REPORT

Relationships between growth, population structure and sea surface temperature in the temperate solitary coral *Balanophyllia europaea* (Scleractinia, Dendrophylliidae)

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Abstract The demographic characteristics of the solitary zooxanthellate scleractinian *Balanophyllia europaea*, endemic to the Mediterranean, were determined in six populations, on a latitudinal gradient along the Italian coast, and compared with the mean annual sea surface temperature (SST). Growth rate correlated negatively, and asymptotic length of the individuals positively with SST. With increasing SST, the distributions of age frequencies moved away from a typical steady state structure (i.e., exponential decrease in the frequency of individuals with age), indicating less stable populations and showed a deficiency of individuals in the younger-age classes. These observations suggest that high temperatures are an adverse factor to the *B. europaea* symbiosis. Using projected increases in seawater temperature, most of the *B. europaea* populations in the Mediterranean are expected to be close to their thermal limits by 2100 and the populations at that time may support few young individuals.

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Introduction

Latitude differences in temperature and irradiance are an important influence on global coral distribution patterns (Kleypas et al. 1999). In general, coral growth decreases with increasing latitude, to a point beyond 30°N and 30°S where coral-reef development no longer occurs (Kinsey and Davies 1979; Grigg 1982). For temperate regions, studies on the relationship between environmental parameters and coral growth are scarce. For *Astrangia danae* (Jacques et al. 1983) and *Plesiastrea versipora* (Howe and Marshall 2002), calcification rate has been shown to increase with temperature, similar to the trend observed in tropical corals (Lough and Barnes 2000; Carricart-Ganivet 2004; McNeil et al. 2004), but for the zooxanthellate coral *Balanophyllia europaea*, Goffredo et al. (2007) reported a negative correlation between sea surface temperature (SST) and skeletal and population density.

There is limited information available on population dynamics of scleractinian corals. In 1973 the modest amount of data collected over the previous 30 years was reviewed and parameters such as growth and survivorship were described (Connell 1973). Since then, demographic processes have been described for some species in the Red Sea (Loya 1976; Chadwick-Furman et al. 2000; Goffredo and Chadwick-Furman 2003; Glassom and Chadwick 2006; Guzner et al. 2007), Northeastern Pacific (Fadlallah 1983), Caribbean (Hughes and Jackson 1985; Johnson 1992; Meesters et al. 2001; Vermeij 2006), Great Barrier Reef (Babcock 1991), and the Mediterranean (Goffredo

et al. 2004; Shenkar et al. 2005). The paucity of information on population dynamics of most scleractinian corals can be attributed, partly, to a distortion of the age–size relationships in this group, resulting from processes of fragmentation, fusion, and partial colony mortality (Hughes and Jackson 1985; Babcock 1991; Hughes et al. 1992). These phenomena prevent the application of traditional growth and population dynamic models based on organism age, and create very complex demographic patterns (Hughes and Jackson 1985). However, in species where the individuals rarely fragment or fuse and partial mortality is discernable by anomalies in the regular growth pattern, it is possible to determine coral age (Chadwick-Furman et al. 2000).

Growth band analysis is a technique that can be used to determine the age of certain forms of gorgonian and scleractinian, solitary and colonial corals, and to describe their demographic characteristics by applying age-based growth and population dynamics models (Knuston et al. 1972; Buddemeier et al. 1974; Grigg 1974; Mistri and Ceccherelli 1994; Peirano et al. 1999; Chadwick-Furman et al. 2000; Goffredo and Chadwick-Furman 2003; Goffredo et al. 2004; Goffredo and Lasker 2006). Demographic parameters reveal relationships between organisms and their environment, contributing to habitat stability assessment (Grigg 1975; Meesters et al. 2001). The demographic analysis of coral populations can reveal the level of stress to which they are subjected (Bak and Meesters 1999; Guzner et al. 2007). In addition, information on population turnover aids in the development of techniques for the restoration of damaged or degraded coastal areas (Chadwick-Furman et al. 2000; Epstein et al. 2001; Goffredo and Chadwick-Furman 2003).

Balanophyllia europaea (Risso 1826) is a solitary, ahermatypic, zooxanthellate scleractinian coral, which is endemic to the Mediterranean (Zibrowius 1980). Because of its symbiosis with zooxanthellae, it is restricted to depths of 0–50 m (Zibrowius 1980), where the 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). Goffredo et al. (2007) examined the correlations between SST, biometry, and population density of this species and a closely related one, the azooxanthellate *Leptopsammia pruvoti*, along the Italian coasts. They found a negative correlation between mean annual SST and skeletal and population density in *B. europaea*, but no correlation in *L. pruvoti*. To explain these results, they hypothesized that the negative effects on *B. europaea* skeletal and population density could be related to an inhibition of the photosynthesis of *B. europaea* symbiotic zooxanthellae at high temperatures.

This present study aimed to assess growth rates and population structure variation of *B. europaea* along a latitudinal gradient of mean annual SST. Considering the negative effects of temperature on the *B. europaea* symbiosis (Goffredo et al. 2007), it was expected that the same negative trend, shown by biometry and population density, would also apply to growth and population structure. Consequently, this study tested the hypothesis that high temperature has a negative effect on growth rates and population structure of *B. europaea*.

Materials and methods

Sample collection

Between 9th November 2003 to 30th September 2005, specimens of *B. europaea* were collected from six populations along a latitudinal gradient, from 44°20′N to 36°45′N (Fig. 1). Latitude is the main factor influencing the variation in SST (Kain 1989), which is the environmental parameter considered in this study because it has been shown to be strongly linked to coral growth, physiology, and demography (Kleypas et al. 1999; Lough and Barnes 2000; Al-Horani 2005). With the exception of the Calafuria population, for which data were obtained from a previous study (Goffredo et al. 2004), samples were
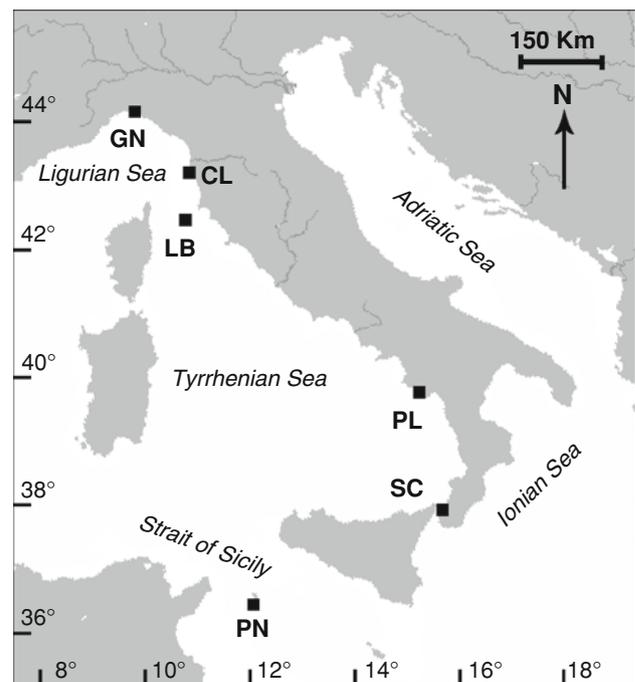

Fig. 1 Map of the Italian coastline indicating sites where corals were collected. Abbreviations and coordinates of the sites in decreasing order of latitude: GN Genova, 44°20′N, 9°08′E; CL Calafuria, 43°27′N, 10°21′E; LB Elba Isle, 42°45′N, 10°24′E; PL Palinuro, 40°02′N, 15°16′E; SC Scilla, 38°01′N,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

collected for each population using transects that consisted of at least 3 patches of 1 m² each, arranged in a line 5 m apart along the southern side of each reef at a depth of 5–7 m. Because the distribution pattern of *B. europaea* is random, the problems associated with regularly spaced quadrats and transects do not apply to this study (Goffredo and Zaccanti 2004; Goffredo et al. 2004). All of the polyps present were collected from each patch. The sampling was at depths known to have high population densities and where the reproductive biology, biometry, and population density of this species had been studied previously (Goffredo et al. 2002, 2004, 2007; Goffredo and Zaccanti 2004). Choosing the sampling depth based on maximum abundance may bias growth toward a higher rate, and in turn underestimate age, but by sampling in the depth range of 5–7 m where 62% of this species are found (Goffredo et al. 2004) this maximum-abundance bias is reduced.

Sample analysis

Corals were dried at 50°C for 4 days and observed under a binocular microscope to remove fragments of substratum and calcareous deposits produced by other organisms. Corallite length was selected as the main biometric parameter, since it is a good indicator of skeletal mass and has been used as the primary measure of size in other biometric, reproductive biology, and population dynamics studies of this species and other solitary corals (Lasker 1981; Foster et al. 1988; Goffredo et al. 2002, 2004, 2007; Goffredo and Chadwick-Furman 2003; Vermeij 2006). Corallite length (*L*: maximum axis of the oral disc) was measured using a caliper, and corallite mass was measured with a precision balance (after Lasker 1981; Goffredo et al. 2002; Goffredo and Chadwick-Furman 2003).

Data modeling

To obtain an objective relationship between corallite size and age, the number of annual growth bands was counted by means of computerized tomography (CT). This technique is commonly applied to scleractinian corals (Bosscher 1993; Helmle et al. 2000) and has been successfully used for *B. europaea* (Goffredo et al. 2004). For each population, CT measurements were taken from about 40 skeletons randomly selected from the collected samples. The age of each skeleton was determined from the growth-band counts, based on one high-density band in winter and a low-density band in summer (Peirano et al. 1999; Goffredo et al. 2004; Fig. 2).

The von Bertalanffy growth model (von Bertalanffy 1938) predicts decreasing growth rate with age, with growth rate that tends to zero approaching an asymptotic size/age, and has been validated by Goffredo et al. (2004)
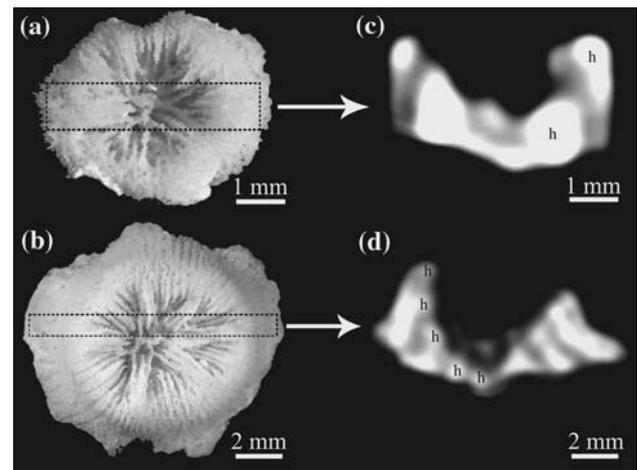

Fig. 2 *Balanophyllia europaea*. Computerized tomography scans (CT) of two corallites from the Elba island population (LB). (**a**, **b**) view of the skeleton from the oral pole. The dotted line shows the section, 1-mm wide, of the CT scan. The Multiple CT views facilitated the recognition of high-density bands (h). (**c**, **d**) sagittal CT scan (the oral pole is turned upward). Age was determined by counting the growth bands of the skeleton. (**c**) In this sample, 4.75-mm long, two high-density bands can be seen, corresponding to 2 years' growth. (**d**) In this sample, 9.95-mm long, five high-density bands can be seen, corresponding to 5 years' growth

for the Calafuria (CL) population of *B. europaea* using CT density bands. To test if the von Bertalanffy function could be used for all populations sampled in this study, the decreasing growth rate of *B. europaea* with age was checked at each location (Fabens 1965). For each sample dated by CT scans, a mean growth rate was obtained by dividing length by age, and the mean growth rate was plotted against individual age (Fig. 3). All the populations showed a marked decrease of mean growth rate with age, the best fit being a negative exponential curve (Fig. 3), from which growth was fitted to the von Bertalanffy function (von Bertalanffy 1938):

$$L_t = L_\infty(1 - e^{-Kt}) \qquad (1)$$

where L_t is individual length at age t, L_∞ is asymptotic length (maximum expected length in the population), K is a growth constant (higher for a fast growth up to the asymptotic length, smaller for a slow one), and t is the age of the individual. The parameters L_∞ and K were determined by applying the "von Bertalanffy plot" method (see Pauly 1984; Sparre et al. 1989 for the exact procedure, and Goffredo and Chadwick-Furman 2003 for examples of applications to corals).

The population size structure was obtained from the survey transects, and age structure was determined using Eq. 1. In a theoretical population in steady state, 100% of the variance of the frequency of age classes is explained by age. To estimate population structure stability, the age-frequency distribution was analyzed using a regression
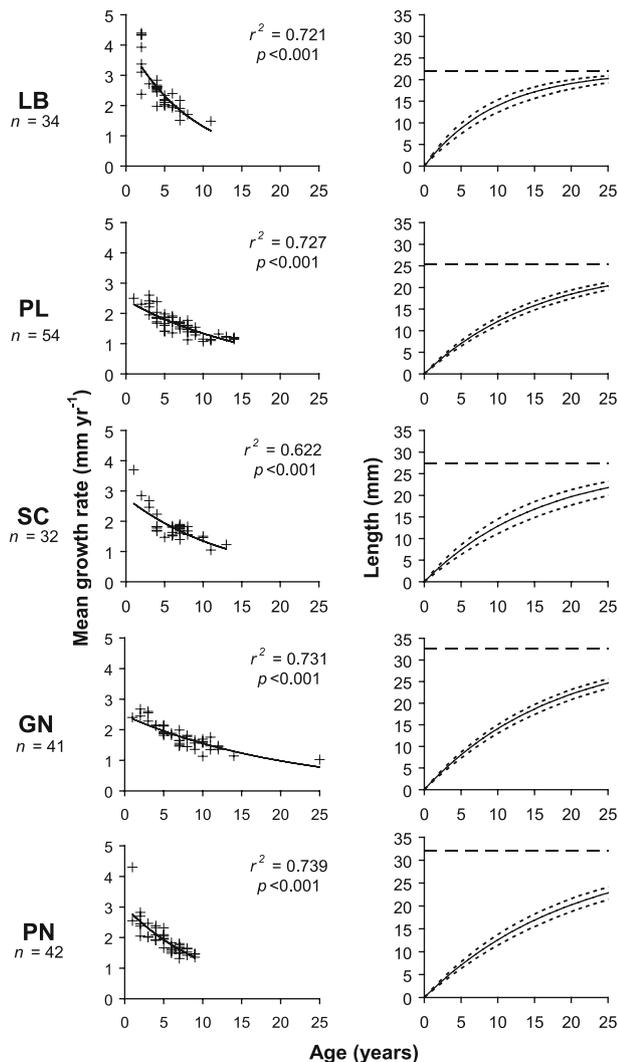
Fig. 3 *Balanophyllia europaea*. Relationships between mean growth rate and age (left hand graphs) and age–length von Bertalanffy growth curves (right hand graphs; see Eq. 1) of each population with 95% confidence interval (dotted lines). The dotted horizontal line represents L_∞ value. n = number of individuals dated by computerized tomography scans (CT)

analysis of the natural logarithm of the numbers of individuals (frequency) in each age class (N_t) against their corresponding age (t), or

$$\ln N_t = at + b \tag{2}$$

the slope a can be used to estimate the theoretical numeric reduction of individuals over time, the intercept b is equal to the natural logarithm of the number of individuals at age zero (N_0) (Pauly 1984; Sparre et al. 1989; Babcock 1991; Chadwick-Furman et al. 2000; Goffredo and Chadwick-Furman 2003; Goffredo et al. 2004). In a theoretical population in a steady state (rate of recruitment equal to rate of mortality; Grigg 1984) the coefficient of determination (r^2)

is equal to unity (Beverton and Holt 1956; Pauly 1984). As natural populations deviate from the steady state, r^2 decreases to zero. In applying this method, the age classes corresponding to lengths <5 mm were ignored, since polyps this small are difficult to see during field surveys, resulting in an underestimate of these age classes (Pauly 1984; Babcock 1991; Chadwick-Furman et al. 2000; Goffredo and Chadwick-Furman 2003; Goffredo et al. 2004). This method for estimating population stability has previously been used for colonial and solitary corals (Grigg 1984; Ross 1984; Babcock 1991; Chadwick-Furman et al. 2000; Goffredo and Chadwick-Furman 2003; Tsounis et al. 2007), including *B. europaea* (Goffredo et al. 2004).

The slope a was used to express the theoretical numerical reduction of the corals over time (survivorship curve):

$$N_t = N_0 e^{at} \tag{3}$$

N_t is the number of individuals in each age class, N_0 is the number of individuals at age 0, a is the slope of Eq. 2, t is the age.

The mean age of the individuals in each population was computed from the mean age of samples from the growth curves (Eq. 1). The observed percentage of individuals below sexual maturity was obtained by summing the frequencies of the age classes below sexual maturity, which is 3–4 years (Goffredo et al. 2002, 2004). The theoretical mean age was estimated as the mean age of the theoretical number of individuals in each population. The theoretical percentage of individuals below sexual maturity was obtained by summing the frequencies of the theoretical number of individuals of the age classes below sexual maturity in each population.

The observed biomass distribution per age class was obtained by adding the mass of each corallite in each age class. A theoretical age–mass growth curve was obtained for each population using the age–length growth curve (Eq. 1) and the length–mass relationship from Goffredo et al. (2007). The theoretical biomass distribution per age class was then obtained by multiplying the theoretical number of individuals in each age class (according to the survivorship curve, Eq. 3) for the expected mass at that age. The theoretical age at maximum percentage biomass was estimated as the age class representing the highest percentage biomass. The observed age at maximum percentage biomass was determined in the same way using the observed biomass distribution. The observed mean age of biomass in the population was calculated as the sum of the products of the observed biomass in each age class multiplied by its age, then divided by the total observed biomass. This parameter estimates how old the biomass is in each population; populations with most of the biomass accumulated in younger corals will have a lower mean age of biomass than populations in which most of the biomass is represented by older individuals. The theoretical mean age

Table 1 Sea surface temperature, L_∞, K, and r^2 (coefficient of determination of the semi-log regression used to estimate population structure stability in Eq. 2) values of the sampled populations

Population	Code	SST (°C), Annual mean (SD)	L_∞ (mm)	K	r^2
Calafuria	CL	18.023 (4.770)	21.3	0.111	0.935
Elba	LB	18.737 (5.057)	22.0	0.101	0.605
Palinuro	PL	19.138 (4.170)	25.5	0.065	0.550
Scilla	SC	19.537 (2.783)	27.4	0.063	0.503
Genova	GN	19.556 (4.723)	32.5	0.057	0.505
Pantelleria	PN	19.875 (4.766)	32.0	0.050	0.423

Growth data of the CL population from Goffredo et al. (2004). The populations are arranged in increasing order of sea temperature

of biomass in the population was calculated in the same way, but using the theoretical biomass in each age class and the total theoretical biomass.

SST data

SST data for the years 2003–2005 were obtained for each location 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). The data were from stations close to the sampling sites (<1 km) at a depth of 1 m below minimum low tide level. Mean annual SST was computed from hourly measurements from January 2001 to January 2005 (Table 1).

Statistical analyses

Analysis of covariance (ANCOVA) was used to examine differences in regression slopes and intercepts. Because of the heteroscedastic data sets, non-parametric Kruskal-Wallis

was used to compare mean SST among the sites. Pearson correlation coefficients were calculated for estimating population structure stability in each population (coefficient of determination of Eq. 2), and for the relationships between SST and L_∞, K, population structure stability, observed and theoretical % of individuals below sexual maturity, observed and theoretical mean age, observed and theoretical age at maximum % biomass, observed and theoretical mean age of biomass. Because of the low n value ($n = 6$) and the assumptions of the Pearson method, correlation coefficients were also estimated with bootstrapping (Efron 1981), with 100,000 resamples. The non-parametric Kolmogorov–Smirnov test was used to compare the age-frequency distributions among the populations. All analyses were computed using SPSS 12.0, except bootstrapping (S-PLUS 6.0 Professional).

Results

Mean annual SST was significantly different between sites (Kruskal-Wallis, $P < 0.001$; Table 1). Mean growth rate was negatively related to age in all populations, with age explaining between 62 and 74% of growth rate variance (Fig. 3). Growth rates decreased from 2–5 mm year^{-1} at ages <5 year to 1–2 mm year^{-1} at ages >10 year (Fig. 3).

L_∞ and K values (Table 1) differed between the populations (ANCOVA for slope of the "von Bertalanffy plot" used to estimate L_∞ and K, $P < 0.05$). These values were therefore used to model the age–length growth curve (Eq. 1) for each population (Fig. 3). L_∞ and K values were significantly correlated with SST (Table 2). SST explained more than 80% of the variance of L_∞ and more than 90% of the variance of K (Table 2).

Table 2 Linear regression and correlation analyses between sea surface temperature (Independent variable) and growth and demographic parameters (Dependent variable) in the sampled populations

Dependent variable	n	Slope (SE)	Intercept (SE)	r^2	R	r^2_{BS}	r_{BS}
L_∞	6	6.373 (1.567)	−95.224 (30.018)	0.805	0.897*	0.826	0.909*
K	6	−0.036 (0.005)	0.757 (0.105)	0.913	−0.956**	0.906	−0.952**
Population structure stability	6	−0.256 (0.039)	5.486 (0.751)	0.914	−0.956**	0.941	−0.970**
Observed % of individuals below sexual maturity	6	−17.826 (7.266)	360.875 (139.179)	0.601	−0.775	0.310	−0.557
Theoretical % of individuals below sexual maturity	6	−12.951 (2.508)	289.102 (48.042)	0.870	−0.932**	0.799	−0.894*
Observed mean age	6	1.639 (0.499)	−24.062 (9.560)	0.729	0.854*	0.548	0.740
Theoretical mean age	6	1.939 (0.488)	−31.851 (9.352)	0.798	0.893*	0.755	0.869*
Observed age at maximum % biomass	6	2.550 (1.046)	−39.652 (20.043)	0.598	0.773	0.588	0.767
Theoretical age at maximum % biomass	6	5.194 (0.922)	−87.777 (17.663)	0.888	0.942**	0.846	0.920**
Observed mean age of biomass	6	2.096 (0.775)	−30.255 (14.852)	0.646	0.804	0.605	0.778
Theoretical mean age of biomass	6	4.780 (0.566)	−77.188 (10.840)	0.947	0.973**	0.889	0.943**

n number of populations. r^2 Pearson's coefficient of determination, r Pearson's correlation coefficient, r^2_{BS} and r_{BS} Pearson's coefficients calculated with bootstrapping, * $P < 0.05$, ** $P < 0.01$. SE = standard error

The age of all collected individuals in the various populations was estimated using the age–length growth curves (Eq. 1). The oldest individual came from the Genova (GN) population with an estimated age of 27 year (25.65 mm length). The age-frequency distributions for each population are shown in Fig. 4. The distributions were significantly different between populations (Kolmogorov–Smirnov, $P < 0.001$), and regressions of the natural logarithm of the numbers of individuals (frequency) in each age class (N_t) were computed (Eq. 2; Table 1, r^2 values). These r^2 values were negatively correlated with SST (Table 2), varying from $r^2 = 0.935$ in the coldest population (CL), to $r^2 = 0.423$ in the warmest population (PN; Table 1), indicating a progressive deviation from the steady state of the populations as temperature increased (Table 2).

The theoretical percentage of individuals under sexual maturity was negatively related to SST, while the theoretical mean age, the theoretical age at maximum percentage biomass, and the theoretical mean age of biomass were all positively related to SST (Table 2).

Discussion

In zooxanthellate corals, photosynthesis enhances calcification, and both processes have temperature optima (Al-Horani 2005). It was previously hypothesized that for *B. europaea*, inhibition of photosynthesis occurs at high temperatures, leading to a reduction in the calcification rate and skeletal density (Goffredo et al. 2007). Also, the reduction in growth rate (*K*) with increasing temperature, highlighted in this study, might be because of a reduced energy input available for skeletal deposition, caused by the inhibition of photosynthesis in zooxanthellae.

A reduced growth rate at high temperatures has been found in the genus *Montastraea* (Carricart-Ganivet 2004), but the opposite has been reported for species of the genera *Porites* (Lough and Barnes 2000), *Acropora* and *Pocillopora* (Crossland 1981) and in mushroom corals (Goffredo and Chadwick-Furman 2003). In a study of the genera *Pocillopora*, *Acropora*, *Turbinaria,* and *Porites*, both increases and decreases in calcification with increases in temperature were reported, suggesting that the influence of temperature on growth may be species-specific (Harriott 1999). These differences might in part be due to the clade of zooxanthellae hosted by the polyp, and it has been proposed that different clades of zooxanthellae associated with corals have different environmental tolerances (e.g., light, temperature, sedimentation; Knowlton and Rohwer 2003). Under experimental conditions, zooxanthellae belonging to clade A (the clade which is hosted by most Mediterranean scleractinian corals; Visram et al. 2006), have proven to be resistant to short-term increases in
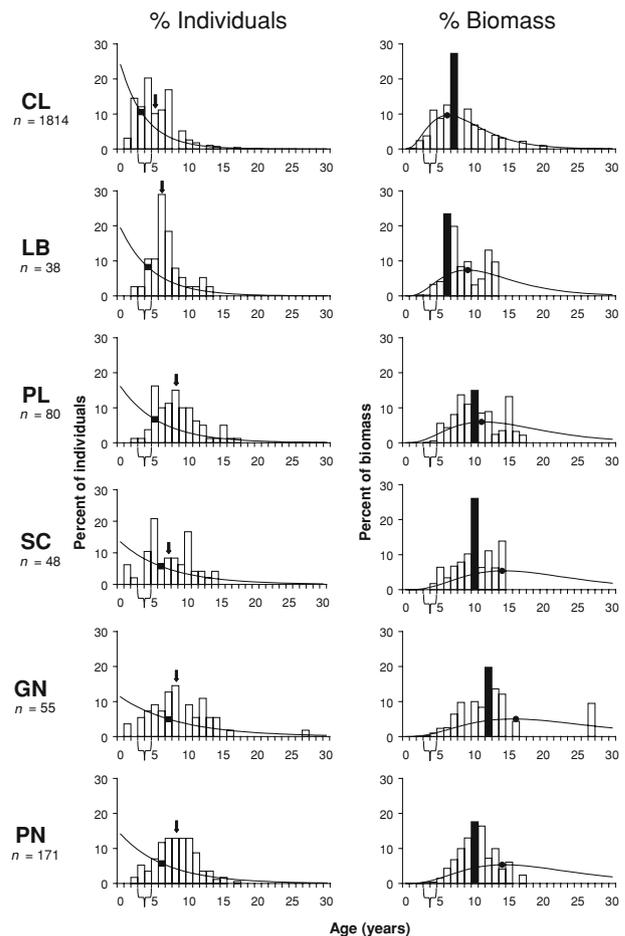

Fig. 4 *Balanophyllia europaea*. Age-class structures of each population. The lines indicate the theoretical distributions. The observed (arrow) and theoretical (black square) age class containing the mean observed age of the individuals of sampled population are indicated. The observed (black column) and theoretical (black circle) age at maximum percentage biomass are indicated. Bracketed ranges indicate the age at sexual maturity. Data for the Calafuria population (CL) are from Goffredo et al. (2004). *n* = number of individuals dated by growth curves

temperature (Rodolfo-Metalpa et al. 2006). However, severe bleaching episodes have been observed in situ in *O. patagonica* which also hosts clade A, in response to high temperatures (Fine et al. 2001).

In the present study the *K* growth constant was negatively correlated with SST and in an earlier study also the skeletal density was negatively correlated with SST (Goffredo et al. 2007). On this basis, calcification would also be expected to decrease at high temperatures (calcification = extension × skeletal density; Lough and Barnes 2000; Carricart-Ganivet 2004). This is in contrast to other studies on latitudinal variations of calcification in tropical and temperate corals, where the trend was an increase in calcification with decreasing latitude (Jacques et al. 1983; Lough and Barnes 2000; Howe and Marshall 2002;

Carricart-Ganivet 2004; McNeil et al. 2004). However, a recent study showed a decline of coral calcification in massive *Porites* from the Great Barrier Reef over a 16-year period (Cooper et al. 2007), and suggested that this reduction is linked to the interactive effects of increasing seawater temperatures and $pCO2$ (Reynaud et al. 2003). Calcification has an optimum temperature, and temperatures above optimum will lead to reduced calcification (Al-Horani 2005). The optimum calcification temperature for *B. europaea* may be equal to or lower than the lowest-recorded temperature in this study (18.023°C), which could explain the observed decrease in calcification with increasing SST.

Despite the theoretical nature of L_∞, in growth models, it is used as a measure of maximum size of individuals in the populations, and this seems to work well in *B. europaea*, fungiids, and gorgonian corals (Grigg 1974; Chadwick-Furman et al. 2000; Goffredo and Chadwick-Furman 2003; Goffredo et al. 2004; Goffredo and Lasker 2006). The increase in maximum corallite size of populations (asymptotic length) with mean SST is in agreement with previous observations, suggesting a positive correlation between biometric parameters (corallite length, width, height, and volume) and temperature in *B. europaea* (Goffredo et al. 2007). Although biologists have been interested in latitudinal variations of organism size for a long time, few studies have been conducted on marine invertebrates, and have often led to contrasting results (Lonsdale and Levinton 1985; Roy and Martien 2001; Olabarria and Thurston 2003). One of the hypotheses relating (terrestrial) body size with latitude is based on latitudinal changes of energy availability (see Wright 1983), and predicts smaller body size at high latitudes where available energy is reduced relative to equatorial regions (Turner and Lennon 1989; Cushman et al. 1993). This theory also seems to explain the present (marine) results, since the populations characterized by higher sea temperature (i.e., higher energy) had higher individual corallite lengths. Nevertheless, the increased length is accompanied by a marked reduction in skeletal density (Goffredo et al. 2007) and growth rate (K; present work). These reductions suggest that the increase in available energy, because of higher temperatures, cannot be exploited by the polyps, because of the reduced photosynthetic efficiency hypothesis (Goffredo et al. 2007). Moreover, the increase in individual size with temperature is accompanied by a reduction in population density (Goffredo et al. 2007), and this is in line with the hypothesis of energetic equivalence (Marquet et al. 1990), which states that, if an animal needs a certain area of space to satisfy its metabolic needs, its abundance will be inversely proportional to body size.

In a theoretical population, in a steady state, the age frequencies follow a negative exponential curve and the coefficient of determination of the semi-logarithmic regression from which a is estimated (Eq. 2) has a value of unity (Beverton and Holt 1956; Pauly 1984). In the populations considered in this study, r^2 was negatively correlated with temperature (i.e., it deviated from the theoretical steady state value as temperature increased) reducing from 0.9 in the coldest population to 0.4 in the warmest one (Tables 1 and 2) indicating that populations characterized by high temperatures were less stable than those from lower temperatures. While some populations only had few individuals, the theoretical growth curves and the parameters derived from them were comparable with those derived from the populations with many individuals, and the derived parameters can be considered good estimates of their population characteristics. Decreasing population stability with increasing temperature is further emphasized in Table 2, where SST was correlated with almost all dependent variables. As temperature increased, the theoretical percentage of immature individuals decreased, while the theoretical mean age of individuals, the theoretical age at maximum percentage biomass, and the theoretical mean age of biomass increased, all indicating a progressive reduction in young individuals. Reduced growth and increased mortality of juvenile tropical corals as temperature increases have been reported in a case study in the US Virgin Islands (Edmunds 2004). The deficiency of younger age classes as the temperature increased might be related to recent local perturbations (e.g., excessively high temperatures) such as the 2°C increase in the maximum SST in the northwest Mediterranean recorded in the year 2003, relative to the previous 50 years, and the short-term increase in SST of 3–4°C relative to the mean values in the year 2003 (Rodolfo-Metalpa et al. 2006; Diaz-Almela et al. 2007). *Balanophyllia europaea* larvae are zooxanthellate and rely on the energy derived from photosynthesis (Goffredo and Zaccanti 2004), and in zooxanthellate corals most of the energetic resources needed for gametogenesis come from photosynthesis (Rinkevich 1989). Reduced photosynthetic efficiency of zooxanthellae at high temperatures, besides limiting energetic resources for polyp gametogenesis (Rinkevich 1989; Goffredo et al. 2007), might decrease the energy available for larvae. Together, high mortality and reduced energy might explain both the low population density (Goffredo et al. 2007), and the reduction in numbers of young individuals with increasing temperature.

An alternative explanation for the negative effects on growth and population structure stability of *B. europaea* with increasing temperature could be related to suspension feeding. In the Mediterranean, 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 proved to be a

stress factor for corals and several benthic suspension feeding taxa (Coma et al. 2000, Coma and Ribes 2003, Peirano et al. 2005). Moreover, in *Stylophora pistillata* colonies, starved corals present significantly lower levels of calcification and photosynthesis than fed corals (Houlbrèque et al. 2004). At high temperatures, low availability of resources would cause slow growth and low population stability in *B. europaea*. However, if this was the case, the inhibition would also be found in *L. pruvoti*, a closely related species which is totally heterotrophic but it is not. Goffredo et al. (2007) found that skeletal and population density of *L. pruvoti* were almost the same at low- and high-temperature study sites, compared to *B. europaea* where they decrease at high temperature. Thus the hypothesis of photosynthetic inhibition at high temperatures seems more likely.

Global increase in sea temperature is one of the greatest threats for reef corals (Hughes et al. 2003). Rising temperatures may pose the greatest threat to populations of *B. europaea* in the warmest areas of its distribution, which could reduce the abundance of recruits. The regression between SST and theoretical percentage of individuals below sexual maturity predicts that at a mean annual SST of 22.3°C, a population will be characterized by no immature individuals, and then will be condemned to a progressive decrease in abundance until extinction. The Intergovernmental Panel on Climate Change (IPCC) projected an increase of global SST of 1–3°C by 2100 (Solomon et al. 2007). Assuming an intermediate and rather conservative increase (2°C), it is expected that most of the populations of *B. europaea* would be near their thermal limit (expected temperature in 2100 in the population of CL = 20.0°C; LB = 20.7°C; PL = 21.1°C; SC = 21.5°C; GN = 21.6°C; PN = 21.9°C). This would result in a large decrease in the input of new individuals to the population. A decrease of population density of this species with increasing SST has already been reported (Goffredo et al. 2007).

Present evidence suggests that corals and their symbiotic zooxanthellae may be unable to acclimate or adapt fast enough to cope with the present rapid rate of water warming (Hoegh-Guldberg 1999; Hoegh-Guldberg et al. 2007). Moreover, being endemic to the Mediterranean, *B. europaea* has very limited possibilities to react to seawater warming by moving northwards toward lower temperatures, since the northern limit of the Mediterranean basin is only 1° of latitude north of the northernmost population considered in this work. The future for *B. europaea* would therefore appear to be bleak.

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