

# Variation in biometry and population density of solitary corals with solar radiation and sea surface temperature in the Mediterranean Sea

Stefano Goffredo · Erik Caroselli · Elettra Pignotti ·  
Guido Mattioli · Francesco Zaccanti

Received: 28 November 2006 / Accepted: 28 March 2007 / Published online: 19 April 2007  
© Springer-Verlag 2007

**Abstract** The correlation between two environmental factors (solar radiation and sea surface temperature), biometry, and population density was assessed along a latitudinal gradient in the zooxanthellate coral *Balanophyllia europaea* and in the azooxanthellate coral *Leptosammia pruvoti*. With increasing polyp size, the oral disc of *B. europaea* assumed an oval shape, while that of *L. pruvoti* retained a circular shape. In both species, biometric parameters varied more with temperature than with solar radiation. In the zooxanthellate species, temperature explained a higher percentage of biometric parameter variance than in the azooxanthellate species. While environmental factors did not co-vary with demographic characteristics in *L. pruvoti*, temperature was negatively related to the population density of *B. europaea*. It is hypothesized that the negative effect of temperature on biometry and population density of *B. europaea* depends on photosynthesis inhibition of symbiotic zooxanthellae at high tem-

peratures, which would lower the calcification rate and availability of energetic resources.

## Introduction

The variation of environmental parameters due to latitude is a substantial causal factor of the global distribution of corals (Kleypas et al. 1999). The distribution of atolls and main coral reefs of the world, confined between 30°N and 30°S latitude (Kinsey and Davies 1979), suggests that coral growth actually decreases at high latitudes to a point where coral reef development no longer occurs (Grigg 1982). Coral “growth” is a composite of the three related characters of annual calcification, skeletal density, and linear extension rate (calcification = skeletal density × linear extension; Lough and Barnes 2000; Carricart-Ganivet 2004), and their measurement is essential when assessing the effects of environmental parameters on coral growth (Dodge and Brass 1984). These three variables have been studied along a latitudinal gradient in the genera *Porites* (Grigg 1982; Lough and Barnes 2000) and *Montastraea* (Carricart-Ganivet 2004) and variation in the three parameters has been related to variation in temperature and light associated with latitude. In colonies of the genus *Porites* in the Hawaiian archipelago, Australian Great Barrier Reef, and Thailand, negative correlations with latitude were found for the linear extension, leading to an increase in skeletal density of the colonies (Grigg 1982; Lough and Barnes 2000). In colonies of the genus *Montastraea* in the Gulf of Mexico and Caribbean Sea, negative correlations with latitude were found for calcification and skeletal density, leading to an increase in linear extension rate (Carricart-Ganivet 2004). Rates of linear extension in

Communicated by R. Cattaneo-Vietti.

S. Goffredo (✉) · E. Caroselli · F. Zaccanti  
Department of Evolutionary and Experimental Biology,  
Alma Mater Studiorum—University of Bologna,  
Via F. Selmi 3, 40126 Bologna, Italy  
e-mail: stefano.goffredo@marinesciencigroup.org

E. Pignotti  
Taskforce for Statistical Analysis,  
Marine and Freshwater Science Group Association,  
Via F. Selmi 3, 40126 Bologna, Italy

G. Mattioli  
Operative Unit of Radiology and Diagnostics by Images,  
Hospital of Porretta Terme, Local Health Enterprise of Bologna,  
Via Roma 16, 40046 Porretta Terme, Bologna, Italy

the colonial corals of the genera *Pocillopora* and *Acropora* and in a number of species of the Faviidae family in subtropical Australia (Crossland 1981; Stimson 1996; Harriott 1999) were considerably slower than those at low latitude. Also in the solitary corals of the Fungiidae family, a negative relationship was found between growth rate and latitude (Goffredo and Chadwick-Furman 2003). In contrast, there seem to be cases where rates of coral growth do not vary with increasing latitude. For instance, *Acropora yongei*, *Acropora formosa*, *Turbinaria frondens*, and *Porites heronensis* from subtropical Australia have linear extension rates similar to those of closely related taxa in the tropics, confounding any causal link between latitude and growth rates of coral colonies or coral reefs (Harriott 1999).

For temperate areas, studies on the relationship between environmental parameters and coral growth are scarce. In *Astrangia danae* (Jacques et al. 1983) and *Plesiastrea versipora* (Howe and Marshall 2002), calcification rate increases with temperature, similar to the trend in tropical corals, albeit at lower temperatures. This study presents the relationship between latitudinal variation of environmental factors [solar radiation and sea surface temperature (SST)] and biometry and population density of two Mediterranean Sea corals, *Balanophyllia europaea* (Risso 1826) and *Leptopsammia pruvoti* (Lacaze-Duthiers 1897).

*Balanophyllia europaea* is a solitary, ahermatypic, zooxanthellate, and scleractinian coral, which is endemic to the Mediterranean Sea (Zibrowius 1980). Due to its symbiosis with zooxanthellae, the distribution of this coral is restricted to 0–50 m depth (Zibrowius 1980), where its population density can reach dozens of individuals per square meter (Goffredo et al. 2004). Its reproductive biology is characterized by simultaneous hermaphroditism and brooding (Goffredo et al. 2002). *L. pruvoti* is an ahermatypic, azooxanthellate, solitary, and scleractinian coral, which is distributed in the Mediterranean basin and along the European Atlantic coast from Portugal to southern England. It is one of the most common organisms under overhangs, in caverns, and crevices at 0–70 m depth, reaching densities of thousands of individuals per square meter (Zibrowius 1980; Goffredo et al. 2006). Its reproductive biology is characterized by gonochorism and brooding (Goffredo et al. 2006).

The aim of this study is to assess the variation in the biometric parameters and population density of the zooxanthellate *B. europaea* and of the azooxanthellate *L. pruvoti* along a solar radiation and SST gradient.

## Materials and methods

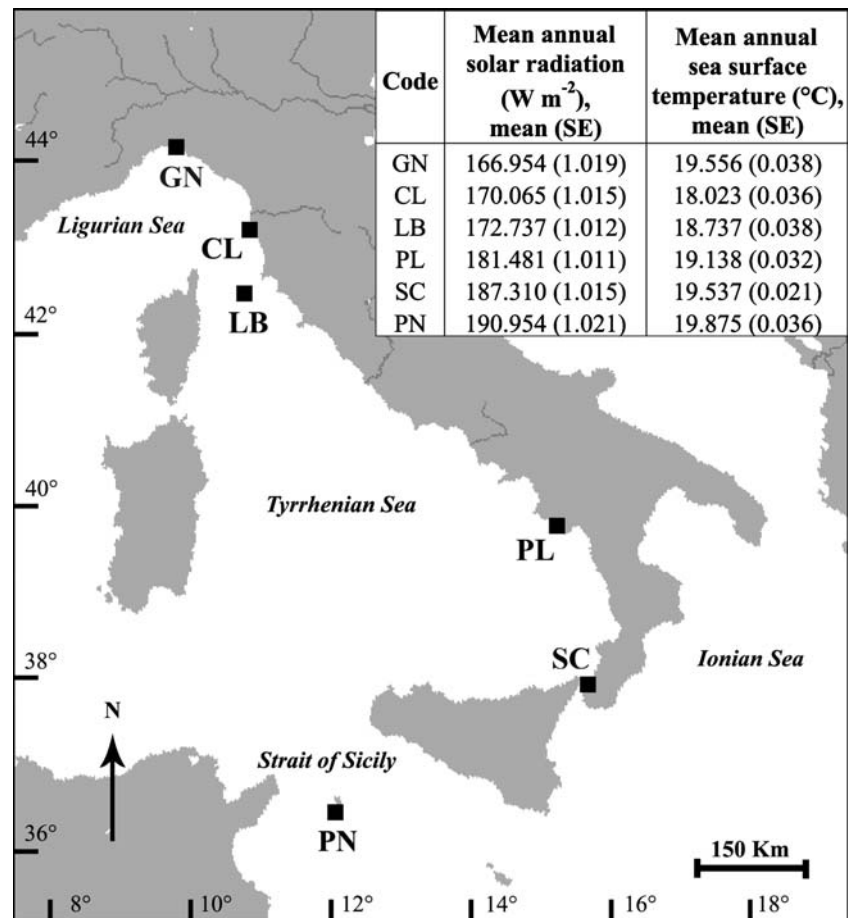
From November 9, 2003 to September 30, 2005, specimens of *B. europaea* and *L. pruvoti* were collected from six sites

along a latitudinal gradient, from 44°20'N to 36°45'N (Fig. 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 strongly linked to coral biometry, physiology, and demography (Kleypas et al. 1999; Lough and Barnes 2000; Harriott and Banks 2002; Al-Horani 2005). At each site, a transect was sampled for both species. For *B. europaea*, the transect consisted of three patches of 1 m<sup>2</sup> each, arranged in a line, 5 m apart and situated along a reef exposed south at a depth of 5–7 m. For *L. pruvoti*, the transect consisted of at least three patches of 0.00425 m<sup>2</sup> each, situated on the vault of crevices 3 m apart, at a depth of 15–17 m (site and number of patches for *B. europaea*: Genova *n* = 8, Calafuria *n* = 18, Elba *n* = 3, Palinuro *n* = 3, Scilla *n* = 8, and Pantelleria *n* = 3; site and number of patches for *L. pruvoti*: Genova *n* = 3, Calafuria *n* = 3, Elba *n* = 4, Palinuro *n* = 3, Scilla *n* = 3, and Pantelleria *n* = 3). 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 these cases since the distributional pattern of the two species is disaggregated (random) (personal observation; Goffredo and Zaccanti 2004; Goffredo et al. 2004). All of the coral polyps present were collected from each patch. The sampling was performed at depths known to have high population densities and where the reproductive biology of the two species had been studied previously (Goffredo and Zaccanti 2004; Goffredo et al. 2002, 2004, 2006). The area of each patch was smaller for *L. pruvoti* than for *B. europaea* because of the very high density of the former species and the difficulty of sampling on the vaults, inside narrow caves.

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 problematic will be investigated using these samples in a diffractometric analysis in preparation. 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 and Chadwick-Furman 2003; Goffredo et al. 2002). Polyp volume (*V*) was determined by applying the formula  $V = \frac{L}{2} \times \frac{W}{2} \times h\pi$  (Goffredo et al. 2002, 2006). Skeletal density (*D*) was calculated by dividing *M* by *V*. The population density was obtained as: (1) *NI*, number of individuals per area unit (N m<sup>-2</sup>), (2) *G*, grams per unit area (g m<sup>-2</sup>), and (3) *P*, percent coverage.

All data relating to the Calafuria site of *B. europaea* were taken from the dataset of Goffredo et al. (2004),

**Fig. 1** 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–Portofino, 44°20'N, and 9°08'E; *CL* Calafuria, 43°27'N, and 10°21'E; *LB* Elba Isle, 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 Isle, 36°45'N, and 11°57'E. For each site, solar radiation and sea surface temperature values are indicated. Solar radiation and SST both varied among the sites (Kruskal–Wallis test and  $P < 0.001$ )



where the biometric analysis was performed on 75 polyps collected randomly at 6 m, and several patches were sampled between 0 and 13 m to examine the bathymetric distribution. For the biometric analysis, the same 75 polyps were used in this work, while for the correlation analysis between biometry, population density, and environmental parameters, only the patches sampled between 5 and 7 m were considered.

As done by a number of authors (e.g., Harriott 1999; Lough and Barnes 2000; Carricart-Ganivet 2004; Peirano et al. 2005a, b) in their studies on the influence of environmental parameters on coral growth, the physical measurement data in our study also (SST and solar radiation) have been obtained from data banks. During 2003–2005, SST data were obtained for each site 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 are measured by mareographic stations SM3810, manufactured by the Italian Society for Precision Apparatuses (SIAP), placed close to the sampling sites. Mean annual SST was obtained from hourly values measured from January 2001 to January 2005 (number of hourly values = 35,064 for each site). Monthly

values of solar radiation ( $\text{W m}^{-2}$ ) were obtained from the International Cloud Climatology Project (ISCCP; available at <http://www.ingrid.ldgo.columbia.edu/>). These estimates are derived from satellite measurements of cloud and atmospheric optical properties. Mean annual solar radiation of each site was obtained for the  $2.5^{\circ}$ -latitude-by-longitude square associated with each of the six sites (number of monthly values = 48 for each site).

#### Statistical analyses

Spearman's rank correlation coefficient is an alternative to Pearson's correlation coefficient (Altman 1991). It is useful when data are non-normally distributed, and thus the assumptions of Pearson's correlation coefficient are not met. Spearman's rank correlation coefficient was used to calculate the significance of the correlations between biometric parameters and environmental variables, and between population density and environmental variables.

Kruskal–Wallis test is a non-parametric alternative to the analysis of variance (ANOVA), and it is used to compare groups of means. The advantage of this test is that the assumption of normality of data is not required, 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 non-normal distribution of sample data, and it is a viable alternative to parametric statistics (Potvin and Roff 1993). Kruskal–Wallis test was used to compare mean solar radiation, SST, polyp length, and population density among study sites.

Covariance analysis (ANCOVA) is a combination of linear regression and variance analysis (Altman 1991). It can be used to compare the regression equations between different groups. For example, given the linear regression equations between the same two variables of three groups of treatments, the analysis compares the slopes and intercepts of the three equations. ANCOVA was used to compare the relationships between biometric parameters and polyp length among study sites.

The Monte Carlo method (Gabriel and Lachenbruch 1969) solves problems in the non-parametric 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). Our Monte Carlo estimate for  $P$  used 100,000 random permutations. This method was used to estimate the significance of the Kruskal–Wallis test when comparing the mean population densities among study sites for both species.

Kruskal–Wallis tests, Spearman's correlation coefficients, and Monte Carlo corrections for small sample size were calculated with SPSS 12.0 (Apache Computer Software Foundation, Forest Hill, MD).

## Results

Solar radiation and SST both varied among the sites (Kruskal–Wallis test, degrees of freedom = 5, and  $P < 0.001$ ; Fig. 1). While solar radiation correlated negatively with latitude, SST correlated significantly after exclusion of Genova–Portofino (GN) site from analysis (Fig. 2). The GN site is characterized by particular local conditions (xerotherm site because of local currents and rock composition; APAT, available at <http://www.apat.gov.it>) and typically has higher SSTs than expected at that latitude (annual SST of Ligurian Sea = 18°C and Genova–Portofino (GN) = 19.6°C); (Fig. 1).

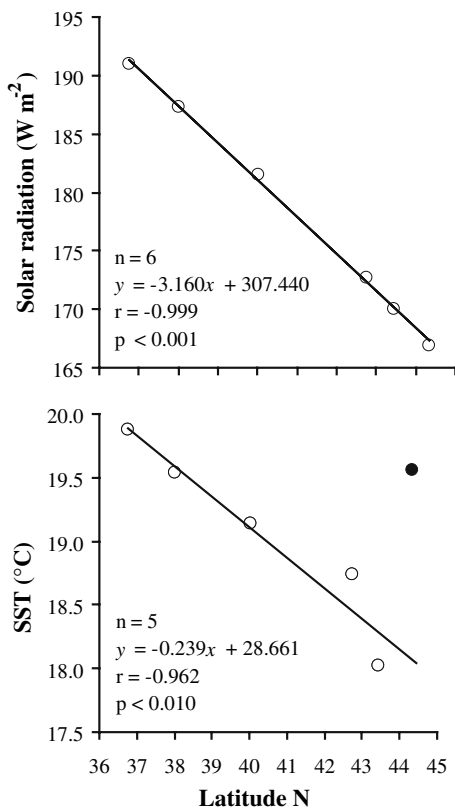
Polyp length (Fig. 3) was selected as the main biometric parameter since it is a good indicator of skeletal mass and has been used as the measure of size in biometric, reproductive biology, and population dynamic studies of *B. europaea*, *L. pruvoti*, and other solitary corals (Hoeksema 1991; Bell and Turner 2000; Goffredo and Chadwick-Furman 2003; Goffredo et al. 2002, 2004, 2006). Polyp width, height, volume, and skeletal mass all correlated positively with polyp length in both the coral species examined

(Figs. 4, 5). Skeletal density correlated positively with polyp length in *B. europaea* at only two sites (Palinuro and Pantelleria). In contrast, skeletal density correlated negatively with polyp length in *L. pruvoti* at all sites (Figs. 4, 5). In both the coral species, the relationships between biometric parameters and polyp length varied significantly among the study sites (ANCOVA, degrees of freedom between exponents = 5, and  $P < 0.05$ ). Each relationship between the biometric parameters and polyp length was linearized and the obtained slopes (representing the original equation exponent) were compared among study sites. None of the slopes was homogeneous among study sites.

The increase in polyp width in comparison with that of polyp length differed in the two species (Figs. 4, 5). In *B. europaea*, an allometric relationship was found; length increased more rapidly than did width, which resulted in an oval oral disc as polyp size increased (at all sites, the confidence interval CI of the regression equation exponent was  $< 1$ , 0.52–0.90, CI 95%, and degrees of freedom = 37–94; Fig. 4). *L. pruvoti* had either isometric growth (at Scilla and Pantelleria, the confidence interval of the regression equation exponent contained 1, 0.96–1.01, CI 95%, and degrees of freedom = 114–143) or allometric growth, with the polyp length increasing less quickly than the width did (at Genova–Portofino, Calafuria, Elba, and Pantelleria, the confidence interval of the regression equation exponent  $> 1$ , 1.00–1.10, CI 95%, and degrees of freedom = 75–209; Fig. 5), which resulted in a circular oral disc as polyp size increased.

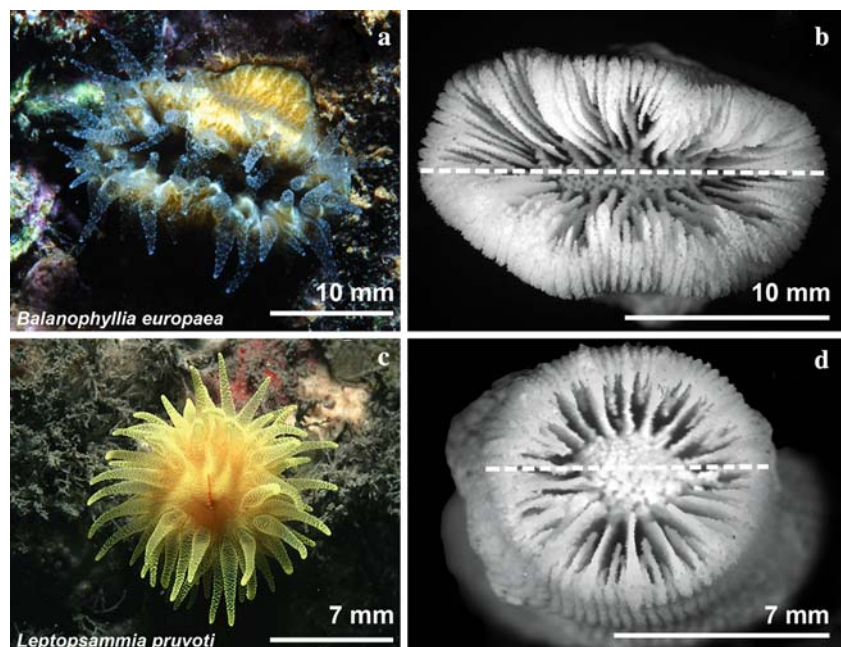
In both species, the lengths of the sampled individuals differed significantly among the sites (Kruskal–Wallis test, degrees of freedom = 5, and  $P < 0.001$ ). For this reason, analyses of correlations between environmental variables and biometric parameters were performed after applying to the data the method of the adjusted values in relation to length (Steel 1980). In *B. europaea*, whereas polyp length, width, height, and volume positively correlated with solar radiation and SST, skeletal mass and skeletal density were negatively correlated (Fig. 6). In all cases, SST explained 2.5–7.4 times more of the variance than did solar radiation (the percentage of biometric parameter variance explained by SST ranged from 3.9% for length to 63.8% for skeletal mass; Fig. 6). In *L. pruvoti*, solar radiation did not correlate with any biometric parameter. Polyp length, height, volume, and skeletal density were correlated with SST, which explained from 0.5% of the variance for volume to 1.2% for length (Fig. 6). SST was more highly correlated with biometric parameters in *B. europaea* than in *L. pruvoti* ( $r^2$  of the relationship between biometric parameters and SST was three times higher for length to 638 times higher for skeletal mass).

In *B. europaea*, population density varied significantly among the sites (Kruskal–Wallis test, Monte Carlo



**Fig. 2** Relationship between environmental parameters (mean annual solar radiation and SST) and the latitude of study sites along the coast of Italy. The *black dot* indicates the site of Genova–Portofino, which was characterized by special local conditions that cause a temperature deviation from the norm at that latitude, and thus was excluded from the correlation coefficient calculation. *n* number of stations; *r* Pearson correlation coefficient

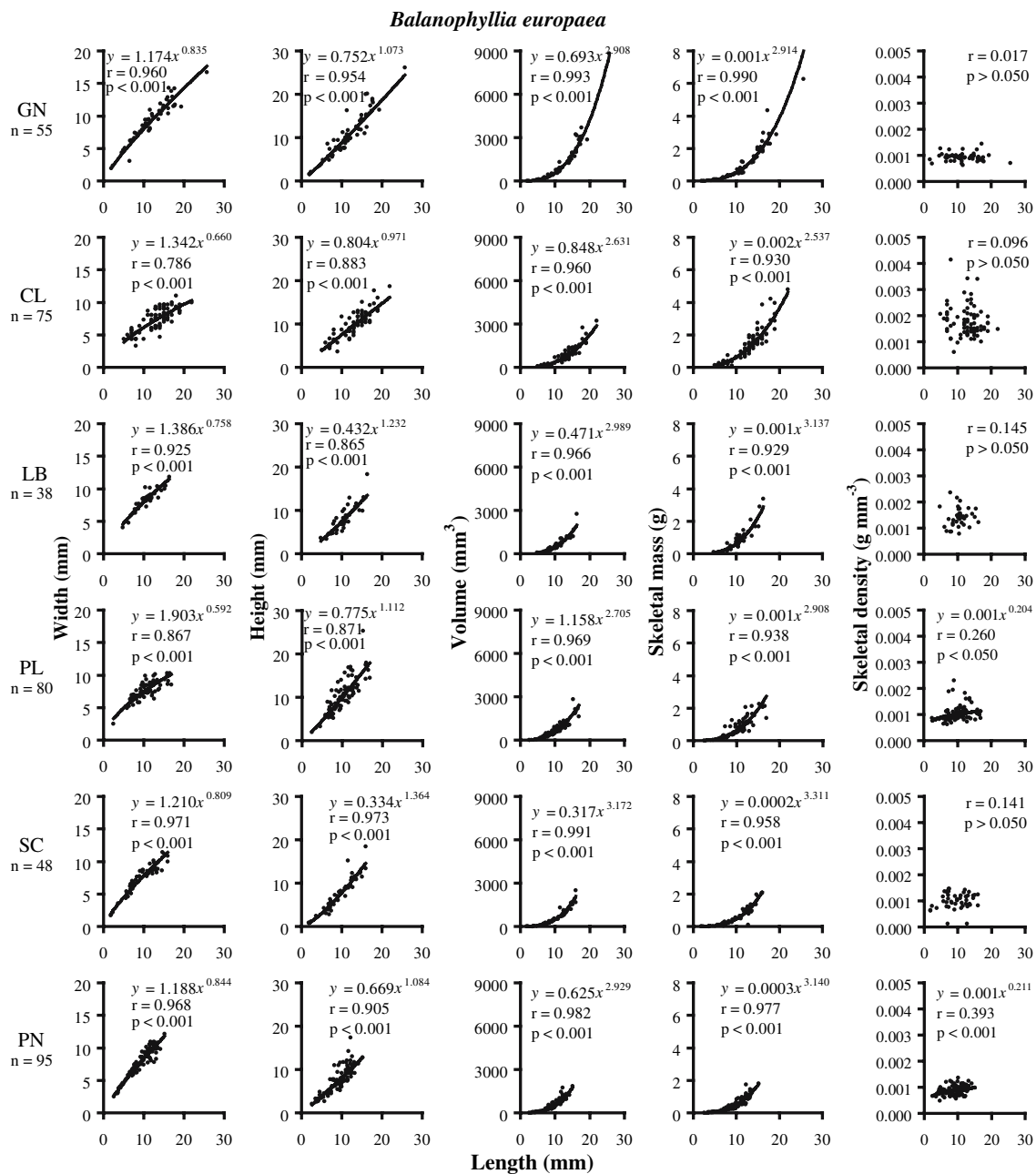
**Fig. 3** *Balanophyllia europaea* (a living polyp; b corallite) and *Leptopsammia pruvoti* (c living polyp; d corallite) specimens from Genova–Portofino. *Dotted line* indicates polyp length (*L*: maximum axis of the oral disc)



correction for small sample size, degrees of freedom = 5, and  $P < 0.001$ ) and was negatively correlated with SST (Fig. 7). In *L. pruvoti*, population density did not vary among the sites (Kruskal–Wallis test, Monte Carlo correction for small sample size, degrees of freedom = 5, and  $P > 0.05$ ). Mean population density for *L. pruvoti* was 10.155 individuals  $m^{-2}$  (SE 1.317), 2,030  $g m^{-2}$  (SE 232), and 15.4% cover (SE 1.4).

## Discussion

The difference between the two species in the relationship between skeletal density and polyp size can be interpreted in terms of relationship between calcification and linear extension. As polyp size of *B. europaea* increases, there is a progressive decrease in linear extension rate (Goffredo et al. 2004). A parallel diminution of the calcification rate could explain the maintenance of skeletal density among mean values of 0.001–0.002  $g mm^{-3}$  regardless of polyp size, at four of the six sites studied (Genova–Portofino, Calafuria, Elba, and Scilla). At the Palinuro and Pantelleria sites, calcification rate could decrease less quickly than did linear extension rate, causing a positive correlation between skeletal density and polyp size. In *L. pruvoti*, as known for several other solitary corals (Bablet 1985; Yamashiro and Nishihira 1998; Goffredo and Chadwick-Furman 2003; Goffredo et al. 2004), the linear extension rate should decrease with increasing polyp size. The diminution of skeletal density with increasing polyp size may have been due to a greater decrease in calcification than in



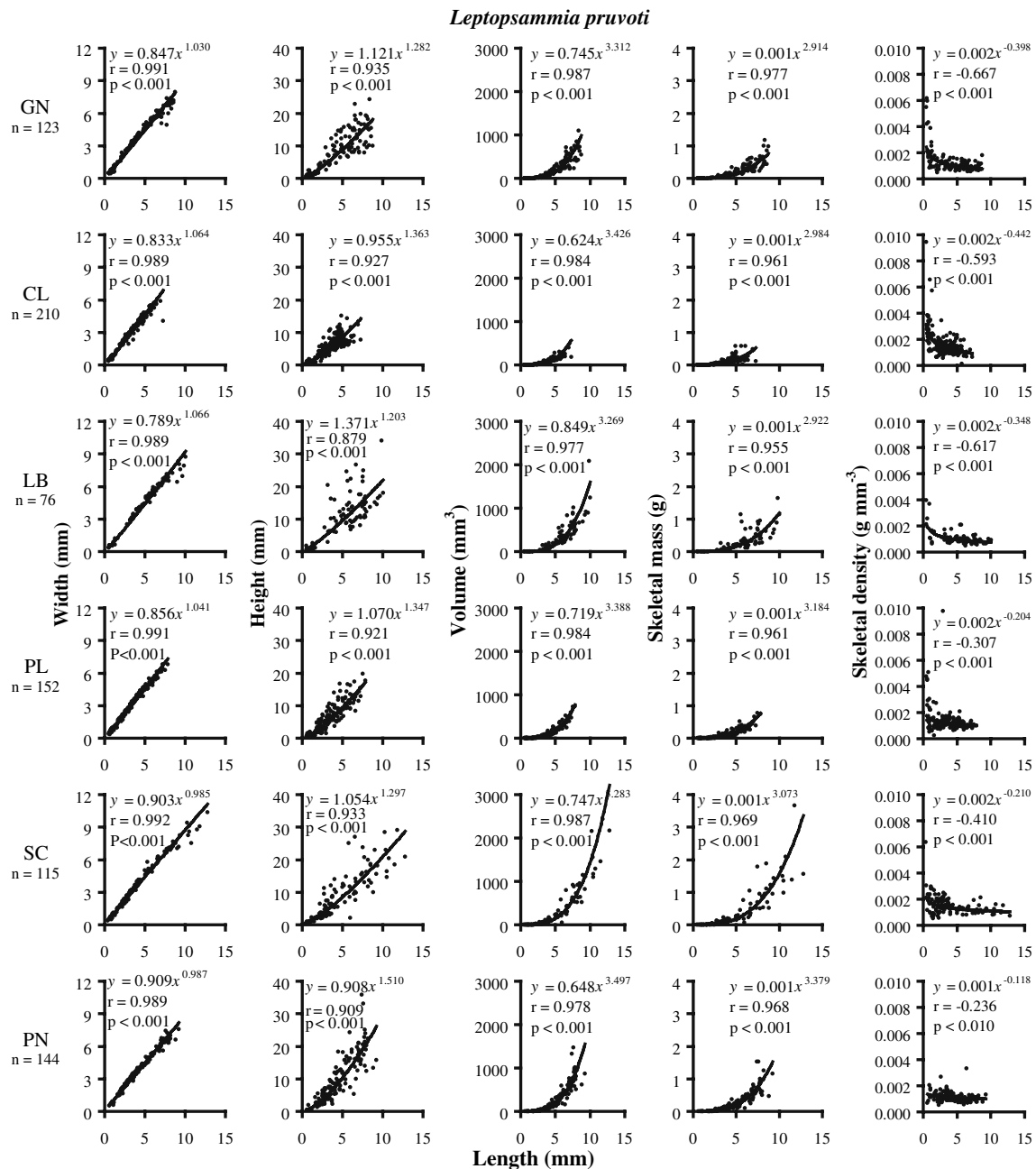
**Fig. 4** *Balanophyllia europaea*. Dependence of biometric parameters on polyp length at six sites along the western coast of Italy (GN Genova–Portofino, CL Calafuria, LB Elba, PL Palinuro, SC Scilla,

and PN Pantelleria). *n* number of individuals; *r* Pearson correlation coefficient. The sites are arranged in order of decreasing latitude

linear extension rate. The radiological analyses underway on both species are expected to provide an understanding of the relationship between calcification and linear extension rates.

The difference in the biometric relationship between the oral disc axes between the two species may relate to sedimentation stress. Sedimentation has many negative effects on corals, including prevention of growth and calcification, interference with respiration, nourishment and photosyn-

thesis, increase in energy dissipation, damaging polyp tissues, lowering the fecundity, and interfering with substratum colonization process (Rosenfeld et al. 1999, and references therein). Corals can adopt different strategies to prevent these negative effects, i.e., sediment rejection behavior or resistant growth forms (Stafford-Smith and Ormond 1992; Bell and Turner 2000). The oval form of the oral disc is one of these resistant forms, since it decreases the area affected by sedimentation and favors the removal



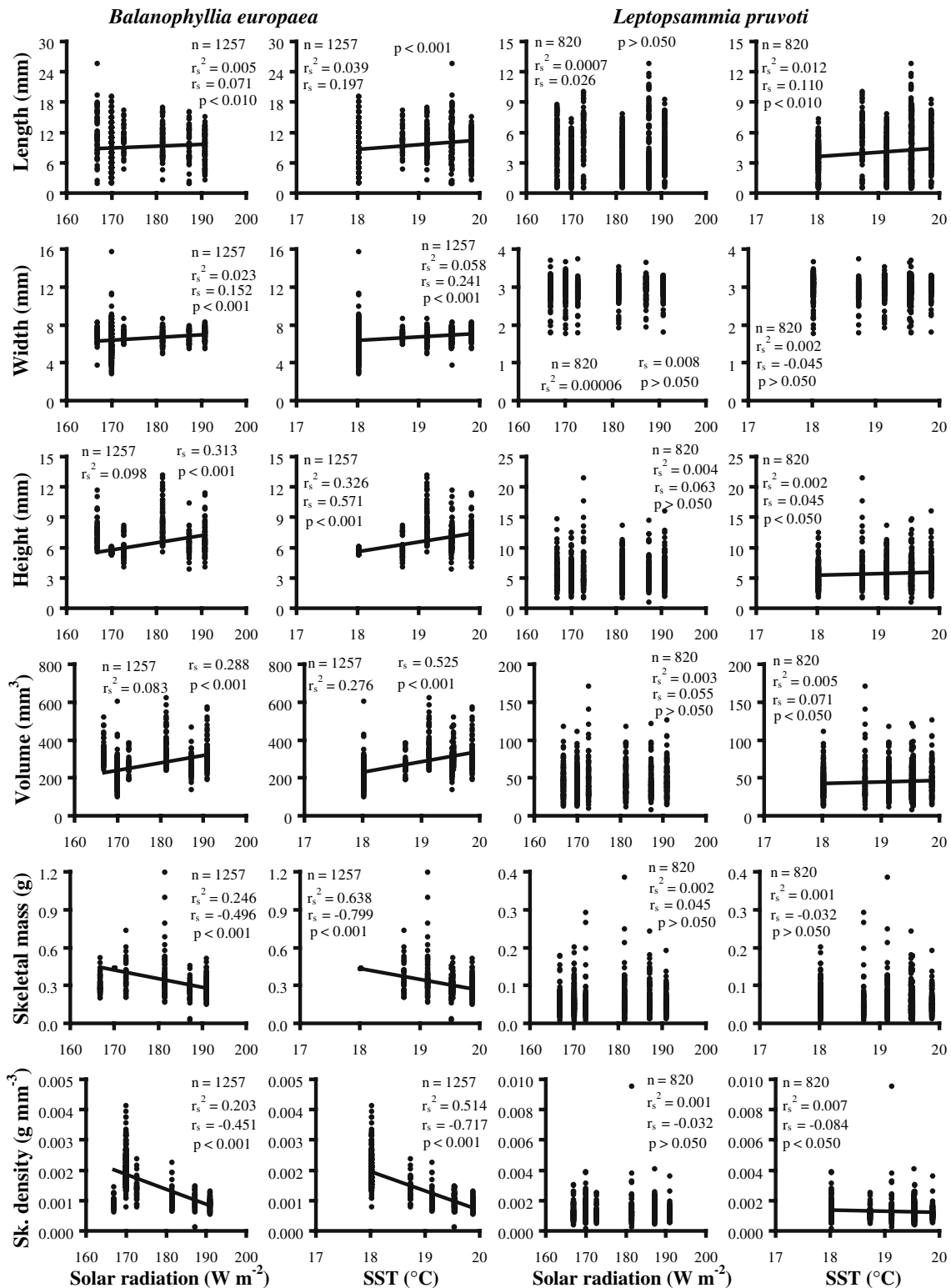
**Fig. 5** *Leptosammia pruvoti*. Dependence of biometric parameters on polyp length at six sites along the western coast of Italy (GN Genova–Portofino, CL Calafuria, LB Elba, PL Palinuro, SC Scilla,

and PN Pantelleria). *n* number of individuals; *r* Pearson correlation coefficient. The sites are arranged in order of decreasing latitude

of sediment from the polyp surface (Hoeksema 1991). The allometric relationship between polyp width and length in *B. europaea*, which produces a progressively oval-shaped oral disc, may prevent damage from sedimentation that might otherwise occur as the polyp becomes larger (Goffredo et al. 2004). In corals living on the vertical walls, the removal of sediment is carried out by gravity, rather than by active mechanisms (Stafford-Smith and Ormond 1992). Moreover, in shallow water overhangs of the

Ligurian Sea, a thin coat of sediment covers the vertical surfaces, while it is absent on the down-facing surfaces (Virgilio et al. 2006). *L. pruvoti* polyps, characterized by circular oral discs, do not need growth forms resistant to damage from sedimentation, since they colonize the vaults of caves and crevices with their oral pole directed downward.

The SST environmental variable correlated with biometric parameters more strongly than did solar radiation in

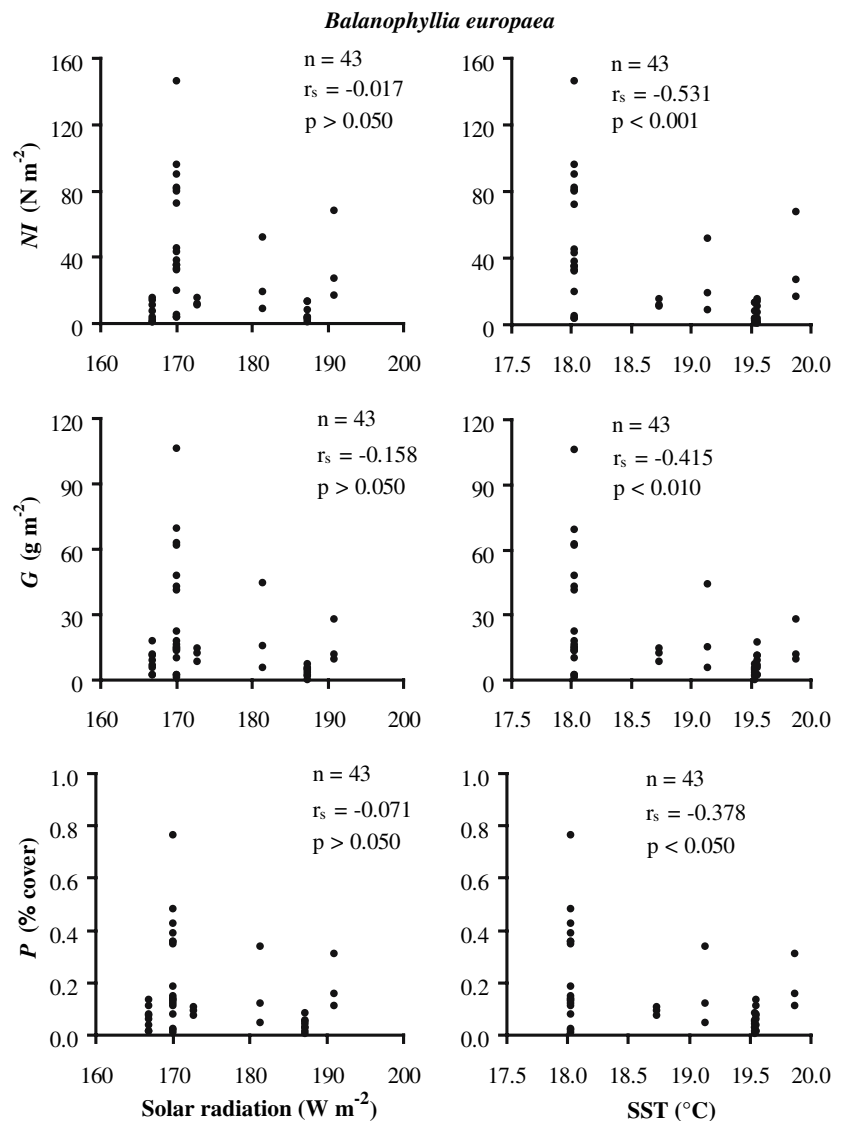


**Fig. 6** Variation in the biometric parameters of two corals, *Balanophyllia europaea* and *Leptopsammia pruvoti* with environmental variables (annual mean solar radiation and SST).  $r_s^2$  Spearman's

determination coefficient;  $n$  number of individuals. Note that scale of the ordinate axes differs between species



**Fig. 7** *Balanophyllia europaea*. Variation in population density parameters with environmental variables (mean annual solar radiation and SST). *NI* number of individuals per square meter, *G* grams per square meter, *P* percent cover.  $r_s$  Spearman's correlation coefficient; *n* number of quadrats examined. Correlations for *Leptopsammia pruvoti* are not shown because population density was homogeneous among the sites examined



both species. This relationship is more marked in *B. europaea*, which is zooxanthellate, suggesting the possible effect of temperature on photosynthesis in the algal symbionts. 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). In *B. europaea*, the decrease in skeletal density with increasing SST could depend on an attenuation of calcification due to an inhibition of the photosynthetic process at higher temperatures. In *L. pruvoti*, the weak relationship between temperature and skeletal density could be due to the absence of zooxanthellae, and thus lack of a physiological dependence of calcification on photosynthesis.

The spatial distribution of adult corals is influenced by the number of offspring produced per reproductive event and their dispersal capability (Hughes et al. 2000). Theoretically, low fecundity combined with wide larval

dispersal results in a low density of local populations. In contrast, high fecundity combined with limited larval dispersal produces high local population density (Gerrodette 1981; Carlon 2002; Goffredo and Zaccanti 2004; Goffredo et al. 2004). In symbiotic corals, a large portion of the energy needed for gametogenesis and larval development is supplied by photosynthate from the zooxanthellae (Rinkevich 1989). The low population density of *B. europaea* relative to that of *L. pruvoti* could be due to lower polyp fecundity and the greater dispersion capability of its larvae (Goffredo and Zaccanti 2004; Goffredo et al. 2002, 2004, 2006). However, population density also depends on recruitment and mortality due to various factors, including predation, so this hypothesis requires further testing. The decrease in population density of *B. europaea* with increasing SST might depend on a polyp's reduced fecundity, consequent to a decrement of the photosynthetic efficiency of the symbiont zooxanthellae at higher than

optimal temperatures (Al-Horani 2005), resulting in lower energy resources for gametogenesis (Rinkevich 1989; Carlon 2002). Without utilizing photosynthesis, *L. pruvoti* would maintain its population density around the mean value regardless of the SST. Further studies on the reproductive biology of these two species at different sites situated along a latitudinal gradient might clarify the relationship between polyp fecundity and SST.

In conclusion, it is hypothesized that high temperature is a negative factor for the zooxanthellate *B. europaea*, since it would lower the photosynthetic efficiency of its symbionts, causing negative effects on both polyp growth and colonization process, while it would not significantly influence the azooxanthellate *L. pruvoti*. An alternative explanation for the decrease of skeletal and population density of *B. europaea* with increasing temperature could be related to suspension feeding. In the Mediterranean Sea, nutrient levels and zooplankton availability are typically lower in summer–fall (i.e., high temperature) than in winter–spring (i.e., low temperature; Coma et al. 2000; Coma and Ribes 2003). Low nutrients and zooplankton availability cause stress and starvation in *Cladocora caespitosa* (Peirano et al. 2005a) and a summer dormancy in the metabolism of several benthic suspension feeding taxa (Coma et al. 2000; Coma and Ribes 2003). Moreover, in *Stylophora pistillata* colonies, starved corals present significantly lower levels of calcification and photosynthesis than fed corals (Houlbrèque et al. 2004). Low energetic resources could be the causes of low skeletal and population density in *B. europaea* at high temperatures. However, if this was the case, the inhibition would be stronger in *L. pruvoti*, which is a full heterotrophic, than in *B. europaea*, which can rely on the symbiont. In contrast, we found that the skeletal and population densities of *L. pruvoti* are almost the same in low and high temperature study sites; thus the hypothesis of a photosynthetic inhibition at high temperatures seems to be more appropriate. Anyway, other factors such as pollution could influence the spatial distributions of populations. During the sampling period of this study, the Italian Ministry of the Environment and Land and Sea Protection conducted sea water quality surveys along the Italian coasts, based on basic oceanographic data ( $\text{NO}_3^-$ ,  $\text{NO}_2^-$ ,  $\text{NH}_4^+$ ,  $\text{PO}_4^{3-}$ ,  $\text{SiO}_4^{4-}$ , salinity, chlorophyll, and transparency, which are parameters included in the Sea Water Classification; Seawater Monitoring Program, available at [www2.minambiente.it/sito/settori\\_azione/sdm/pubblicazioni/pubblicazioni.asp](http://www2.minambiente.it/sito/settori_azione/sdm/pubblicazioni/pubblicazioni.asp); [www.sidimar.ipzs.it](http://www.sidimar.ipzs.it)). Ministry data exhibited negative correlations between latitude and environmental quality along the western coasts of Italy, but this is hardly linkable to our data since we found that the population density of both species does not co-vary with latitude.

Future work to test the hypothesis of an inhibition of photosynthetic efficiency of *B. europaea* at high temperatures will involve experimental measurements of photosynthesis at different temperatures and stable isotopes analyses on *B. europaea* skeletons to reconstruct the photosynthetic efficiency of the polyps.

**Acknowledgments** We wish to thank L. Bortolazzi, M. Ghelia, G. Neto, and L. Tomesani for their underwater assistance in collecting the samples. The diving centers Centro Immersioni Pantelleria, Il Pesciolino, Polo Sub, and Sub Maldive supplied logistic assistance in the field. The Bologna Scuba Team collaborated in the underwater activities. The Marine Science Group (<http://www.marinescience-group.org>) supplied scientific, technical, and logistical support. H. R. Lasker, J. Bilewitch, and N. Kirk (State University of New York at Buffalo), N. E. Chadwick-Furman (Auburn University), and two anonymous reviewers gave comments that improved the manuscript. This research was financed by the Associazione dei Tour Operator Italiani (ASTOI), the Marine and Freshwater Science Group Association (<http://www.msgassociation.net>), the Canziani foundation of the Department of Evolutionary and Experimental Biology of the Alma Mater Studiorum—University of Bologna, and the Ministry of Education, University and Research (MIUR). The experiments complied with current Italian law.

## References

- Al-Horani FA (2005) Effects of changing seawater temperature on photosynthesis and calcification in the scleractinian coral *Galaxea fascicularis*, measured with  $\text{O}_2$ ,  $\text{Ca}^{2+}$  and pH micro-sensors. *Sci Mar* 69:347–354
- Al-Horani FA, Ferdelman T, Al-Moghrabi SM, de Beer D (2005) Spatial distribution of calcification and photosynthesis in the scleractinian coral *Galaxea fascicularis*. *Coral Reefs* 24:173–180
- Altman DG (1991) Practical statistics for medical research. Chapman & Hall, London
- Babiet JP (1985) Report on the growth of a scleractinia (*Fungia paumotensis*). In: Proceedings of the 5th International Coral Reef Symposium 4:361–365
- Bell JJ, Turner JR (2000) Factors influencing the density and morphometrics of the cup coral *Caryophyllia smithii* in Lough Hyne. *J Mar Biol Assoc UK* 80:437–441
- Carlon DB (2002) Production and supply of larvae as determinants of zonation in a brooding tropical coral. *J Exp Mar Biol Ecol* 268:33–46
- Carricart-Ganivet JP (2004) Sea surface temperature and the growth of the West Atlantic reef-building coral *Montastraea annularis*. *J Exp Mar Biol Ecol* 302:249–260
- 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 JM, Zabala M (2000) Seasonality in coastal ecosystems. *Trends Ecol Evol* 12:448–453
- Crossland CJ (1981) Seasonal growth of *Acropora cf. formosa* and *Pocillopora damicornis* on a high latitude reef (Houtman Abrolhos, Western Australia). In: Proceedings of the 4th International Coral Reef Symposium 1:663–667
- Dodge RE, Brass GW (1984) Skeletal extension, density and calcification of the reef coral *Montastrea annularis*: St Croix, US Virgin Islands. *Bull Mar Sci* 34:288–307
- Gabriel KR, Lachenbruch PA (1969) Non-parametric ANOVA in small samples: a Monte Carlo study of the adequacy of the asymptotic approximation. *Biometrics* 25:593–596

- Gattuso JP, Allemand D, Frankignoulle M (1999) Photosynthesis and calcification at cellular, organismal and community levels in coral reefs: a review on interaction and control by carbonate chemistry. *Am Zool* 39:160–183
- Gerrodette T (1981) Dispersal of the solitary coral *Balanophyllia elegans* by demersal planular larvae. *Ecology* 62:611–619
- 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, Chadwick-Furman NE (2003) Comparative demography of mushroom corals (Scleractinia, Fungiidae) at Eilat, northern Red Sea. *Mar Biol* 142:411–418
- 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, 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, Airi V, Radetić J, Zaccanti F (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
- Grigg RW (1982) Darwin point: a threshold for atoll formation. *Coral Reefs* 1:29–34
- Harriott VJ (1999) Coral growth in subtropical eastern Australia. *Coral Reefs* 15:281–291
- Harriott VJ, Banks SA (2002) Latitudinal variation in coral communities in eastern Australia: a qualitative biophysical model of factors regulating coral reefs. *Coral Reefs* 21:83–94
- Hoeksema BW (1991) Evolution of body size in mushroom corals (Scleractinia: Fungiidae) and its ecomorphological consequences. *Neth J Zool* 41:112–129
- Houlbrèque F, Tambuttè E, Allemand D, Ferrier-Pagès C (2004) Interactions between zooplankton feeding, photosynthesis and skeletal growth in the scleractinian coral *Stylophora pistillata*. *J Exp Biol* 207:1461–1469
- Howe SA, Marshall AT (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 TP, Baird AH, Dinsdale EA, Moltschanivskyj NA, Pratchett MS, Tanner JE, Willis BL (2000) Supply-side ecology works both ways: the link between benthic adults, fecundity, and larval recruits. *Ecology* 81:2241–2249
- Jacques TG, Marshall N, Pilson MEQ (1983) Experimental ecology of the temperate scleractinian coral *Astrangia danae*: II. Effect of temperature, light intensity and symbiosis with zooxanthellae on metabolic rate and calcification. *Mar Biol* 76:135–148
- Kain JM (1989) The seasons in the subtidal. *Br Phycol J* 24:203–215
- Kinsey DW, Davies PJ (1979) Carbon turnover calcification and growth in coral reefs. In: Trudinger PA, Swaine DJ (eds) Biogeochemical cycling of mineral forming elements. Elsevier, Amsterdam, pp 131–162
- Kleypas JA, McManus JW, Menez LAB (1999) Environmental limits to coral reef development: where do we draw the line? *Am Zool* 39:146–159
- Lough JM, Barnes DJ (2000) Environmental controls on growth of the massive coral *Porites*. *J Exp Mar Biol Ecol* 245:225–243
- 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 CN (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
- Potvin C, Roff DA (1993) Distribution-free and robust statistical methods: viable alternatives to parametric statistics? *Ecology* 74:1617–1628
- Rinkevich B (1989) The contribution of photosynthetic products to coral reproduction. *Mar Biol* 101:259–263
- Rosenfeld M, Bresler V, Abelson A (1999) Sediment as a possible source of food for corals. *Ecol Lett* 2:345–348
- Senchaudhuri P, Mehta CR, Patel NR (1995) Estimating exact p-values by the method of control variates, or Monte Carlo rescue. *J Am Stat Assoc* 90:640–648
- Stafford-Smith MG, Ormond RFG (1992) Sediment-rejection mechanisms of 42 species of Australian Scleractinian. *Aust J Mar Freshw Res* 43:683–705
- Steel RGD (1980) Principles and procedures of statistics: a biometrical approach, 2nd edn. McGraw-Hill College, New York
- Stimson J (1996) Wave-like outward growth of some table- and plate-forming corals, and a hypothetical mechanism. *Bull Mar Sci* 58:301–313
- Virgilio M, Airoidi L, Abbiati M (2006) Spatial and temporal variations of assemblages in a Mediterranean coralligenous reef and relationships with surface orientation. *Coral Reefs* 25:265–272
- Vongsavat V, Winotai P, Meejoo S (2006) Phase transitions of natural corals monitored by ESR spectroscopy. *Nucl Instr Meth B* 243:167–173
- Yamashiro H, Nishihira M (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
- Zibrowius H (1980) Les scléactiniaires de la Méditerranée et de l'Atlantique nord-oriental. *Mem Inst Oceanogr (Monaco)* 11:1–284