N. R. Patel. 1995. Estimating exact p-values by the method of control variates, or Monte Carlo rescue. J. Am. Stat. Assoc. **90**: 640-648. doi:10.2307/2291077
- Solomon, S., and others. 2007. Climate change 2007: The physical science basis. Cambridge Univ. Press.
- Stafford-Smith, M. G., and R. F. G. Ormond. 1992. Sediment-rejection mechanisms of 42 species of Australian Scleractinian. Aust. J. Mar. Fresh Res. **43**: 683-705. doi:10.1071/MF9920683
- Steel, R. G. D. 1980. Principles and procedures of statistics: a biometrical approach, 2nd ed. McGraw-Hill College.
- Tanzil, J. T. I., B. E. Brown, A. W. Tudhope, and R. P. Dunne. 2009. Decline in skeletal growth of the coral *Porites lutea* from the Andaman Sea, South Thailand between 1984 and 2005. Coral Reefs **28**: 519-528. doi:10.1007/s00338-008-0457-5
- Thornhill, D. J., D. W. Kemp, B. U. Bruns, W. K. Fitt, and G. W. Schmidt. 2008. Correspondence between cold tolerance and temperate biogeography in a Western Atlantic *Symbiodinium* (Dinophyta) lineage. J. Phycol. **44**: 1126-1135. doi:10.1111/j.1529-8817.2008.00567.x
- Van Woesik, R., K. Sakai, A. Ganase, and Y. Loya. 2011. Revisiting the winners and the losers a decade after coral

- bleaching. *Mar. Ecol. Prog. Ser.* **434**: 67-76. doi:[10.3354/meps09203](https://doi.org/10.3354/meps09203)
- 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. Ass. U.K.* **86**: 1281-1283. doi:[10.1017/S0025315406014299](https://doi.org/10.1017/S0025315406014299)
- Vongsavat, V., P. Winotai, and S. Meejoo. 2006. Phase transitions of natural corals monitored by ESR spectroscopy. *Nucl. Instrum. Methods* **243**: 167-173. doi:[10.1016/j.nimb.2005.07.197](https://doi.org/10.1016/j.nimb.2005.07.197)
- Wilkinson, C. 2004. Status of coral reefs of the World: 2004, v. 2. Status of coral reefs of the World. Australian Institute of Marine Science.
- Yamashiro, H., and M. Nishihira. 1998. Experimental study of growth and asexual reproduction in *Diaseris distorta* (Michelin, 1843), a free-living fungiid coral. *J. Exp. Mar. Biol. Ecol.* **225**: 253-267. doi:[10.1016/S0022-0981\(97\)00229-3](https://doi.org/10.1016/S0022-0981(97)00229-3)
- Zibrowius, H. 1978. Les scléractiniaires des grottes sous-marines en Méditerranée et dans l'Atlantique nord-oriental (Portugal, Madère, Canaries, Açores). *P. S. Z. N. I.: Mar. Ecol.* **40**: 516-545.
- Zibrowius, H. 1980. Les scléractiniaires de la Méditerranée et de l'Atlantique nord-oriental. *Mem. Inst. Oceanogr. (Monaco)* **11**: 1-284.

Acknowledgments

We wish to thank S. Branchini, F. Gizzi, M. Marinozzi, S. Prantoni, and F. Turano for their underwater assistance in collecting the samples. The diving centers Centro Immersioni Pantelleria, Il Pesciolino, Bubble Lounge and Sub Maldive supplied logistic assistance in the field. The Scientific Diving School (www.sdseducational.org) supplied scientific, technical, and logistical support. Field coral photographs by G. Neto (www.giannineto.it). Two anonymous reviewers gave precious comments that improved manuscript's quality. The research leading to these results has received funding from the European Research Council under the European Union's Seventh Framework Programme (FP7/2007-2013)/ERC grant agreement n° [249930-CoralWarm: Corals and global warming: the Mediterranean versus the Red Sea]. This research was financed by the Associazione dei Tour Operator Italiani (ASTOI), The Marine and Freshwater Science Group Association, and the Ministry of Education, University and Research (MIUR). The experiment complied with current Italian law.

Received 13 November 2014

Revised 10 March 2015

Accepted 9 April 2015

Associate editor: Anthony Larkum