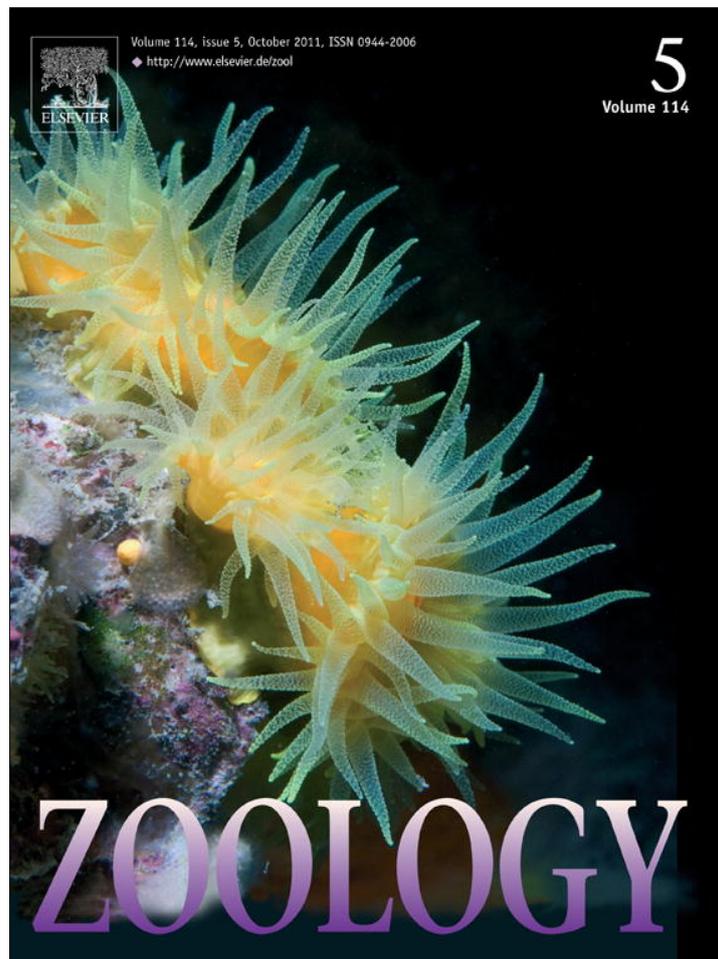


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Environmental implications of skeletal micro-density and porosity variation in two scleractinian corals

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ABSTRACT

The correlations between skeletal parameters (bulk density, micro-density and porosity), coral age and sea surface temperature were assessed along a latitudinal gradient in the zooxanthellate coral *Balanophyllia europaea* and in the azooxanthellate coral *Leptopsammia pruvoti*. In both coral species, the variation of bulk density was more influenced by the variation of porosity than of micro-density. With increasing polyp age, *B. europaea* formed denser and less porous skeletons while *L. pruvoti* showed the opposite trend, becoming less dense and more porous. *B. europaea* skeletons were generally less porous (more dense) than those of *L. pruvoti*, probably as a consequence of the different habitats colonized by the two species. Increasing temperature had a negative impact on the zooxanthellate species, leading to an increase of porosity. In contrast, micro-density increased with temperature in the azooxanthellate species. It is hypothesized that the increase in porosity with increasing temperatures observed in *B. europaea* could depend on an attenuation of calcification due to an inhibition of the photosynthetic process at elevated temperatures, while the azooxanthellate species appears more resistant to variations of temperature, highlighting possible differences in the sensitivity/tolerance of these two coral species to temperature changes in face of global climate change.

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1. Introduction

Studying how terrestrial and marine ecosystems respond to present and future environmental shifts related to climate change is a fundamental challenge for ecologists (Karl and Trenberth, 2003; Harley et al., 2006). The rate of climate change is accelerating, and the average surface temperature of the Earth is likely to increase by 1.1–6.4 °C until the end of the 21st century, with a best estimate of 1.8–4.0 °C (Solomon et al., 2007). Growing evidence suggests that climate change is having more substantial and rapid effects on marine communities than on terrestrial ones (Richardson and Poloczanska, 2008). Increased seawater temperature, enhanced ultraviolet-B radiation, upper-ocean acidification, and anthropogenic stress will affect all levels of ecological hierarchies and a broad array of marine ecosystems (Walther et al., 2002).

The magnitude of temperature change is expected to be greater in temperate areas than in tropical ones (Solomon et al., 2007).

Climatic models further predict that the Mediterranean basin will be one of the regions most affected by the ongoing warming trend and by an increase in extreme events (Lejeune et al., 2010). This commends the Mediterranean Sea as a potential model of global scenarios to occur in the world's marine biota, and a natural focus of interest for research. The Mediterranean is already one of the most impacted seas in the world, since climate change interacts synergistically with many other disturbances such as eutrophication caused by increased use of agricultural phosphates and the damming of rivers (Tsimplis et al., 2006). In recent years, the coralligenous community of the Mediterranean Sea, one of the most diverse communities there (~1666 species; Ballesteros, 2006) where suspension feeders are dominant, has been strongly affected by several mass mortality events (Cerrano et al., 2000; Perez et al., 2000; Rodolfo-Metalpa et al., 2000; Romano et al., 2000; Coma et al., 2009; Garrabou et al., 2009). Ecosystem engineers, including gorgonians and sponges, have been the most affected taxa down to depths of 45 m (Cerrano et al., 2000; Perez et al., 2000; Garrabou et al., 2009).

The present study focuses on two scleractinian species commonly occurring in the Mediterranean Sea: *Balanophyllia europaea* and *Leptopsammia pruvoti*.

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B. europaea is a solitary, ahermatypic, zooxanthellate, and scleractinian coral, which is endemic to the Mediterranean Sea and is distributed at 0–50 m depth due to its symbiosis with zooxanthellae (Zibrowius, 1980). Along the Italian coasts, its skeletal density and population abundance are negatively correlated with sea surface temperature (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 due to a progressive

deficiency of young individuals (Goffredo et al., 2008). Its calcification is negatively correlated with SST (Goffredo et al., 2009). It has been hypothesized that photosynthesis of the symbiotic algae of *B. europaea* is inhibited at high temperatures, consequently causing an inhibition of calcification (Goffredo et al., 2009). There is concern for the future of this species (Goffredo et al., 2008, 2009) with regard to the current predictions of global warming by the Intergovernmental Panel on Climate Change (IPCC).

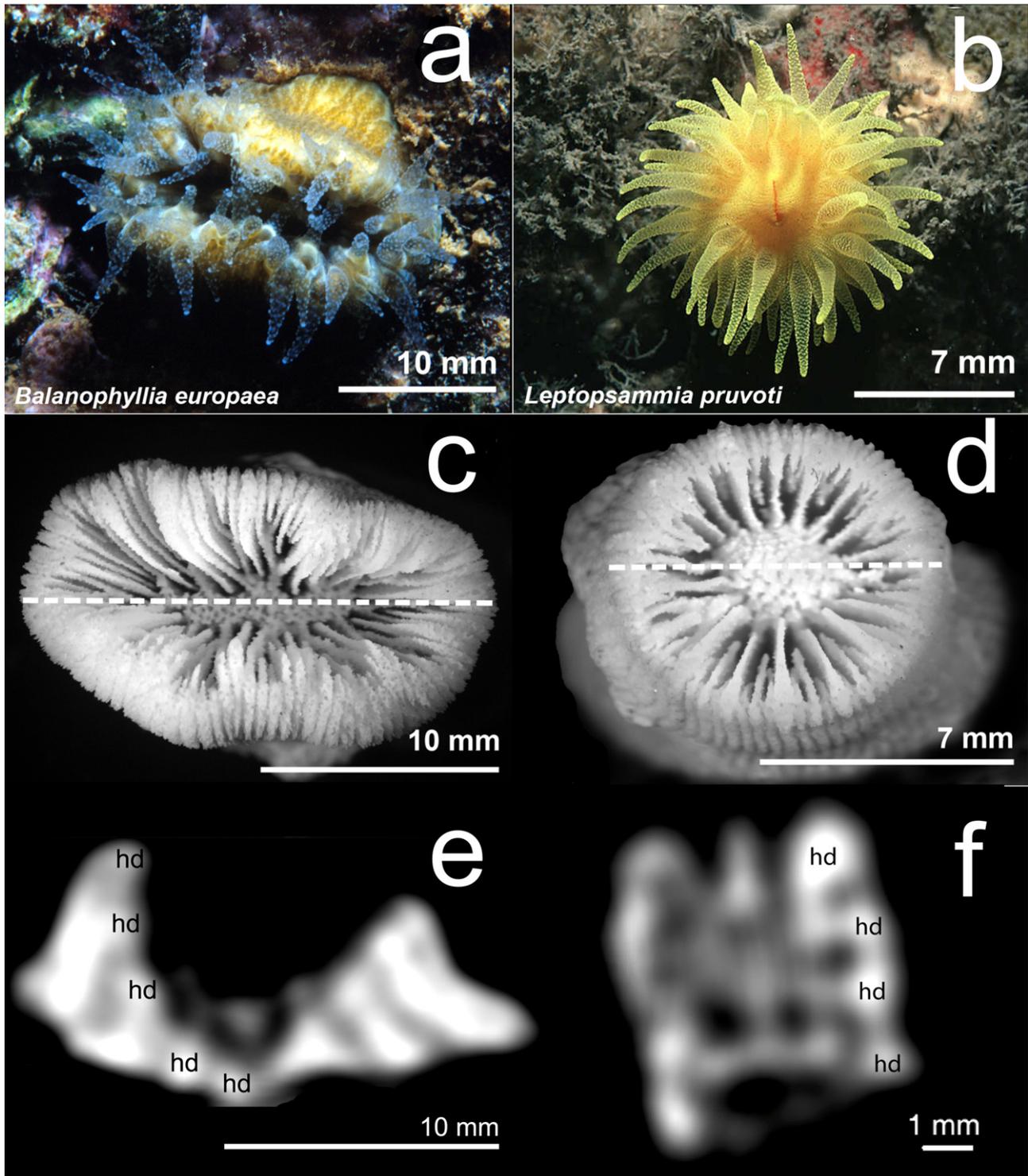


Fig. 1. Living specimens (top), skeletons (middle) and corallites (bottom) of (a, c and e) *Balanophyllia europaea* and (b, d and f) *Leptopsammia pruvoti*. Dotted lines in (b) and (d) indicate polyp lengths (L = maximum axis of the oral disc). (e and f) Computerized tomography scans of two corallites. Age was determined by counting the high density growth bands (hd). In these samples, the skeleton of *B. europaea* is 5 years old, while the skeleton of *L. pruvoti* is 4 years old.

L. pruvoti is an ahermatypic, non-zooxanthellate, and solitary scleractinian coral, which is distributed in the Mediterranean basin and along the European Atlantic coast from Portugal to Southern England and Ireland (Zibrowius, 1980). It is one of the most common organisms in semi-enclosed rocky habitats, under overhangs, in caverns, and small crevices at 0–70 m depth (Zibrowius, 1980). Sea surface temperature and solar radiation have been reported not to significantly influence its skeletal density, corallite length, width, height or population abundance along an 850-km latitudinal gradient on the west coast of Italy (Goffredo et al., 2007).

SST, whose variation is mainly influenced by latitude (Kain, 1989), is strongly linked to coral biometry, physiology, and demography (Kleypas et al., 1999; Lough and Barnes, 2000; Harriott and Banks, 2002; Al-Horani, 2005). Several studies have shown that coral growth is strongly related to temperature (Goreau and Goreau, 1959; Bak, 1974; Jokiel and Coles, 1978; Highsmith, 1979; Crossland, 1984; Kleypas et al., 1999; Lough and Barnes, 2000; Goffredo et al., 2007, 2008, 2009). Coral growth is defined by three related characteristics: calcification, skeletal density, and linear extension rate (calcification = skeletal density \times linear extension; Lough and Barnes, 2000; Carricart-Ganivet, 2004). Most studies on coral skeletal density have focused on bulk density, which is the mass divided by the total enclosed volume, including the volume of the enclosed skeletal voids (porosity). Bulk density has been found to vary with exposure, latitude, depth, temperature, location within a colony, and also between different growth forms (see, e.g., Dustan, 1975; Schneider and Smith, 1982; Oliver et al., 1983; Hughes, 1987; Jiménez and Cortés, 1993; Harriott, 1997; Carricart-Ganivet, 2004; Goffredo et al., 2007, 2009; Dar and Mohammed, 2009; Tanzil et al., 2009). Another measure of skeletal density appearing in the literature is micro-density (mass per unit volume of the material which composes the skeleton; Barnes and Devereux, 1988). As porosity decreases, bulk density will approach micro-density, and neither can exceed the density of pure aragonite (2.94 mg mm^{-3} ; Marszałek, 1982; Bucher et al., 1998), due to the presence of an intra-crystalline organic matrix which is absent in abiotic carbonates (Cuif et al., 1999). Bulk density, porosity and micro-density have rarely been investigated together (Barnes and Devereux, 1988; Bucher et al., 1998), even though they are the factors influencing the ability of coral skeletons to resist natural and anthropogenic breakage (Wainwright et al., 1976; Chamberlain, 1978; Tunnicliffe, 1979; Schumacher and Plewka, 1981; Vosburgh, 1982; Liddle and Kay, 1987; Jiménez and Cortés, 1993; Rodgers et al., 2003). Variability in micro-density among colonies within and among species, localities, and environmental conditions remains largely unstudied (Bucher et al., 1998). This is the first study exploring all of these three skeletal parameters (bulk density, micro-density and porosity) in temperate corals, with the aim of defining their relationships with coral age and SST and highlighting possible differences in the sensitivity/tolerance of the two investigated coral species to temperature changes in face of global climate change.

2. Materials and methods

2.1. Collection and treatment of specimens

Specimens of *B. europaea* (Risso, 1826) and *L. pruvoti* Lacaze-Duthiers, 1897 (Fig. 1A and B) were collected between 9 November 2003 and 24 June 2008 from 6 sites along a latitudinal gradient, from $44^{\circ}20'N$ to $36^{\circ}45'N$ (Fig. 2). Corals of *B. europaea* were randomly collected along a reef with southerly exposure at a depth of 5–7 m. Corals of *L. pruvoti* were randomly collected on the vault of crevices at a depth of 15–17 m. The sampling was performed at depths known to have high population densities and where the reproductive biology of the two species had been

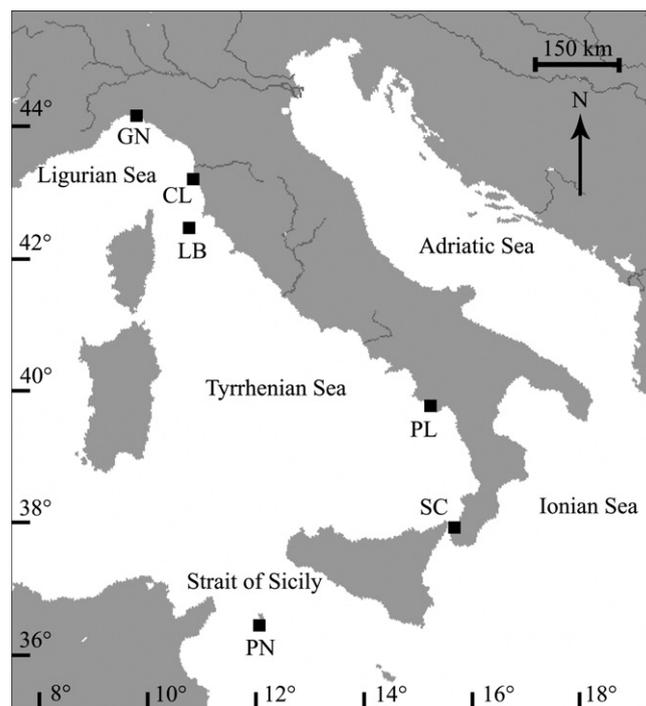


Fig. 2. Map of the Italian coastline indicating the sites where the corals were collected. Abbreviations and coordinates of the sites in decreasing order of latitude: GN, Genova, $44^{\circ}20'N$, $9^{\circ}08'E$; CL, Calafuria, $43^{\circ}27'N$, $10^{\circ}21'E$; LB, Elba Isle, $42^{\circ}45'N$, $10^{\circ}24'E$; PL, Palinuro, $40^{\circ}02'N$, $15^{\circ}16'E$; SC, Scilla, $38^{\circ}01'N$, $15^{\circ}38'E$; PN, Pantelleria Isle, $36^{\circ}45'N$, $11^{\circ}57'E$.

studied previously (Goffredo et al., 2002, 2004, 2006; Goffredo and Zaccanti, 2004).

Coral tissue was totally removed by immersing the samples in a solution of 10% commercial bleach for 3 days. Corals were dried for 4 days at a maximum temperature of $50^{\circ}C$ to avoid phase transitions in the skeletal carbonate phases (Vongsavat et al., 2006). Each sample was inspected under a binocular microscope to remove fragments of substratum and calcareous deposits produced by other organisms. During this microscopic inspection, the few specimens that showed evident signs of bioerosion were separated and excluded from the analysis. Polyp length (L : longest axis of the oral disc), width (W : shortest axis of the oral disc), and height (h : oral–aboral axis) were measured using a pair of calipers (Fig. 1C and D; cf. Goffredo et al., 2007).

2.2. Age determination

Coral age was obtained by growth band analysis of about 40 skeletons randomly selected from the samples collected for each population, by means of computerized tomography (CT; von Bertalanffy, 1938; Goffredo et al., 2008; Fig. 1E and F). This technique is commonly applied to scleractinian corals (Bosscher, 1993; Helmle et al., 2000) and has also been successfully used in solitary corals (Goffredo et al., 2004, 2008, 2010). The age of each skeleton was determined by counting the growth bands, which are distinguished by a high-density band in winter and a low-density band in summer (Peirano et al., 1999; Goffredo et al., 2004, 2008). For *L. pruvoti*, a power function model was used to correlate the age/length data obtained by the CT scans of each population, since it produced the best fit. Using this model, the age of each coral sample was determined from its length. For *B. europaea*, the age of each sample was estimated using the von Bertalanffy's growth function for analyzing the data obtained by CT growth band analysis (cf. Goffredo et al., 2008).

2.3. Determination of skeletal parameters

To obtain the skeletal parameters, the buoyant weight of 250 specimens of *B. europaea* and 248 specimens of *L. pruvoti* was measured using the density determination kit of the Ohaus Explorer Pro balance (± 0.0001 g; Ohaus Corp., Pine Brook, NJ, USA). For buoyant weight measurements, the standard pan was replaced by a suspended weighing cradle attached to an underwater weighing pan submerged in a glass beaker filled with distilled water. A cover isolated the device from air flow within the laboratory. Measurements required for calculating the skeletal parameters were:

ρ	density of the fluid medium (in this case, distilled water: 1 g cm^{-3} at 20°C and 1 atm)
DW	dry weight of the skeleton
BW	buoyant weight of the skeleton = weight of the skeleton minus weight of the water displaced by it. To obtain this measurement, corals were placed in a desiccator connected to a mechanical vacuum pump for about 4 h in order to suck out all of the water and air from the pores (Barnes and Devereux, 1988). Still under vacuum conditions, the dry corals were soaked by gradually pouring distilled water inside the desiccator. The coral was then slowly lowered onto the underwater weighing pan, ensuring that no air bubbles adhered to its surface. The buoyant weight measurement was taken when the reading was stable, to avoid errors caused by measurement instability in the first few seconds due to water movement. This simple and nondestructive method has been widely used on various corals (Franzisket, 1964; Bak, 1973, 1976; Jokiel et al., 1978; Graus and Macintyre, 1982; Hughes, 1987; Barnes and Devereux, 1988; Davies, 1989; Mann, 1994; Marubini et al., 2003; Ammar et al., 2005; Spiske et al., 2008; Shi et al., 2009).
SW	saturated weight of the coral = weight of the skeleton plus weight of the water enclosed in its pores. The coral was taken out of the water, quickly blotted with a humid paper towel to remove surface water, and weighed in air, making sure that no water droplets were left on the weighing platform, which would lead to an overestimation.
$V_{\text{MATRIX}} = \frac{DW - BW}{\rho}$	matrix volume = volume of the skeleton, excluding the volume of its pores.
$V_{\text{PORES}} = \frac{SW - DW}{\rho}$	pore volume = volume of the pores in the skeleton.
$V_{\text{TOT}} = (V_{\text{MATRIX}} + V_{\text{PORES}})$	total volume = volume of the skeleton including its pores.

Additionally, the following skeletal parameters were calculated:

Micro-density (matrix density) = DW/V_{MATRIX}

Porosity = $(V_{\text{PORES}}/V_{\text{TOT}}) \times 100$

Bulk density = DW/V_{TOT} .

Table 1
Balanophyllia europaea and *Leptopsammia pruvoti*. Values of sea surface temperature (SST), date of sample collection, number of collected samples and age of the samples at each site. The Genova site is characterized by particular local conditions (xerotherm site due to local currents and rock composition; see www.apat.gov.it) and typically has higher SST than expected for this latitude (annual SST of Ligurian Sea: 18°C ; Genova: 19.6°C). In both coral species, the ages of sampled individuals differed significantly among the sites (Kruskal–Wallis test, $df = 5$; *B. europaea*: $p < 0.050$; *L. pruvoti*: $p < 0.001$). The sites are arranged in order of increasing seawater temperature.

Population	Code	SST ($^\circ\text{C}$)		Date of collection	Species	n	Age (years)	
		Annual mean (SE)	Range				Mean (SE)	Range (years)
Calafuria	CL	18.02 (0.04)	12.6–29.4	31 January 2004/24 June 2008	<i>B. europaea</i>	38	7.05 (0.80)	1.5–17.1
					<i>L. pruvoti</i>	44	4.52 (0.19)	2.0–6.6
Elba	LB	18.74 (0.04)	12.5–26.7	10–11 November 2003	<i>B. europaea</i>	17	6.16 (0.21)	4.0–7.5
					<i>L. pruvoti</i>	42	8.05 (0.40)	3.2–13.7
Palinuro	PL	19.14 (0.03)	12.9–27.1	2–3 April 2004	<i>B. europaea</i>	49	7.77 (0.36)	1.6–16.2
					<i>L. pruvoti</i>	45	5.07 (0.31)	1.6–9.5
Scilla	SC	19.54 (0.02)	15.3–25.3	6–7 January 2005	<i>B. europaea</i>	8	7.59 (0.49)	5.7–9.7
					<i>L. pruvoti</i>	29	8.69 (0.10)	1.4–19.7
Genova	GN	19.56 (0.04)	13.1–34.7	24 October 2004	<i>B. europaea</i>	23	8.42 (0.63)	1.3–13.8
					<i>L. pruvoti</i>	43	8.29 (0.52)	1.6–13.8
Pantelleria	PN	19.88 (0.04)	13.1–26.8	29–30 September 2005/1 August 2006	<i>B. europaea</i>	115	7.92 (0.23)	1.7–13.5
					<i>L. pruvoti</i>	45	7.74 (0.60)	1.7–14.8

n, number of individuals; SE, standard error.

The above method was slightly different from the one proposed by Bucher et al. (1998), since we decided not to use acetone or wax in order to preserve the samples for further analyses. However, the results of this buoyant weighing technique were confirmed by the strong relationship between bulk density and porosity obtained for both species and all locations (see Section 3).

As in other studies on the influence of environmental parameters on coral growth (i.e., Harriott, 1999; Lough and Barnes, 2000; Carricart-Ganivet, 2004; Peirano et al., 2005a,b), SST data were obtained from data banks. During 2003–2005, SST data for each site were obtained from the National Mareographic Network of the Agency for the Protection of the Environment and Technical Services (APAT, available at <http://www.apat.gov.it>). These data were measured by mareographic stations (SM3810; SIAP, Bologna, Italy), which were located close to the sampling sites (<1 km). Mean annual SST was obtained from hourly values measured from January 2001 to January 2005 (number of hourly values = 35,064 for each site; Table 1).

2.4. Statistical analyses

Spearman's rank correlation coefficient was used to calculate the significance of the correlations between skeletal parameters and sea surface temperature. Spearman's rank correlation coefficient is an alternative to Pearson's correlation coefficient (Altman, 1991). It is useful for data that are non-normally distributed and do not meet the assumptions of Pearson's correlation coefficient. The Kruskal–Wallis test was used to compare SST, age, and skeletal parameter characteristics among study sites. The Kruskal–Wallis test is a non-parametric alternative to the analysis of variance (ANOVA) and is used to compare groups of means. The advantage of this test is that it does not require normality of the data, as the test is based on the ranks of data. This distribution-free test proved to be more robust than its parametric counterpart in the case of a non-normal distribution of sample data, and it is a viable alternative to parametric statistics (Potvin and Roff, 1993). All analyses were computed using SPSS. 12.0.

3. Results

SST varied among the sites, with mean values spanning from 18.0°C to 19.9°C (Kruskal–Wallis test, $df = 5$, $p < 0.001$; Table 1). In both coral species, the ages of the sampled individuals differed significantly among the sites (Kruskal–Wallis test, $df = 5$; *B. europaea*: $p < 0.050$; *L. pruvoti*: $p < 0.001$; Table 1).

Table 2

Balanophyllia europaea. Correlation analysis between polyp age (independent variable) and skeletal parameters (dependent variable) at 6 sites along the west coast of Italy. Relationships were fitted to a power function model $y = ax^b$. The exponent (b) and factor (a) values are indicated only where the relationship was significant. The sites are arranged in order of increasing seawater temperature.

Population	Code	n	Dependent variable	Factor	Exponent	r^2	r
Calafuria	CL	38	Micro-density	–	–	0.051	0.226
			Porosity	35.293	–0.117	0.109	–0.330 [†]
			Bulk density	1.740	0.052	0.123	0.350 [†]
Elba	LB	17	Micro-density	–	–	0.012	0.110
			Porosity	–	–	0.013	0.116
			Bulk density	–	–	0.005	–0.068
Palinuro	PL	49	Micro-density	–	–	0.026	–0.162
			Porosity	–	–	0.058	–0.241
			Bulk density	–	–	0.030	0.173
Scilla	SC	8	Micro-density	2.485	0.043	0.591	0.768 [†]
			Porosity	–	–	0.377	0.614
			Bulk density	–	–	0.194	–0.440
Genova	GN	23	Micro-density	2.559	0.030	0.531	0.729 [†]
			Porosity	–	–	0.026	–0.162
			Bulk density	–	–	0.084	0.290
Pantelleria	PN	115	Micro-density	2.528	0.032	0.494	0.703 ^{***}
			Porosity	41.548	–0.084	0.056	–0.237 [†]
			Bulk density	1.461	0.086	0.156	0.394 ^{***}

n , number of individuals; r^2 , Pearson's coefficient of determination; r , Pearson's correlation coefficient.

[†] $p < 0.050$.

^{***} $p < 0.001$.

In *B. europaea*, when bulk density correlated positively with age (Calafuria and Pantelleria), porosity correlated negatively, regardless of the response of micro-density. When bulk density did not vary with age (Genova, Elba, Palinuro and Scilla), neither did porosity vary, regardless of micro-density patterns (Table 2). In two cases (Scilla and Genova), micro-density was positively correlated with age (Table 2).

In *L. pruvoti*, when bulk density correlated negatively with age (Genova, Calafuria, Elba and Scilla), porosity correlated positively, regardless of the response of micro-density. When bulk density remained constant (Palinuro and Pantelleria), porosity was also

unchanged, irrespective of micro-density (Table 3). In three cases (Calafuria, Genova and Pantelleria), micro-density was positively correlated with age (Table 3).

Thus, in both species, the variation of bulk density with age was determined by the variation of porosity rather than by the variation of micro-density. Whenever the relationship between bulk density and micro-density or age was significant, it showed a positive trend.

The mean porosity of *B. europaea* was significantly lower than that of *L. pruvoti* in 4 out of 6 populations (Genova, Calafuria, Elba and Pantelleria; Student's t -test, $p < 0.001$). In the Palinuro population, porosity was significantly lower in *L. pruvoti* (Student's t -test,

Table 3

Leptopsammia pruvoti. Correlation analysis between polyp age (independent variable) and skeletal parameters (dependent variable) at 6 sites along the west coast of Italy. Relationships were fitted to a power function model $y = ax^b$. The exponent (b) and factor (a) values are indicated only where the relationship was significant. The sites are arranged in order of increasing seawater temperature.

Population	Code	n	Dependent variable	Factor	Exponent	r^2	r
Calafuria	CL	44	Micro-density	2.525	0.031	0.14	0.374 [*]
			Porosity	27.600	0.285	0.19	0.431 ^{**}
			Bulk density	1.943	–0.178	0.13	–0.361 [†]
Elba	LB	42	Micro-density	–	–	0.07	–0.273
			Porosity	23.156	0.250	0.12	0.349 [†]
			Bulk density	2.331	–0.188	0.13	–0.365 [†]
Palinuro	PL	45	Micro-density	–	–	0.01	0.071
			Porosity	–	–	0.00	–0.049
			Bulk density	–	–	0.01	0.069
Scilla	SC	29	Micro-density	–	–	0.09	–0.298
			Porosity	26.852	0.128	0.17	0.417 [†]
			Bulk density	2.029	–0.074	0.19	–0.437 [†]
Genova	GN	43	Micro-density	2.634	0.012	0.20	0.445 ^{***}
			Porosity	27.799	0.205	0.24	0.491 ^{***}
			Bulk density	1.917	–0.112	0.15	–0.382 [†]
Pantelleria	PN	45	Micro-density	2.532	0.036	0.39	0.621 ^{***}
			Porosity	–	–	0.04	0.194
			Bulk density	–	–	0.03	0.157

n , number of individuals; r^2 , Pearson's coefficient of determination; r , Pearson's correlation coefficient.

^{*} $p < 0.050$.

^{**} $p < 0.010$.

^{***} $p < 0.001$.

Table 4
Balanophyllia europaea and *Leptopsammia pruvoti*. Mean porosity of the samples at each site and significance of Student's *t*-test used to compare the values between the two species. The sites are arranged in order of increasing seawater temperature.

Population	Code	Species	<i>n</i>	Mean porosity (%)	SE	Significance
Calafuria	CL	<i>B. europaea</i>	1814	29.58	0.04	<i>p</i> < 0.001
		<i>L. pruvoti</i>	210	37.35	0.48	
Elba	LB	<i>B. europaea</i>	38	30.00	0.25	<i>p</i> < 0.001
		<i>L. pruvoti</i>	76	36.05	0.78	
Palinuro	PL	<i>B. europaea</i>	80	38.20	0.20	<i>p</i> < 0.001
		<i>L. pruvoti</i>	152	31.02	0.05	
Scilla	SC	<i>B. europaea</i>	48	30.78	0.94	ns
		<i>L. pruvoti</i>	115	30.99	0.44	
Genova	GN	<i>B. europaea</i>	55	31.44	0.16	<i>p</i> < 0.001
		<i>L. pruvoti</i>	123	36.26	0.80	
Pantelleria	PN	<i>B. europaea</i>	171	35.11	0.09	<i>p</i> < 0.001
		<i>L. pruvoti</i>	144	41.84	0.10	

n, number of individuals; SE, standard error.

p < 0.001), while in the Scilla population both species exhibited the same porosity (Table 4).

In both species and in all locations, a strong correlation was observed between bulk density and porosity. In *B. europaea*, the relationship between bulk density and porosity was 1.8–45.0 times stronger than that with micro-density, as indicated by the ratio of the r^2 values of the regressions (Table 5). In *L. pruvoti*, this relationship was even more emphasized, the correlation with porosity being 1.7–185.0 times stronger than that with micro-density (Table 6).

Since the average age of the samples differed among the sites (Table 1), analyses of correlations between SST and skeletal parameters were performed after applying to the data the method of the adjusted values in relation to age (Steel, 1980; see Goffredo et al., 2007 for an example of application on corals). In *B. europaea*, SST did not correlate with micro-density, while it was positively correlated with porosity, explaining 4.5% of its variation, and negatively correlated with bulk density, explaining 4.2% of its variation (Fig. 3). In *L. pruvoti*, SST was positively correlated with micro-density, explaining 15.4% of its variation, but showed no correlation with porosity and bulk density (Fig. 3).

Table 5
Balanophyllia europaea. Correlation analysis between bulk density, micro-density and porosity at the 6 sites. The exponent and factor values are indicated only where the relationship was significant. The sites are arranged in order of increasing seawater temperature.

Population	Code	<i>n</i>	Dependent variable	Independent variable	Factor	Exponent	r^2	<i>r</i>
Calafuria	CL	38	Bulk density	Porosity	7.532	−0.409	0.963	0.981***
			Bulk density	Micro-density	0.160	2.462	0.241	0.491**
			Micro-density	Porosity	3.035	−0.032	0.143	0.378*
Elba	LB	17	Bulk density	Porosity	9.701	−0.490	0.956	0.978***
			Bulk density	Micro-density	0.003	6.515	0.532	0.729***
			Micro-density	Porosity	2.992	−0.036	0.417	0.646**
Palinuro	PL	49	Bulk density	Porosity	13.728	−0.581	0.931	0.965***
			Bulk density	Micro-density	0.377	1.510	0.125	0.353*
			Micro-density	Porosity	–	–	0.015	0.122
Scilla	SC	8	Bulk density	Porosity	8.436	−0.440	0.950	0.975***
			Bulk density	Micro-density	–	–	0.021	0.145
			Micro-density	Porosity	–	–	0.003	0.055
Genova	GN	23	Bulk density	Porosity	8.273	−0.435	0.920	0.959***
			Bulk density	Micro-density	–	–	0.037	0.192
			Micro-density	Porosity	–	–	0.0001	0.01
Pantelleria	PN	115	Bulk density	Porosity	14.315	−0.593	0.936	0.967***
			Bulk density	Micro-density	0.157	2.427	0.253	0.503***
			Micro-density	Porosity	3.093	−0.039	0.093	0.305**

n, number of individuals; r^2 , Pearson's coefficient of determination; *r*, Pearson's correlation coefficient.

* *p* < 0.050.

** *p* < 0.010.

*** *p* < 0.001.

4. Discussion

4.1. Relationships among skeletal parameters

In both species and in all locations, the strong relationship between bulk density and porosity was expected and indicates that the buoyant weighing technique we used gave reasonable results (Tables 5 and 6; Bucher et al., 1998). Bulk density trends were always diametrically opposed to porosity trends (Tables 2, 3, 5 and 6; Fig. 3), regardless of the trend of micro-density, thus indicating that the variations in micro-density, even when significant, were not strong enough to cause significant variations in bulk density.

4.2. Relationships between micro-density and age

Bulk density is determined by the pattern in which the material is laid down (micro-density) and by the volume of skeletal voids it encloses (porosity) (Bucher et al., 1998). Micro-density is the specific gravity of the material of which the skeleton is made. The scleractinian coral skeleton is a two-phase composite material

Table 6

Leptosammia pruvoti. Correlation analysis between bulk density, micro-density and porosity at the 6 sites. The exponent and factor values are indicated only where the relationship was significant. The sites are arranged in order of increasing seawater temperature.

Population	Code	n	Dependent variable	Independent variable	Factor	Exponent	r ²	r
Calafuria	CL	44	Bulk density	Porosity	21.824	-0.717	0.925	0.961 ^{***}
			Bulk density	Micro-density	0.091	2.881	0.230	0.480 ^{**}
			Micro-density	Porosity	-	-	0.092	0.303
Elba	LB	42	Bulk density	Porosity	19.874	-0.692	0.924	0.961 ^{***}
			Bulk density	Micro-density	0.003	6.398	0.547	0.740 ^{***}
			Micro-density	Porosity	3.250	-0.054	0.417	0.646 ^{***}
Palinuro	PL	45	Bulk density	Porosity	8.798	-0.458	0.900	0.949 ^{***}
			Bulk density	Micro-density	-	-	0.011	0.105
			Micro-density	Porosity	-	-	0.016	0.126
Scilla	SC	29	Bulk density	Porosity	11.711	-0.536	0.950	0.975 ^{***}
			Bulk density	Micro-density	-	-	0.015	0.122
			Micro-density	Porosity	-	-	1.00E-06	0.001
Genova	GN	43	Bulk density	Porosity	19.743	-0.685	0.943	0.971 ^{***}
			Bulk density	Micro-density	-	-	0.019	0.138
			Micro-density	Porosity	-	-	0.0001	0.01
Pantelleria	PN	45	Bulk density	Porosity	13.069	-0.569	0.742	0.861 ^{***}
			Bulk density	Micro-density	-	-	0.004	0.063
			Micro-density	Porosity	1.581	0.144	0.195	0.442 ^{**}

n, number of individuals; r², Pearson's coefficient of determination; r, Pearson's correlation coefficient.

* p < 0.050.

** p < 0.010.

*** p < 0.001.

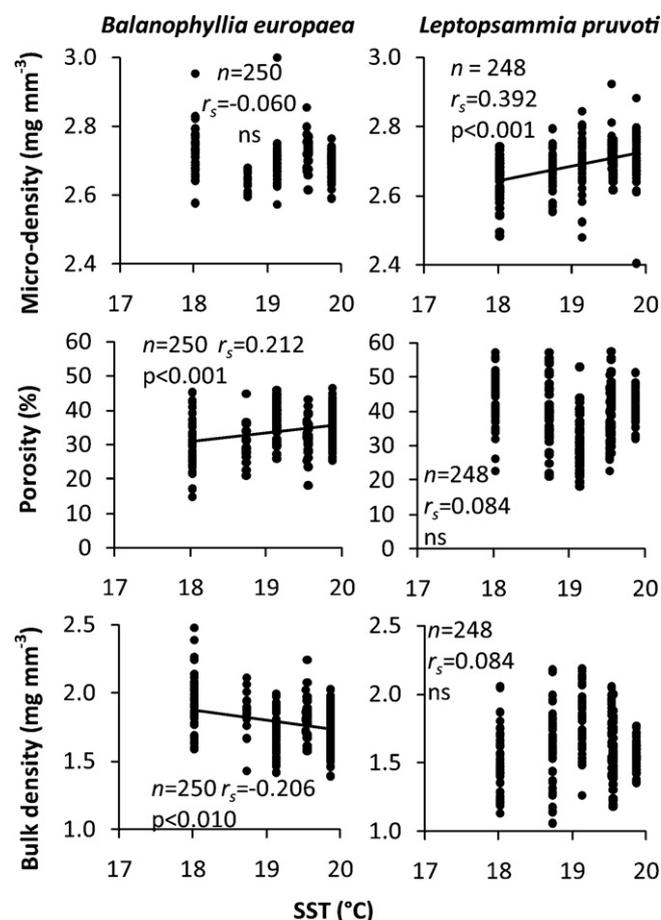


Fig. 3. Variation in the skeletal parameters of two corals, *Balanophyllia europaea* and *Leptosammia pruvoti*, with sea surface temperature (SST). r² Spearman's determination coefficient, r_s Spearman's correlation coefficient, n number of individuals.

consisting of fiber-like crystals of aragonitic calcium carbonate phases (crystal fibers and micro-spherulites) intimately associated with an intra-crystalline organic matrix (OM) (Cuif et al., 1999). OM generally constitutes <0.1% of the total skeleton weight (Constantz and Weiner, 1988) and is believed to initiate nucleation of calcium carbonate and provide a framework for crystallographic orientation and species-specific architecture (Towe, 1972; Addadi and Weiner, 1985; Lowenstam and Weiner, 1989).

For both species, in the populations where the relationship between micro-density and age was significant (Scilla, Genova and Pantelleria for *B. europaea* and Calafuria, Genova and Pantelleria for *L. pruvoti*; Tables 2 and 3), micro-density increased from 2.6 mg mm⁻³ at minimum age (1.3–5.7 years) to 2.8 mg mm⁻³ at maximum age (9.7–17.1 years). This variation is quite relevant with respect to the density of inorganic CaCO₃ (2.94 mg mm⁻³ for aragonite and 2.71 mg mm⁻³ for calcite; Marszalek, 1982) and might be determined by the influence of OM. A decrease of intracrystalline OM content with increasing age could explain the increase of micro-density with age found in this study. As an alternative hypothesis, which is currently being tested, the production of different kinds of OM along the life cycle of the polyp could lead to the precipitation of crystal phases with different densities, thus causing the observed increase of micro-density with age. The different densities of crystal phases could result from different processes, e.g., an increased isomorphic substitution of strontium to calcium in the aragonite structure, a different polymorphic selection between calcium carbonate polymorphs (aragonite is denser than calcite) or a decrease of the relative number of low-density centers of calcification (possibly amorphous calcium carbonate; Cohen and McConnaughey, 2003) with respect to the aragonitic fibrous structure. Indeed, preliminary data on *B. europaea* skeletons show a decreasing calcite content (and increasing aragonite content) with age (S. Goffredo, personal observation), thus supporting the latter hypothesis.

4.3. Relationships between porosity and age

In *L. pruvoti*, porosity increased with age in 4 out of 6 populations (Genova, Calafuria, Elba and Scilla). Thus, younger individuals were less porous and, as they got older, the skeleton's porosity increased.

In most populations of *B. europaea*, porosity did not vary with age, while in 2 out of 6 populations (Calafuria and Pantelleria) porosity decreased with age.

To compare the average porosity between the two species, the relationships between porosity and age obtained in the present study (when significant) were used to estimate the porosity values of samples collected for previous analyses (Goffredo et al., 2007). For this earlier study, a higher number of samples of the two species had been collected within quadrats in the same sites as used for the present study. The inverse of the age–porosity relationship obtained in the present work was applied to their age, thus obtaining their porosity. For those populations with a non-significant age–porosity relationship, the average porosity value calculated in the present study was assigned to all the samples of Goffredo et al. (2007). The mean porosity of *B. europaea* was significantly lower than that of *L. pruvoti* in 4 out of 6 populations (Genova, Calafuria, Elba and Pantelleria; Student's *t*-test, $p < 0.001$). In the Palinuro population, porosity was significantly lower in *L. pruvoti* (Student's *t*-test, $p < 0.001$), while in the Scilla population both species showed no differences in porosity (Table 4). A possible explanation for the generally lower porosity of *B. europaea* compared to *L. pruvoti* might be the adaptation to two very different habitats. Several studies show that in protected habitats extension is faster, but branches are more lightly calcified, so skeletal porosity is higher than in non-protected habitats. Where water movement is high, branches are thicker, shorter and more heavily calcified, making them more resistant to wave action (Chamberlain, 1978; Oliver et al., 1983; Harriott, 1997, 1998). Indeed, *B. europaea* is found in open and light habitats often subject to currents and water motion and may need stronger skeletons, while *L. pruvoti* lives in much more sheltered environments such as crevices and caves.

4.4. Relationships between skeletal parameters and sea surface temperature

While in *B. europaea* there was an increase of porosity with increasing temperature and no correlation with micro-density, in *L. pruvoti* there was an increase of micro-density with increasing temperature and no correlation with porosity.

The relationship between temperature and porosity in *B. europaea*, which is a zooxanthellate coral, suggests a possible effect of temperature on photosynthesis in the algal symbionts. The same hypothesis was proposed in earlier studies (Goffredo et al., 2007, 2008, 2009) investigating the relationship between SST and biological parameters (population density, population stability, percentage of immature individuals, calcification) in this species. In zooxanthellate corals, photosynthesis enhances calcification (Gattuso et al., 1999; Al-Horani et al., 2005), and both processes have temperature optima (Howe and Marshall, 2002; Al-Horani, 2005). Thus, the increase of porosity with increasing SST in *B. europaea* could result from an attenuation of calcification due to an inhibition of the photosynthetic process at higher temperatures (Goffredo et al., 2009).

Alternatively, suspension feeding could also explain the increase of porosity with increasing SST observed in *B. europaea*. In the Mediterranean Sea, nutrient levels and zooplankton availability are typically lower in summer (i.e., at higher SST) than in winter (i.e., at lower SST; Coma et al., 2000; Coma and Ribes, 2003). Low nutrient and zooplankton availability causes stress and starvation in *Cladocora caespitosa* (Peirano et al., 2005a) and a summer dormancy in the metabolism of several benthic suspension feeders (Coma et al., 2000; Coma and Ribes, 2003). In colonies of the tropical corals *Stylophora pistillata* and *Galaxea fascicularis*, calcification and photosynthesis are significantly lower in starved corals than in fed ones (Houlbrèque et al., 2004; Borell and Bischof, 2008; Borell et al., 2008). The high skeletal porosity observed in *B. europaea* at high SST

might thus be explained as being a consequence of low energetic resources. However, if this were the case, the inhibition would have to be stronger in *L. pruvoti*, which is fully heterotrophic, than in *B. europaea*, which can also rely on the symbiont. In the present study, however, skeletal porosity of *L. pruvoti* did not vary with increasing temperature. Thus, the hypothesis of photosynthetic inhibition at high SST seems to be more appropriate for explaining the results regarding porosity in *B. europaea*. Yet, the role of feeding in determining the increase of porosity cannot be completely excluded, since the proportion of energy obtained by autotrophy versus heterotrophy has never been quantified for this species in the currently available literature.

In *L. pruvoti*, the fact that temperature did not correlate with porosity could be due to the absence of zooxanthellae, and thus the lack of a physiological dependence of calcification on photosynthesis. However, the increase of micro-density with increasing temperature observed in *L. pruvoti* is intriguing. A possible explanation could be that aragonite, whose density is greater than that of calcite (2.94 mg mm^{-3} for aragonite vs. 2.71 mg mm^{-3} for calcite; Marszalek, 1982), is more stable at high temperatures than is calcite. In many carbonate-producing taxa, the precipitation of biominerals depends on several aspects of the environment they live in, such as temperature and chemistry, which strongly influence aragonite and magnesium calcite deposition (Morse et al., 1997; Stanley and Hardie, 1998; Montañez, 2002; Skinner and Jahren, 2003; Feely et al., 2004; Smith and Key, 2004). In particular, the abundance of various polymorphs of calcium carbonate strongly depends on SST (Wray and Daniels, 1957; Ogino et al., 1987). Calcite is the dominant polymorph at low temperatures. With increasing temperature, calcite abundance decreases in favor of aragonite (Sawada, 1997). High-Mg calcites and aragonite are predominantly associated with warm tropical to subtropical waters and low-Mg calcite levels are generally found at higher latitudes or in cold, deep waters (Lopez et al., 2009). An increase of aragonite with increasing temperature could cause the increase of micro-density with temperature in *L. pruvoti* found in the present study (Fig. 3).

5. Conclusion

In conclusion, it is hypothesized that high SST has a negative impact on the zooxanthellate *B. europaea*, since it compromises the photosynthetic efficiency of its symbionts, lowering its skeletal resistance due to increasing porosity. In contrast, the porosity of the azooxanthellate *L. pruvoti* is unaffected by temperature, and the skeletal resistance of this species may even benefit from the increased micro-density achieved in warmer waters. These results have to be considered in the context of global climate change, since they highlight possible differences of these two coral species in their sensitivity/tolerance to temperature change. Interestingly, *B. europaea*, which can count on both heterotrophy and symbiotic algae for its nourishment, seems to be negatively affected by increasing temperatures, while *L. pruvoti*, which is fully heterotrophic, seems to be tolerant to higher temperatures. It seems likely that photosynthesis plays a role in determining the different sensibilities of these two species, and experimental measurements of photosynthesis at different temperatures may clarify its role in determining the observed patterns of skeletal parameters.

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References

- Addadi, L., Weiner, S., 1985. Interactions between acidic proteins and crystals: stereochemical requirements in biomineralization. *Proc. Natl. Acad. Sci. U.S.A.* 82, 4110–4114.
- Al-Horani, F.A., 2005. Effects of changing seawater temperature on photosynthesis and calcification in the scleractinian coral *Galaxea fascicularis*, measured with O_2 , Ca^{2+} and pH microsensors. *Sci. Mar.* 69, 347–354.
- Al-Horani, F.A., Ferdelman, T., Al-Moghrabi, S.M., de Beer, D., 2005. Spatial distribution of calcification and photosynthesis in the scleractinian coral *Galaxea fascicularis*. *Coral Reefs* 24, 173–180.
- Altman, D.G., 1991. *Practical Statistics for Medical Research*. Chapman & Hall, London.
- Ammar, M.S., Mohammed, T.A., Mahmoud, M.A., 2005. Skeletal density (strength) of some corals in an actively flooding and a non flooding site, south Marsa Alam, Red Sea, Egypt. *J. Egypt. Germ. Soc. Zool.* 46, 125–139.
- Bak, R.P.M., 1973. Coral weight increment in situ. A new method to determine coral growth. *Mar. Biol.* 20, 40–49.
- Bak, R.P.M., 1974. Available light and other factors influencing growth of stony corals through the year in Curacao. In: *Proceedings of the 2nd International Coral Reef Symposium*, vol. 2, pp. 229–233.
- Bak, R.P.M., 1976. The growth of coral colonies and the importance of crustose coralline algae and burrowing sponges in relation with carbonate accumulation. *Neth. J. Sea Res.* 10, 285–337.
- Ballesteros, E., 2006. Mediterranean coralligenous assemblages: a synthesis of the present knowledge. *Oceanogr. Mar. Biol. Annu. Rev.* 44, 123–195.
- Barnes, D.J., Devereux, M.J., 1988. Variations in skeletal architecture associated with density banding in the hard corals *Porites*. *J. Exp. Mar. Biol. Ecol.* 121, 37–54.
- Borell, E.M., Bischof, K., 2008. Feeding sustains photosynthetic quantum yield of a scleractinian coral during thermal stress. *Oecologia* 157, 593–601.
- Borell, E.M., Yuliantri, A.R., Bischof, K., Richter, C., 2008. The effect of heterotrophy on photosynthesis and tissue composition of two scleractinian corals under elevated temperature. *J. Exp. Mar. Biol. Ecol.* 364, 116–123.
- Bosscher, H., 1993. Computerized tomography and skeletal density of coral skeletons. *Coral Reefs* 12, 97–103.
- Bucher, D.J., Harriott, V.J., Roberts, L.G., 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 *Montastrea annularis*. *J. Exp. Mar. Biol. Ecol.* 302, 249–260.
- Cerrano, C., Bavestrello, G., Bianchi, C.N., Cattaneo-Vietti, R., Bava, S., Morganti, C., Morri, C., Picco, P., Sara, G., Schiaparelli, S., Siccardi, A., Sponga, F., 2000. A catastrophic mass-mortality episode of gorgonians and other organisms in the Ligurian Sea (NW Mediterranean), summer 1999. *Ecol. Lett.* 3, 284–293.
- Chamberlain, J.A., 1978. Mechanical properties of coral skeleton: compressive strength and its adaptive significance. *Paleobiology* 4, 419–435.
- Cohen, A.L., McConnaughey, T.A., 2003. Geochemical perspectives on coral mineralization. *Rev. Miner. Geochem.* 54, 151–187.
- Coma, R., Ribes, M., 2003. Seasonal energetic constraints in Mediterranean benthic suspension feeders: effects at different levels of ecological organization. *Oikos* 101, 205–215.
- Coma, R., Ribes, M., Gili, J.M., Zabala, M., 2000. Seasonality in coastal ecosystems. *Trends Ecol. Evol.* 12, 448–453.
- Coma, R., Ribes, M., Serrano, E., Jimenez, E., Salat, J., Pascual, J., 2009. Global warming-enhanced stratification and mass mortality events in the Mediterranean. *Proc. Natl. Acad. Sci. U.S.A.* 106, 6176–6181.
- Constant, B., Weiner, S., 1988. Acidic macromolecules associated with the mineral phase of scleractinian coral skeletons. *J. Exp. Zool.* 248, 253–258.
- Crossland, C.J., 1984. Seasonal variations in the rates of calcification and productivity in the coral *Acropora formosa* on a high latitude reef. *Mar. Ecol. Prog. Ser.* 15, 135–140.
- Cuif, J.P., Dauphin, Y., Gautret, P., 1999. Compositional diversity of soluble mineralizing matrices in some recent coral skeletons compared to fine-scale growth structures of fibres: discussion of consequences for biomineralization and diagenesis. *Int. J. Earth Sci.* 88, 582–592.
- Dar, M.A., Mohammed, T.A., 2009. Seasonal variations in the skeletogenesis process in some branching corals of the Red Sea. *Thalassas* 25, 31–44.
- Davies, P.S., 1989. Short-term growth measurements of corals using an accurate buoyant weighing technique. *Mar. Biol.* 101, 389–395.
- Dustan, P., 1975. Growth and form in the reef-building coral *Montastrea annularis*. *Mar. Biol.* 33, 101–107.
- Franzisket, L., 1964. The metabolic intensity of the reef corals and their ecological, phylogenetic and sociological significance. *Z. Vergl. Physiol.* 49, 91–113 (in German).
- Feely, R.A., Sabine, C.L., Lee, K., Berelson, W., Kleypas, J., Fabry, V.J., Millero, F.J., 2004. Impact of anthropogenic CO_2 on the $CaCO_3$ system in the ocean. *Science* 305, 362–366.
- Garrabou, J., Coma, R., Bensoussan, N., Bally, M., Chevaldonne, P., Cigliano, M., Diaz, D., Harmelin, J.G., Gambi, M.C., Kersting, D.K., Ledoux, J.B., Lejeune, C., Linares, C., Marschal, C., Perez, T., Ribes, M., Romano, J.C., Serrano, E., Teixido, N., Torrens, O., Zabala, M., Zuberer, F., Cerrano, C., 2009. Mass mortality in the NW Mediterranean rocky benthic communities: effects of the 2003 heat wave. *Glob. Change Biol.* 15, 1090–1103.
- Gattuso, J.P., Allemand, D., Frankignoulle, M., 1999. Photosynthesis and calcification at cellular, organismal and community levels in coral reefs: a review on interactions and control by carbonate chemistry. *Am. Zool.* 39, 160–183.
- Goffredo, S., Zaccanti, F., 2004. Laboratory observations of larval behavior and metamorphosis in the Mediterranean solitary coral *Balanophyllia europaea* (Scleractinia, Dendrophylliidae). *Bull. Mar. Sci.* 74, 449–458.
- Goffredo, S., Arnone, S., Zaccanti, F., 2002. Sexual reproduction in the Mediterranean solitary coral *Balanophyllia europaea* (Scleractinia, Dendrophylliidae). *Mar. Ecol. Prog. Ser.* 229, 83–94.
- Goffredo, S., Mattioli, G., Zaccanti, F., 2004. Growth and population dynamics model of the Mediterranean solitary coral *Balanophyllia europaea* (Scleractinia, Dendrophylliidae). *Coral Reefs* 23, 433–443.
- Goffredo, S., Airo, V., Radetić, J., Zaccanti, F., 2006. Sexual reproduction of the solitary sunset cup coral *Leptostammia pruvoti* (Scleractinia, Dendrophylliidae) in the Mediterranean. 2. Quantitative aspects of the annual reproductive cycle. *Mar. Biol.* 148, 923–932.
- Goffredo, S., Caroselli, E., Mattioli, G., Pignotti, E., Zaccanti, F., 2007. Variation in biometry and demography of solitary corals with environmental factors in the Mediterranean Sea. *Mar. Biol.* 152, 351–361.
- Goffredo, S., Caroselli, E., Mattioli, G., Pignotti, E., Zaccanti, F., 2008. Relationships between growth, population structure and sea surface temperature in the temperate solitary coral *Balanophyllia europaea* (Scleractinia, Dendrophylliidae). *Coral Reefs* 27, 623–632.
- Goffredo, S., Caroselli, E., Mattioli, G., Pignotti, E., Dubinsky, Z., Zaccanti, F., 2009. Inferred level of calcification decreases along an increasing temperature gradient in a Mediterranean endemic coral. *Limnol. Oceanogr.* 54, 930–937.
- Goffredo, S., Caroselli, E., Mattioli, G., Zaccanti, F., 2010. Growth and population dynamic model for the non-zooxanthellate temperate solitary coral *Leptostammia pruvoti* (Scleractinia, Dendrophylliidae). *Mar. Biol.* 157, 2603–2612.
- Goreau, T.F., Goreau, N.I., 1959. The physiology of skeleton formation in corals. II. Calcium deposition by hermatypic corals under different conditions. *Biol. Bull.* 117, 239–250.
- Graus, R.R., Macintyre, I.G., 1982. Variation in growth forms of the reef coral *Montastrea annularis* (Ellis and Solander): a quantitative evaluation of growth response to light distribution using computer simulation. In: Rützler, K., Macintyre, I.G. (Eds.), *The Atlantic Barrier Reef Ecosystem at Carrie Bow Cay, Belize*. Smithsonian Inst. Press, Washington, DC, pp. 441–465.
- Harley, C.D.G., Hughes, A.R., Hultgren, K.M., Miner, B.G., Sorte, C.J.B., Thornber, C.S., Rodriguez, L.F., Tomanek, L., Williams, S.L., 2006. The impacts of climate change in coastal marine systems. *Ecol. Lett.* 9, 228–241.
- Harriott, V.J., 1997. Skeletal bulk density of the scleractinian coral *Acropora formosa* (Dana 1846) in tropical and subtropical Western Australia. In: Wells, F.E. (Ed.), *The Flora and Fauna of the Houtman Abrolhos Islands, Western Australia*. Western Australian Museum Publications, Perth, pp. 75–82.
- Harriott, V.J., 1998. Growth of the staghorn coral *Acropora formosa* in Houtman Abrolhos, Western Australia. *Mar. Biol.* 132, 319–325.
- Harriott, V.J., 1999. Coral growth in subtropical eastern Australia. *Coral Reefs* 15, 281–291.
- Harriott, V.J., Banks, S.A., 2002. Latitudinal variation in coral communities in eastern Australia: a qualitative biophysical model of factors regulating coral reefs. *Coral Reefs* 21, 83–94.
- Helmle, K.P., Dodge, R.E., Ketcham, R.A., 2000. Skeletal architecture and density banding in *Diploria strigosa* by X-ray computed tomography. *Proceedings of the 9th International Coral Reef Symposium* 1, 365–371.
- Highsmith, R.C., 1979. Coral growth rates and environmental control of density banding. *J. Exp. Mar. Biol. Ecol.* 37, 105–125.
- Houlbrèque, F., Tambutté, E., Allemand, D., Ferrier-Pagès, C., 2004. Interactions between zooplankton feeding, photosynthesis and skeletal growth in the scleractinian coral *Stylophora pistillata*. *J. Exp. Mar. Biol. Ecol.* 207, 1461–1469.
- Howe, S.A., Marshall, A.T., 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., 1987. Skeletal density and growth form of corals. *Mar. Ecol. Prog. Ser.* 35, 259–266.
- Jiménez, C., Cortés, J., 1993. Density and compressive strength of the coral *Siderastrea sideraea* (Scleractinia: Siderastreidae): intraspecific variability. *Rev. Biol. Trop.* 41, 39–43.

- Jokiel, P.L., Coles, S.L., 1978. Effects of temperature on the mortality and growth of Hawaiian reef corals. *Mar. Biol.* 43, 201–208.
- Jokiel, P.L., Maragos, J.E., Franzisket, L., 1978. Coral growth: buoyant weight technique. In: Stoddart, D.R., Johannes, R.E. (Eds.), *Coral Reef: Research Methods*. UNESCO Publishing, Paris, pp. 379–396.
- Kain, J.M., 1989. The seasons in the subtidal. *Br. Phycol. J.* 24, 203–215.
- Karl, T.R., Trenberth, K.E., 2003. Modern global climate change. *Science* 302, 1175–1177.
- Kleypas, J.A., McManus, J.W., Menez, L.A.B., 1999. Environmental limits to coral reef development: where do we draw the line? *Am. Zool.* 39, 146–159.
- Lejeune, C., Chevaldonné, P., Pergent-Martini, C., Boudouresque, C.F., Pérez, T., 2010. Climate change effects on a miniature ocean: the highly diverse, highly impacted Mediterranean Sea. *Trends Ecol. Evol.* 25, 250–260.
- Liddle, M.J., Kay, A.M., 1987. Resistance, survival and recovery of trampled corals on the Great Barrier Reef. *Biol. Conserv.* 42, 1–18.
- Lopez, O., Zuddas, P., Faivre, O., 2009. The influence of temperature and seawater composition on calcite crystal growth mechanisms and kinetics: implications for Mg incorporation in calcite lattice. *Geochim. Cosmochim. Acta* 73, 337–347.
- Lough, J.M., Barnes, D.J., 2000. Environmental controls on growth of the massive coral *Porites*. *J. Exp. Mar. Biol. Ecol.* 245, 225–243.
- Lowenstam, H.A., Weiner, S., 1989. *On Biomineralization*. Oxford University Press, New York.
- Mann, G.S., 1994. Distribution, abundance and life history of the reef coral *Favia fragum* (Esper) in Barbados: effects of eutrophication and of the black sea urchin *Diadema antillarum* (Philippi). M. Sc. Thesis, McGill University, Montreal.
- Marszalek, D.S., 1982. The role of heavy skeletons in vertical movements of non-motile zooplankton. *Mar. Freshw. Behav. Physiol.* 8, 295–303.
- Marubini, F., Ferrier-Pages, C., Cuif, J.P., 2003. Suppression of skeletal growth in scleractinian corals by decreasing ambient carbonate-ion concentration: a cross-family comparison. *Proc. R. Soc. Lond. B* 270, 179–184.
- Montañez, I.P., 2002. Biological skeletal carbonate records changes in major ion chemistry of paleo-oceans. *Proc. Natl. Acad. Sci. U.S.A.* 99, 5852–5854.
- Morse, J.W., Wang, Q., Tsio, M.Y., 1997. Influence of temperature and Mg:Ca ratio on CaCO₃ precipitates from seawater. *Geology* 25, 85–87.
- Ogino, T., Suzuki, T., Sawada, K., 1987. The formation and transformation mechanism of calcium carbonate in water. *Geochim. Cosmochim. Acta* 51, 2757–2767.
- Oliver, J.K., Chalker, B.E., Dunlap, W.C., 1983. Bathymetric adaptations of reef-building corals at Davies Reef, Great Barrier Reef, Australia. I. Long-term growth responses of *Acropora formosa* (Dana 1846). *J. Exp. Mar. Biol. Ecol.* 73, 11–35.
- Peirano, A., Morri, C., Bianchi, C.N., 1999. Skeleton growth and density pattern of the temperate, zooxanthellate scleractinian *Cladocora caespitosa* from the Ligurian Sea (NW Mediterranean). *Mar. Ecol. Prog. Ser.* 185, 195–201.
- Peirano, A., Abbate, M., Cerrati, G., Difesca, V., Peroni, C., Rodolfo-Metalpa, R., 2005a. Monthly variations in calyx growth, polyp tissue, and density banding of the Mediterranean scleractinian *Cladocora caespitosa* (L.). *Coral Reefs* 24, 404–409.
- Peirano, A., Damasso, V., Montefalcone, M., Morri, C., Bianchi, C.N., 2005b. Effects of climate, invasive species and anthropogenic impacts on the growth of the seagrass *Posidonia oceanica* (L.) Delile in Liguria (NW Mediterranean Sea). *Mar. Pollut. Bull.* 50, 817–822.
- Perez, T., Garrabou, J., Sartoretto, S., Harmelin, J.G., Francour, P., Vacelet, J., 2000. Mass mortality of marine invertebrates: an unprecedented event in the Northwestern Mediterranean. *C. R. Acad. Sci. Paris, Ser. III* 323, 853–865.
- Potvin, C., Roff, D.A., 1993. Distribution-free and robust statistical methods: viable alternatives to parametric statistics? *Ecology* 74, 1617–1628.
- Richardson, A.J., Poloczanska, E.S., 2008. Under-resourced, under threat. *Science* 320, 1294–1295.
- Rodgers, K., Cox, E., Newston, C., 2003. Effects of mechanical fracturing and experimental trampling on Hawaiian corals. *Environ. Manage.* 31, 377–384.
- Rodolfo-Metalpa, R., Bianchi, C.N., Peirano, A., Morri, C., 2000. Coral mortality in NW Mediterranean. *Coral Reefs* 19, 24.
- Romano, J.C., Bensoussan, N., Younes, W.A.N., Arlhac, D., 2000. Thermal anomaly in the waters of the Gulf of Marseilles during summer 1999. A partial explanation of the mortality of certain fixed invertebrates? *C. R. Acad. Sci. Paris Ser. III* 323, 415–427.
- Sawada, K., 1997. The mechanisms of crystallization and transformation of calcium carbonates. *Pure Appl. Chem.* 69, 921–928.
- Schneider, R.C., Smith, S.V., 1982. Skeletal Sr content and density in *Porites* spp. in relation to environmental factors. *Mar. Biol.* 66, 121–131.
- Schumacher, H., Plewka, M., 1981. The adaptive significance of mechanical properties versus morphological adjustments in skeletons of *Acropora palmata* and *Acropora cervicornis* (Cnidaria, Scleractinia). In: *Proceedings of the 4th International Coral Reef Symposium*, vol. 2, pp. 121–128.
- Shi, Q., Zhao, M.X., Zhang, Q.M., Yu, K.F., Chen, T.R., Li, S., Wang, H.K., 2009. Estimate of carbonate production by scleractinian corals at Luhuitou fringing reef, Sanya, China. *Chin. Sci. Bull.* 54, 696–705.
- Skinner, H.C.W., Jahren, A.H., 2003. Biomineralization. In: Schlesinger, W.H. (Ed.), *Treatise on Geochemistry*. Elsevier, Amsterdam, pp. 117–184.
- Smith, A.M., Key Jr., M.M., 2004. Controls, variation, and a record of climate change in detailed stable isotope record in a single bryozoan skeleton. *Quat. Res.* 61, 123–133.
- Solomon, S., Qin, D., Manning, M., Marquis, M., Averyt, K., Tignor, M.M.B., Le Roy Miller Jr., H., Chen, Z., 2007. *Climate Change 2007: The Physical Science Basis*. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.
- Spiske, M., Böröcz, Z., Bahlburg, H., 2008. The role of porosity in discriminating between tsunami and hurricane emplacement of boulders—a case study from the Lesser Antilles, southern Caribbean. *Earth Planet. Sci. Lett.* 268, 384–396.
- Stanley, S.M., Hardie, L.A., 1998. Secular oscillations in carbonate mineralogy of reef-building and sediment producing organisms driven by tectonically forced shifts in seawater chemistry. *Palaeogeogr. Palaeoclimat. Palaeoecol.* 144, 3–19.
- Steel, R.G.D., 1980. *Principles and Procedures of Statistics: A Biometrical Approach*, 2nd ed. McGraw-Hill College, New York.
- Tanzil, J.T.I., Brown, B.E., Tudhope, A.W., Dunne, R.P., 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.
- Towe, K.M., 1972. Invertebrate shell structure and the organic matrix concept. *Biominer. Res. Rep.* 4, 2–14.
- Tsimplis, M.N., Zervakis, V., Josey, S., Peeneva, E., Struglia, M.V., Stanev, E., Lionello, P., Malanotte-Rizzoli, P., Artale, V., Theocharis, A., Tragou, E., Oguz, T., 2006. Changes in the oceanography of the Mediterranean Sea and their link to climate variability. In: Lionello, P., Malanotte-Rizzoli, P., Boscolo, R. (Eds.), *Mediterranean Climate Variability*. Elsevier, Amsterdam, pp. 227–282.
- Tunncliffe, V., 1979. The role of boring sponges in coral fracture. In: Levi, C., Bowry-Esnaul, N. (Eds.), *Biologie des Spongiaires*, vol. 291. *Colloq. Int. C.N.R.S.*, pp. 309–315.
- von Bertalanffy, L., 1938. A quantitative theory of organic growth (inquiries on growth laws II). *Hum. Biol.* 10, 181–213.
- Vongsavat, V., Winotai, P., Meejoo, S., 2006. Phase transitions of natural corals monitored by ESR spectroscopy. *Nucl. Instr. Meth. Phys. Res. B* 243, 167–173.
- Vosburgh, F., 1982. *Acropora reticulata*: structure, mechanics and ecology of a reef coral. *Proc. R. Soc. Lond. B* 214, 481–499.
- Wainwright, S.A., Biggs, W.D., Curry, J.D., Gosline, J.M., 1976. *Mechanical Design in Organisms*. Edward Arnold, London.
- Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate change. *Nature* 416, 389–395.
- Wray, J.L., Daniels, F., 1957. Precipitation of calcite and aragonite. *J. Am. Chem. Soc.* 79, 2031–2034.
- Zibrowius, H., 1980. The scleractinians of the Mediterranean and of the North-Eastern Atlantic. *Mem. Inst. Oceanogr.* 11, 1–284 (in French).