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REPORT

Relationships between growth, population dynamics, and environmental parameters in the solitary non-zooxanthellate scleractinian coral *Caryophyllia inornata* along a latitudinal gradient in the Mediterranean Sea

E. Caroselli[1] · F. Ricci[1] · V. Brambilla[1] · G. Mattioli[2] · O. Levy[3] · G. Falini[4] ·
Z. Dubinsky[3] · S. Goffredo[1]

Abstract The ecology of scleractinian corals may be understood through comparisons between population demographic data and environmental parameters. Growth (growth constant and maximum size) and demographic parameters (population structure stability, instantaneous mortality rate, average age of individuals, percentage of immature individuals, age at maximum biomass, and average age of biomass) of the solitary, non-zooxanthellate, and temperate coral *Caryophyllia inornata* were investigated at six sites along an 8° latitudinal gradient of temperature and solar radiation (SR) on the western Italian coasts. Growth parameters were homogeneous among populations across the investigated latitudinal range. While demographic parameters were not correlated with depth temperature, populations were progressively less stable and showed a deficiency of young individuals with increasing SR, likely as a result of the lowered energetic resources due to reduced zooplankton availability. These results contrast with data from another Mediterranean non-zooxanthellate solitary coral, *Leptopsammia pruvoti*, investigated along the same gradient, which shows no correlation between population demography and temperature or SR.

Introduction

Many scleractinians are sensitive to environmental factors such as nutrients (Muscatine et al. 1989; Orejas et al. 2011), water flow (Purser et al. 2010), substrate slope and structure (Vertino et al. 2010), waves (Lasker 1990), pH (Goffredo et al. 2014; Fantazzini et al. 2015), light (Rodolfo-Metalpa et al. 2008), and temperature (Goffredo et al. 2008; Kružić et al. 2012). Latitude is the main factor influencing variation in solar radiation (SR) and sea surface temperature (SST; Kain 1989), which are widely used as monitoring parameters for ecological studies (Gerrodette 1979; Goffredo et al. 2008; Caroselli et al. 2012) and have notable implications for organism biology (Carricart-Ganivet 2004; Cantin et al. 2010; Caroselli et al. 2011; Kružić et al. 2012). The Mediterranean Sea extends for about 14° of latitude, making it a good system model to study whether and how biological processes vary with SR and temperature along a latitudinal gradient (e.g., Goffredo et al. 2007). The latitudinal variation of SR and SST generally influences scleractinian demography and growth (Dodge et al. 1974; Hughes 1984; Goffredo et al. 2008; Cantin et al. 2010; Hamel et al. 2010), such as in the Mediterranean species *Cladocora caespitosa* that shows differential growth rates in response to temperature and nutrients (Kružić et al. 2012). Net calcification rates are frequently related to temperature in both temperate

Communicated by Biology Editor Dr. Mark J. A. Vermeij

✉ S. Goffredo
s.goffredo@unibo.it

[1] Marine Science Group, Department of Biological, Geological and Environmental Sciences, University of Bologna, Via F. Selmi 3, 40126 Bologna, Italy

[2] Operative Unit of Radiology and Diagnostics by Images, Hospital of Porretta Terme, Local Health Enterprise of Bologna, Via O. Zagnoni 5, 40046 Porretta Terme, Italy

[3] The Mina and Everard Goodman Faculty of Life Sciences, Bar-Ilan University, 52900 Ramat Gan, Israel

[4] Department of Chemistry "Giacomo Ciamician", University of Bologna, Via F. Selmi 2, 40126 Bologna, Italy

(Goffredo et al. 2009) and tropical corals (Lough and Barnes 2000; Rodolfo-Metalpa et al. 2006; Cooper et al. 2008; Cantin et al. 2010; Carricart-Ganivet et al. 2012). Coral reproductive cycles are often regulated by temperature and photoperiod (Chornesky and Peters 1987; Goffredo et al. 2006; Airi et al. 2014), and larval survivorship and development are influenced by many environmental parameters (Jokiel and Guinther 1978; Edmunds et al. 2001; Brooke and Young 2005; Graham et al. 2008). Physiological processes (e.g., calcification, photosynthesis, and respiration) of organisms, including corals, are strongly dependent on environmental conditions (Edmunds and Gates 2002; Reynaud et al. 2003; Krief et al. 2010).

Some aspects of the ecology of scleractinians may be understood by comparing population demographic data and environmental parameters (Goffredo et al. 2008; Caroselli et al. 2012). Some gorgonians, reef-building corals, and solitary scleractinians record annual growth bands in their skeleton (Dodge et al. 1974; Chadwick-Furman et al. 2000; Goffredo and Lasker 2008; Goffredo et al. 2010; Caroselli et al. 2012), which can be counted to determine their individual age. In some species where mechanisms decoupling growth from age (e.g., colony fragmentation, fusion, and partial mortality) are negligible (Hughes and Jackson 1985; Babcock 1991), growth and population dynamic models based on age can be applied to describe demographic characteristics (Grigg 1984; Chadwick-Furman et al. 2000; Goffredo et al. 2010; Caroselli et al. 2012). The Beverton–Holt age-based model is a population dynamic model that estimates demographic data based on the previous generation's data (Beverton and Holt 1956). Data on demographic parameters such as population turnover time can be used to design strategies for reef restoration and bioremediation of degraded coastal areas (Goffredo and Chadwick-Furman 2003; Goffredo and Lasker 2008).

This study focuses on Caryophyllia inornata (Duncan 1878), a non-zooxanthellate solitary scleractinian coral widely distributed in the Mediterranean Sea and in the eastern Atlantic Ocean, from the UK to Azores Islands, up to 100 m depth (Zibrowius 1980). The species colonizes shaded hard substrates like the vaults and walls of caves, crevices, and wrecks and, in some cases, can dominate coral cover (Zibrowius 1980; Caroselli et al. 2015b). Its abundance along western Italian coasts ranges from 100 to 1500 individuals m^{-2} (Caroselli et al. 2015b). Caryophyllia inornata is gonochoric, brooding and displays an unusual reproductive cycle characterized by continuous production of brooded and apparently agamic embryos by females, males, and sexually inactive individuals (Goffredo et al. 2012a; Marchini et al. 2015).

The aims of this study were (1) to determine whether the growth and demographic parameters of C. inornata from six populations were related to SR and temperature variation along a wide latitudinal gradient, and (2) to compare the responses of C. inornata and two solitary dendrophyllids, Balanophyllia europaea (zooxanthellate) and Leptopsammia pruvoti (non-zooxanthellate), previously investigated along the same latitudinal gradient with the same methods (Goffredo et al. 2008; Caroselli et al. 2012).

## Materials and methods

Sample collection

Specimens of C. inornata (Fig. 1a) were collected between May 14, 2009, and April 14, 2011, from six sites along a latitudinal gradient in the Mediterranean Sea from 44°20′N to 36°45′N (Caroselli et al. 2015b; Fig. 2). The samples were collected at depths ranging from 11 to 16 m, where a high population density of C. inornata has been reported (Caroselli et al. 2015b). Samples were collected from crevices (see Table 1 for the number of samples collected at each site), excluding the Elba site where they were collected under the wings of a sunken plane wreck. At each site, all samples were collected along a transect ranging between 4 and 8 square patches of 0.01 m^2 each (number of patches: Genova, GN, $n = 6$; Calafuria, CL, $n = 8$; Elba, LB, $n = 4$; Palinuro, PL, $n = 6$; Scilla, SC, $n = 6$; Pantelleria, PN, $n = 7$; Table 1).

Sample analysis

Specimens were dried at 50 °C for 4 d and observed under a stereoscope to remove fragments of substratum and calcareous deposits produced by other organisms. The low drying temperature was selected to avoid phase transitions in the skeletal aragonite/calcite composition (Vongsavat et al. 2006), under investigation in these samples by diffractometric analyses (Goffredo et al. 2012b). Polyp length (L: maximum axis of the oral disk, Fig. 1b), width (W: minimum axis of the oral disk), and height (h: oral–aboral axis) were measured with Vernier calipers (Metrica, Milano, Italy). The dry skeletal mass (M) was measured with a digital precision balance. The number of annual growth bands was counted in approximately 30 skeletons randomly selected from each population, to obtain an empirical relationship between size and age. The selected samples were subjected to computerized tomography (CT) for growth band counts, as some forms of scleractinian corals (such as temperate corals) record two annual growth bands in their skeletons, a high-density band in winter and a low-density band in summer (Dodge et al. 1974; Goffredo et al. 2008, 2010; Caroselli et al. 2012; Fig. 1c, d).

Fig. 1 *Caryophyllia inornata:*
a living polyp; **b** corallite.
Dotted line indicates polyp
length (*L* maximum axis of the
oral disk); **c** computerized
tomography (CT) scan of a
mature corallite (8 yr); **d** CT
scan of a juvenile corallite
(3 yr). The multiple CT views
facilitated the recognition of
high-density bands (h)
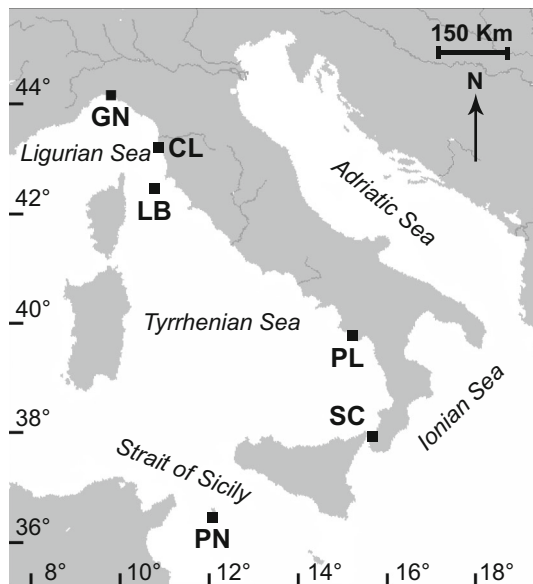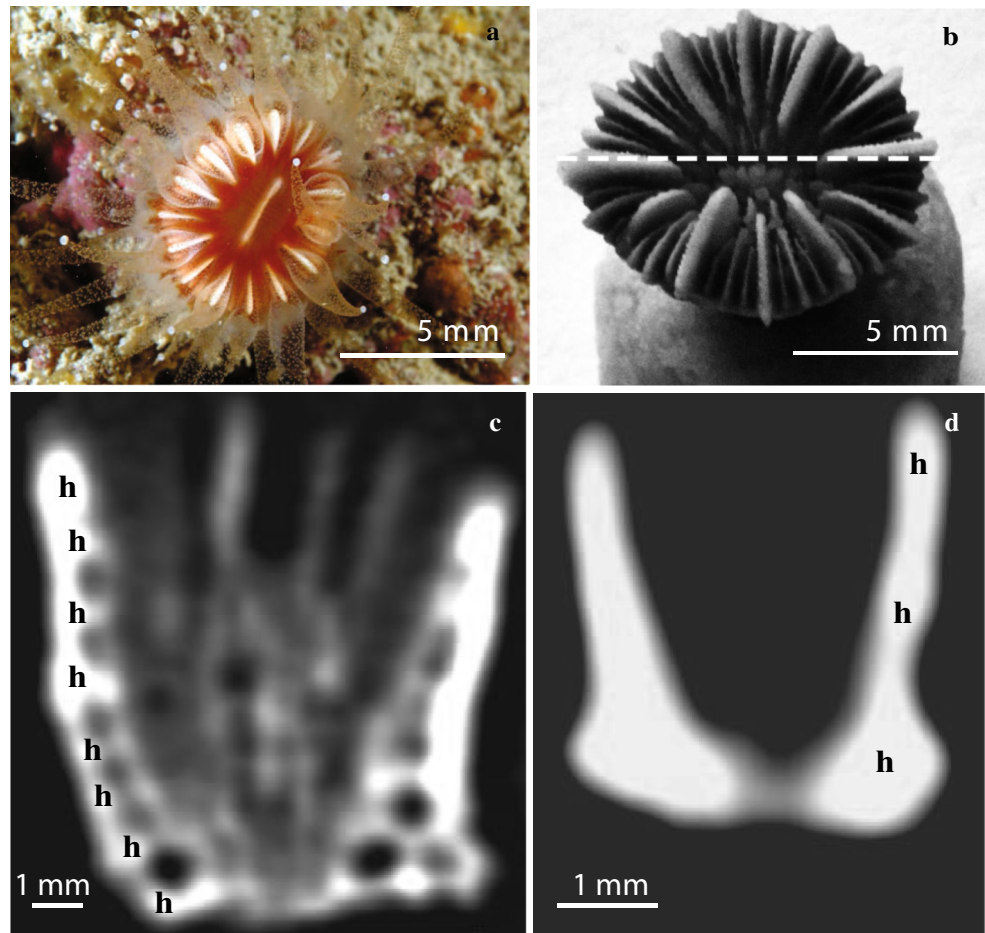
Fig. 2 Map of the Italian coastline indicating sites where samples
were collected. *GN* Genova, 44°20′N, 9°08′E; *CL* Calafuria, 43°27′N,
10°21′E; *LB* Elba Isle, 42°45′N, 10°24′E; *PL* Palinuro, 40°02′N,
15°16′E; *SC* Scilla, 38°01′N, 15°38′E; *PN* Pantelleria Isle, 36°45′N,
11°57′E

Growth and population demography modeling

The age of each scanned individual was obtained using CT
(Fig. 1c, d), and the mean annual growth rate was esti-
mated by dividing a polyp's length by its age. As for other
Mediterranean solitary corals (Goffredo et al. 2008; Car-
oselli et al. 2012), the mean annual growth rate showed an
exponential negative relationship with individual age
(Fig. 3), as required for the application of the von Berta-
lanffy growth model (von Bertalanffy 1938):

$$L_t = L_\infty \left(1 - e^{-kt}\right) \tag{1}$$

where L_t is individual length at age t, L_∞ is the asymptotic
length (maximum expected length in the population), k is a
growth constant (larger for fast growth up to the asymptotic
length, smaller for slow growth), and t is the age of the
individual. To apply this growth model, L_∞ and k, along
with their confidence intervals (CI), were estimated for
each population through a regression analysis by least
squares procedure developed in the software MATLAB
R2012a (MathWorks, Natick, USA), since this method has
superior fitting properties (Sparre and Venema 1998) than
traditional methods (e.g., Pauly 1984). The obtained von

Table 1 Depth temperature (DT), mean annual solar radiation (SR), number of patches and collected samples, asymptotic length (L_∞), growth constant (k), coefficient of determination of the semilog regression of Eq. 2, which is an estimator of population structure stability (r^2) and demographic parameters of each population

Variable	Site						
	Genova	Calafuria	Elba	Palinuro	Scilla	Pantelleria	General
Code	GN	CL	LB	PL	SC	PN	
DT (°C), annual mean (SE)	18.24 (0.45)	16.74 (0.38)	17.63 (0.38)	18.94 (0.44)	18.20 (0.41)	19.15 (0.41)	
SR (W m^{-2}), annual mean (SE)	161.8 (9.3)	174.9 (10.6)	183.4 (10.6)	194.9 (10.8)	203.2 (10.4)	214.2 (10.1)	
Number of patches	6	8	4	6	6	7	
Number of samples collected	86	62	241	93	47	39	
L_∞ (mm) (95 % confidence limit)	21.9 (0.0–56.7)	7.1 (3.8–10.4)	22.5 (12.1–32.9)	22.5 (10.2–34.7)	12.3 (6.9–17.6)	16.1 (11.4–20.9)	15.8 (13.1–18.5)
k (95 % confidence limit)	0.048 (0.000–0.099)	0.234 (0.035–0.432)	0.041 (0.017–0.066)	0.048 (0.015–0.082)	0.101 (0.022–0.180)	0.073 (0.040–0.105)	0.072 (0.054–0.090)
r^2	0.803	0.853	0.829	0.523	0.437	0.449	
Instantaneous rate of mortality Z (95 % confidence limit)	0.354 (0.180–0.530)	0.541 (0.283–0.799)	0.223 (0.156–0.290)	0.136 (0.058–0.259)	0.102 (0.014–0.190)	0.081 (0.013–0.149)	
Observed% of immature individuals	81.4	95.2	58.9	39.8	42.6	38.5	
Theoretical% of immature individuals	91.9	98.0	79.3	67.3	51.3	43.4	
Observed mean age (yr) (95 % confidence limit)	4.6 (4.0–5.1)	3.3 (2.9–3.7)	6.5 (6.0–7.0)	8.5 (7.7–9.2)	8.3 (7.2–9.4)	8.8 (7.5–10.1)	
Theoretical mean age (yr)	2.3	1.4	3.9	5.7	9.1	11.6	
Observed age at max% of biomass (yr)	5	2	11	10	10	15	
Theoretical age at max% of biomass (yr)	6	4	9	11	15	18	
Observed mean age of biomass (yr)	6.7	4.4	10.2	10.8	11.1	11.5	
Theoretical mean age of biomass (yr)	7.7	4.9	11.7	14.8	21.1	25.3	

Bertalanffy age–length relationship was used to estimate the age of all samples for which CT scans were not performed.

The theoretical population age structure and the population age structure stability were estimated by a linear regression analysis of the natural logarithm of the number
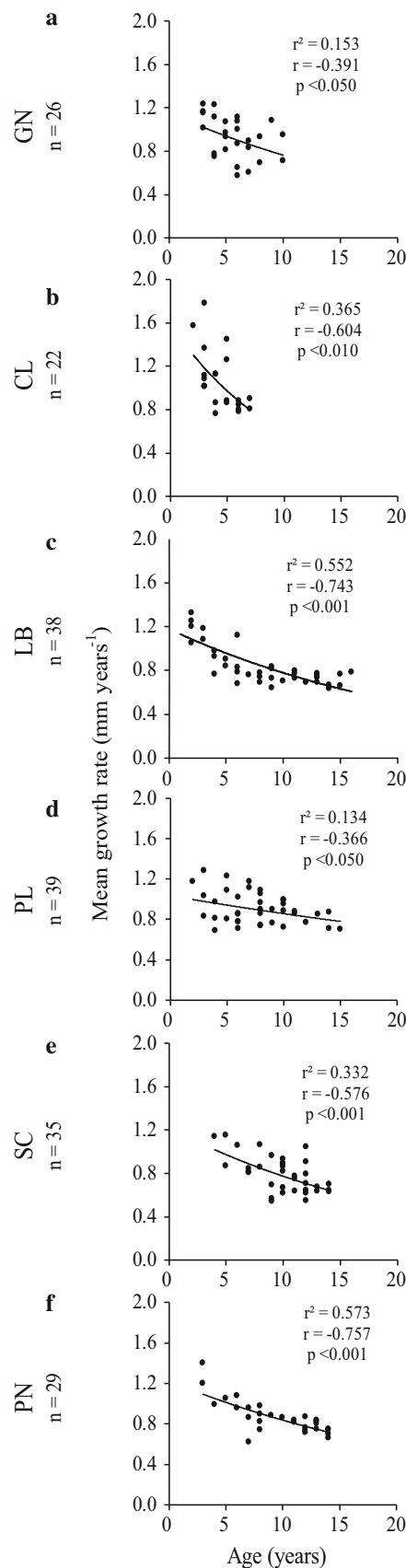
Fig. 3 Relationship between mean growth rate and individual age at **a** Genova, **b** Calafuria, **c** Elba Isle, **d** Palinuro, **e** Scilla, **f** Pantelleria Isle. Data were fitted with exponential curves to verify the assumptions of the von Bertalanffy growth model. n = number of individuals dated by computerized tomography (CT) scans

of individuals (frequency) in each age class (N_t) against their corresponding age (t):

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

where a is the slope, indicated also with sign changed as Z (instantaneous rate of mortality), which represents the decrement of the number of individuals with age and is the reciprocal of the turnover time of the population (Pauly 1984; Goffredo and Chadwick-Furman 2003; Goffredo et al. 2010). The intercept b corresponds to the natural logarithm of the number of individuals at age zero (N_0) (Pauly 1984; Caroselli et al. 2012). In a theoretical steady-state population (i.e., no age cohort missing or overrepresented, as would be the case if a major disturbance event had recently altered recruitment patterns; Grigg 1984), 100 % of the variance in the frequency of age classes is explained by age and the r^2 of the regression line of Eq. 2 is equal to one. Populations deviating from the steady state will have lower r^2 values (Sparre et al. 1989; Goffredo et al. 2004; Caroselli et al. 2012).

The Beverton and Holt model was applied to describe the population dynamics of *C. inornata* in each population and to obtain the theoretical population parameters (Beverton and Holt 1956; Chadwick-Furman et al. 2000; Goffredo et al. 2008, 2010; Goffredo and Lasker 2008; Caroselli et al. 2012). Population age structures sampled in the field are usually underrepresented in the younger age classes, as smaller individuals are difficult to observe and collect in situ while diving. The "theoretical" population obtained with the Beverton and Holt demographic model also reconstructs the youngest age classes and is an additional estimation of population demographic traits. The observed mean age of the individuals at each site was computed from the age of collected samples dated with the growth curve (Eq. 1). The theoretical mean age was estimated as that of the theoretical number of individuals at each site. The observed percentage of individuals below sexual maturity was obtained by summing the frequencies of the age classes below sexual maturity, which is ~8 yr (~6.1 mm length; Marchini et al. 2015). The theoretical percentage of individuals below sexual maturity was determined by summing the frequencies of the theoretical number of individuals in the age classes below sexual maturity at each site. The observed biomass distribution per age class was obtained by the sum of each corallite mass in each age class. The theoretical biomass distribution per age

class was then obtained by multiplying the theoretical number of individuals in each age class for the expected biomass at that age. The observed age at maximum percentage biomass was estimated as the age class representing the highest percentage biomass, using the observed biomass distribution. The theoretical age at maximum percentage biomass was determined in the same way, using the theoretical distribution. The observed mean age of biomass in the populations was calculated as the sum of the products of the observed biomass in each age class multiplied by its age and then divided by the total observed biomass. The theoretical mean age of biomass in each site was calculated in the same way, but using the theoretical biomass.

Temperature and solar radiation

In this study, for each site, environmental parameters (DT and SR) were collected for a period equal to the mean turnover time of populations, which was 6 yr (calculated as the reciprocal of the instantaneous rate of mortality, Z). Thus, for each site, 72 average monthly values of DT and SR were collected for the 6 yr prior to the month of sampling. With this method, the mean values of environmental parameters considered were those experienced by the polyps for most of their lifespan. Data were obtained from data banks, as commonly done to study the influence of environmental parameters on coral growth (e.g., Harriott 1999; Peirano et al. 1999, 2005; Lough and Barnes 2000; Carricart-Ganivet 2004; Cantin et al. 2010).

Temperature data (°C) were recorded every 2–3 h by digital thermometers (i-Button, DS1921G-F5#, Maxim Integrated Products, Dallas Semiconductors) placed at the experimental sites to record seawater temperature over time intervals that varied by site. Thermometers were replaced every 3 months to avoid problems of encrustation and overgrowth by marine organisms. SST historical data (°C) were obtained for each site from the National Mareographic Network of the Superior Institute for Environmental Protection and Research (ISPRA; http://isprambiente.gov.it). These data are measured by SM3810 mareographic stations located close to the sampling sites and provided by the Society for Environmental and Industrial Monitoring (SIAP + MICROS). For each site, historical at-depth temperatures were estimated by linear regression between DT and SST. In this study, the average DT of the 6 yr preceding sampling ($n = 72$ monthly temperatures) was considered.

Monthly values of SR (W m⁻²) were obtained from the data bank of the Satellite Application Facility on Climate Monitoring (CM-SAF/EUMETSAT; http://www.cmsaf.eu). These are estimates derived from real-time satellite measurements and datasets registered with intersensor calibrated radiances. Mean annual solar radiation was

calculated for the 15 km square associated with each study site by averaging 72 monthly values for each site.

Statistical analyses

An analysis of variance (ANOVA) was used to compare the mean DT and SR among the six sites, after checking that the assumptions for parametric statistics were fulfilled. Pearson's correlation coefficients were calculated between physical parameters (DT and SR) and population parameters, namely instantaneous rate of mortality (Z), population structure stability (r^2), observed and theoretical percentage of individuals below sexual maturity, observed and theoretical mean age, observed and theoretical age at maximum percentage of biomass, and observed and theoretical mean age of biomass. Pearson's correlation coefficients were also calculated with a bootstrapping procedure (1000 resamples) for a more careful and reliable analysis (Efron 1981). A nonparametric Kolmogorov–Smirnov test was used to test for differences in the age frequencies of the six populations. All analyses were done using SPSS Statistics 22.

Results

The mean annual values of SR ranged from 161.8 W m⁻² at GN to 214.2 W m⁻² at PN (Table 1). Mean annual values of DT ranged from 16.74 °C at CL to 19.15 °C at PN (Table 1). Mean SR and DT were significantly different among sites (ANOVA, $p < 0.01$). While SR decreased with higher latitude, DT did not correlate with latitude (Fig. 4).

Each population showed an exponential decrease in mean growth rate with increasing age, with age variance explaining 13–57 % of mean growth rate variation (Fig. 3). Mean growth rate decreased from 0.8–1.2 mm yr⁻¹ for immature individuals (0–7 yr) to 0.5–0.7 mm yr⁻¹ for mature individuals (7–14 yr; Fig. 3).

L_∞ and k for each population were homogeneous among sites (95 % CI overlapped; Table 1); therefore, data from all the individuals dated by growth bands in all populations were pooled. The general L_∞ and k values were then estimated (Table 1) to obtain a general von Bertalanffy growth curve (Fig. 5) describing the age–length relationship across all sampling sites. All 95 % CI of k values for each population overlapped with the 95 % CI of the general k value (Table 1). The 95 % CI of L_∞ of the CL population did not overlap with the 95 % CI of the general L_∞ value (Table 1). However, for the CL population, the difference between the age of each sample estimated with the general growth curve and that estimated with the CL growth curve had a mean of 0.060 yr and a 95 % CI in the
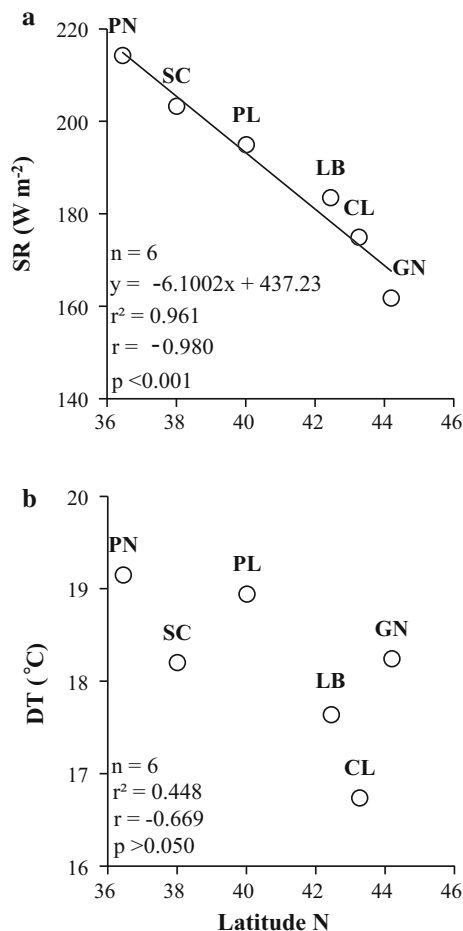
Fig. 4 Relationships between latitude and **a** solar radiation (SR) and **b** depth temperature (DT) at study sites (*GN* Genova, *CL* Calafuria, *LB* Elba Isle, *PL* Palinuro, *SC* Scilla, *PN* Pantelleria Isle). *n* = number of sites; *r* = Pearson's correlation coefficient
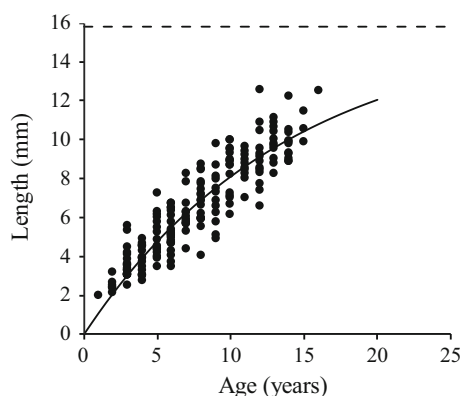
Fig. 5 General age–length von Bertalanffy growth curve (see Eq. 1) describing the growth in all populations. *Dotted line* indicates the maximum expected length of corals in all populations ($L_\infty = 15.8$ mm). *Points* indicate the age/size of all samples in all populations, dated by computerized tomography (CT) scans (*n* = 189) from which the general growth curve was obtained

range −0.324 to 0.444 yr (i.e., containing zero), indicating that the difference in the age estimated by the two curves was negligible. Moreover, for the CL population, the difference between the age of each sample estimated with the general growth curve and the one obtained by growth band counts had a mean of 0.111 yr and a 95 % CI in the range −0.348 to 0.570 yr (i.e., containing zero), indicating that the general growth curve was a good estimator of coral age at CL. All 568 individuals collected were dated using the general growth curve (Eq. 1; Fig. 5). The oldest individual came from the Scilla population (SC) with an estimated age of 22 yr and a length of 12.55 mm.

The age–frequency distributions (Fig. 6) differed among populations (Kolmogorov–Smirnov test, $p < 0.001$). The observed and theoretical population demographic parameters are given in Table 1 and shown in Fig. 6. Based on the bootstrapping correlation coefficients, the instantaneous rate of mortality (Z, ranging from 0.541 at CL to 0.081 at PN; Table 1), population structure stability (r^2, ranging from 0.803 at GN to 0.437 at SC; Table 1), and observed and theoretical percentage of individuals below sexual maturity (ranging from 95.2 % at CL to 38.5 % at PN, and 98.0 % at CL to 43.4 % at PN, respectively; Table 1) were negatively correlated with SR (decreasing southward), while the observed and theoretical mean age (ranging from 3.3 yr at CL to 8.8 yr at PN, and 1.4 yr at CL to 11.6 yr at PN, respectively; Table 1) and theoretical age at maximum percentage of biomass (ranging from 4 yr at CL to 18 yr at PN; Table 1) were positively correlated with SR (increasing southward; Table 2). No demographic parameter was correlated with DT.

Discussion

In all populations along the investigated latitudinal gradient, *C. inornata* showed determinate growth, characterized by a decreasing growth rate with increasing age, as previously demonstrated in other animals (Sebens 1987). Latitudinal variation in environmental conditions can affect the size of organisms (Lough and Barnes 2000), influencing coral growth rate and maximum size within the limits allowed by the organism's biology (Carricart-Ganivet 2004; Cantin et al. 2010). Determinate growth is a characteristic of some colonial octocorals (Goffredo and Lasker 2008) and scleractinians, such as branching *Pocillopora* spp. (Grigg and Maragos 1974), massive *Goniastrea aspera* (now renamed as *Coelastrea aspera*; Sakai 1998; Huang et al. 2014), and free-living *Manicina areolata* (Johnson 1992), but this characteristic is mainly found in solitary corals, such as *B. europaea* (Goffredo et al. 2008), *B. elegans, Paracyathus stearnsii* (Gerrodette 1979), *L. pruvoti* (Goffredo et al. 2010; Caroselli et al. 2012), the

Fig. 6 Age class structures by abundance and proportion of biomass of populations of *Caryophyllia inornata* at **a** Genova, **b** Calafuria, **c** Elba Isle, **d** Palinuro, **e** Scilla, **f** Pantelleria Isle. The *lines* indicate the theoretical distributions. The observed (*grey column*) and theoretical (*black square*) age classes containing the mean age of the individuals of sampled population are indicated. The observed age at maximum percentage biomass (*black column*) and theoretical (*black circle*) age at maximum percentage biomass are indicated. *Asterisks* indicate the age at sexual maturity
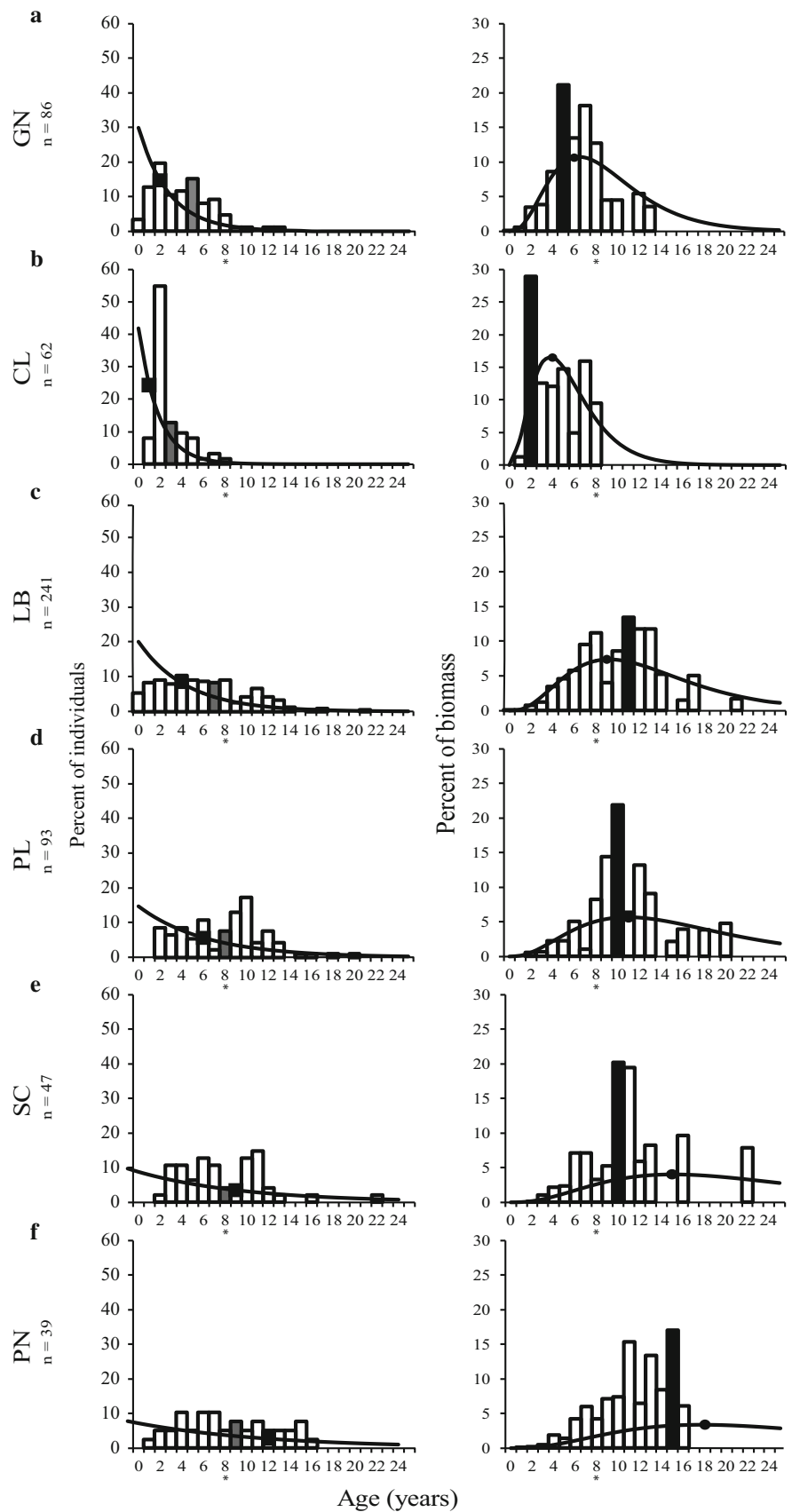
Table 2 Correlation analyses between solar radiation and depth temperature (independent variables) and demographic parameters (dependent variables) in the sampled populations ($n = 6$ sites)

	n	r^2	r	r^2_{BS}	r_{BS}
Solar radiation					
Instantaneous rate of mortality (Z)	6	0.654	−0.883*	0.759	−0.871*
Population structure stability (r^2)	6	0.778	−0.809	0.759	−0.871*
Observed% of individuals below sexual maturity	6	0.744	−0.862*	0.785	−0.886*
Theoretical% of individuals below sexual maturity	6	0.899	−0.949**	0.906	−0.952**
Observed mean age	6	0.768	−0.876*	0.794	0.891*
Theoretical mean age	6	0.883	0.939**	0.889	0.943**
Observed age at maximum% of biomass	6	0.687	0.829*	0.643	0.802
Theoretical age at maximum% of biomass	6	0.878	0.937**	0.874	0.935**
Observed mean age of biomass	6	0.657	0.811	0.740	0.860*
Theoretical mean age of biomass	6	0.877	0.937**	0.884	0.940**
Depth temperature					
Instantaneous rate of mortality (Z)	6	0.690	−0.769	0.558	−0.743
Population structure stability (r^2)	6	0.592	−0.830	0.552	−0.747
Observed% of individuals below sexual maturity	6	0.654	−0.809	0.587	−0.766
Theoretical% of individuals below sexual maturity	6	0.555	−0.745	0.483	−0.695
Observed mean age	6	0.674	−0.821*	0.598	0.773
Theoretical mean age	6	0.526	0.725	0.489	0.699
Observed age at maximum% of biomass	6	0.564	0.751	0.387	0.622
Theoretical age at maximum% of biomass	6	0.565	0.751	0.491	0.701
Observed mean age of biomass	6	0.579	0.761	0.483	0.695
Theoretical mean age of biomass	6	0.555	0.745	0.497	0.705

r^2 = Pearson's coefficient of determination, r = Pearson's correlation coefficient, r^2_{BS} and r_{BS} = Pearson's coefficients calculated with bootstrapping

* $p < 0.05$; ** $p < 0.01$

free-living deep coral *Flabellum alabastrum* (Hamel et al. 2010), and the free-living fungiids *Diaseris distorta* (now renamed as *Cycloseris distorta*; Yamashiro and Nishihira 1998; Gittenberger et al. 2011), *Ctenactis echinata*, *Fungia scutaria* (now renamed as *Lobactis scutaria*; Gittenberger et al. 2011), *F. fungites*, the subgenus *Fungia* (*Danafungia*) spp. (now renamed as *Danafungia* spp.; Goffredo and Chadwick-Furman 2003; Gittenberger et al. 2011), and *Heliofungia actiniformis* (Knittweis et al. 2009). The growth rate of colonies or single polyps can be affected by several environmental factors and differs greatly among scleractinians (Chornesky and Peters 1987; Goffredo et al. 2008; Caroselli et al. 2012; Kružić et al. 2012). Measurements of growth in natural populations refer mostly to zooxanthellate scleractinians, while only few studies have focused on non-zooxanthellate species. Exceptions include studies on deepwater *Lophelia pertusa* (Gass and Roberts 2006), temperate *B. regia* from the French Atlantic coast (Brahmi et al. 2010), and *L. pruvoti* from the Mediterranean Sea (Caroselli et al. 2012). Since the age–length relationships of *C. inornata* were homogeneous among sites, a general growth curve was obtained (Fig. 5) to describe the growth of individuals across the whole

Mediterranean latitudinal range of this species. It must be noted that the species range also extends to the Atlantic, where environmental conditions are very different and growth could respond differently to latitudinal gradients. Growth rates estimated in this study agree with the only previous study of growth in this species, from Spain (Teixidó et al. 2011). In the Mediterranean Sea, the latitudinal variation of temperature greatly influences the population characteristics of some scleractinian corals (Goffredo et al. 2008; Kružić et al. 2012; Airi et al. 2014; Caroselli et al. 2015b), even though some exceptions have been reported. Previous studies on solitary scleractinians living in the same sites and analyzed using the same methods as in the present study showed homogeneous growth for the non-zooxanthellate *L. pruvoti* along the same latitudinal gradient (Caroselli et al. 2012), while in the zooxanthellate *B. europaea*, k decreased and L_∞ increased with increasing temperature (Goffredo et al. 2008). The apparent insensitivity of the growth of *C. inornata* and *L. pruvoti* (i.e., homogeneous growth parameters) to SR and temperature variations along the latitudinal gradient may be explained by their biology and/ or ecological mechanisms: (1) the lack of photosynthetic

symbionts, which generally stimulate calcification and growth in zooxanthellate corals (Al-Horani 2005; Goffredo et al. 2009) and lower their photosynthetic efficiency when exposed to excessive temperature (Al-Horani 2005); (2) a wide range of optimal temperatures for calcification in this species; (3) synergies between 1 and 2; or (4) a notable adaptation capability of these species to environmental conditions. Assessment of demographic characteristics provided new insights into these hypotheses.

The lack of significant correlation between demographic parameters and DT was expected. Temperature is an important environmental parameter whose latitudinal variation influences the biometry, abundance, growth, and demography of some Mediterranean zooxanthellate corals (Goffredo et al. 2007, 2008, 2009), while the only asymbiotic scleractinian studied in the Mediterranean (*L. pruvoti*) seemed unaffected by temperature differences among sites (Caroselli et al. 2012). However, any comparison between *C. inornata* and *B. europaea* must be interpreted cautiously, since the two species were sampled at different depths ($\sim$14 and $\sim$6 m, respectively) that may be subjected to slightly different thermal regimes throughout the year. Calcification is depressed when temperature is outside of the species-specific optimal range (Howe and Marshall 2002). A recent study indicated that *C. inornata* calcification was unaffected by temperature differences along the same Mediterranean latitudinal gradient investigated in this study (Caroselli et al. unpublished). The calcification tolerance to a wide range of temperature as observed in the non-zooxanthellate *L. pruvoti* studied at the same sites (Caroselli et al. 2012) may be due to the absence of symbiotic zooxanthellae, which need appropriate temperatures for regular metabolism (Carricart-Ganivet et al. 2012). Supporting the possible high adaptation capability of *C. inornata* to latitudinal variation in temperature, the Caryophylliidae family (Dana 1846) is widespread from shallow (Cairns et al. 2005) to deep waters (Squires 1959), from coastal Antarctic (Cairns 1982) to the Arctic Circle (Roberts et al. 2003), and *Caryophyllia* is the most diverse genus within non-zooxanthellate scleractinians (Kitahara et al. 2010).

Unexpectedly, most of the parameters of this non-zooxanthellate species analyzed were significantly correlated with SR along the investigated Mediterranean latitudinal range. The stability of population structure (r^2 of Eq. 2), the instantaneous rate of mortality (Z), and the percentage of immature individuals decreased with increasing SR (southward) (Table 1). In addition, the average age of populations (from 4.6 yr for the northernmost site, GN, to 8.8 yr for the southernmost, PN), the mean age of biomass (from 6.7 at GN to 11.5 at PN), and the age at maximum biomass (from 5 yr at GN to 15 yr at PN) increased with increasing SR (Tables 1, 2). All these

correlations indicate that with increasing SR (southward), populations were less stable and presented deficits of young individuals. This trend strictly refers to the investigated latitudinal range in the Mediterranean Sea and cannot predict the response of Atlantic populations, which could be very different. Since this species is non-zooxanthellate, SR is likely to have no direct effect on the species, but the SR latitudinal gradient could be related to other abiotic and/or biotic parameters that were not investigated in this study. For example, plankton in seawater of the western Mediterranean Sea decreases moving southward (D'Ortenzio and Ribera d'Alcalà 2009). The wind effect, winter layers mixing, and coastal upwelling create a biomass gradient for phyto- and zooplankton from north to south along the western Italian coastline (D'Ortenzio and Ribera d'Alcalà 2009). Low presence of zooplankton may cause feeding deficits and reduced available energy for polyps (Coma and Ribes 2003; Leuzinger et al. 2012); thus, the observed deficit of immature individuals could be related to an energetic trade-off between growth and reproduction (Kozłowski and Wiegert 1986). The reduced stability and deficit of immature individuals in southern populations (high SR) could be explained through the allocation of energy to growth at the expense of reproduction. While there are few studies on energy allocation of shallow non-zooxanthellate corals under energetic deficit, there are several studies on zooxanthellate species. Tropical *Montipora digitata* subjected to low light regime (and thus energetic depletion) for 1 yr showed a reduced growth rate, while the energy allocation for reproduction increased at intermediate levels of resource availability, ceasing completely only at the lowest resource availability (Leuzinger et al. 2012). Populations of Mediterranean *B. europaea* showed reduced k growth constant with increasing temperature (Goffredo et al. 2008), probably due to the inhibition of photosynthesis by zooxanthellae, which reduced the availability of energy (Caroselli et al. 2015a). Growth rate decreased in populations of *Orbicella* sp. characterized by high temperatures (Carricart-Ganivet 2004), while species of *Porites* (Lough and Barnes 2000), *Acropora*, and *Pocillopora* (Crossland 1981) showed the opposite growth trend. *Caryophyllia inornata* growth parameters do not correlate with environmental gradients; thus, skeletal deposition seems unaffected by temperature and light regime, while reproduction could be affected. The species may reduce energetic investment in reproductive output in favor of growth as a response to the zooplankton deficit. This could explain the lack of immature corals in the southernmost populations, suggesting a correlation between SR and abundance along the investigated latitudinal gradient. However, a recent study at the same sites showed that population abundance was not correlated with SR (Caroselli et al. 2015b). This could depend on the lower

mortality rate (Z) in the southernmost populations; the deficit of young individuals could be counterbalanced by the decreasing morality rate, resulting in the observed homogeneous abundance across sites. As an alternative hypothesis, the deficit of immature individuals in southern populations of the Mediterranean Sea could be related to larval vicariance as a result of the marine flow that follows the western Italian coastline from south to north throughout the year (Istituto Idrografico della Marina 1982). The northern Italian populations may benefit from the flow of larvae from north-flowing currents, while southern populations cannot benefit from the same effect because they lie on the southern border of the species' distribution (Zibrowius 1980). However, the relevance of this effect also depends on the competency period of the planulae, which is affected by the reproductive mode. Brooding corals such as *C. inornata* (Goffredo et al. 2012a) tend to have larvae that rapidly reach competency relative to broadcast-spawning corals (Jackson 1986; Harrison and Wallace 1990; Goffredo and Zaccanti 2004). However, the larval traits of this species are not known, and further studies on larval behavior are needed to clarify whether larval vicariance could contribute to the observed deficit of young individuals in southern populations. In any case, these data must be interpreted cautiously because the mass mortality in the northwestern Mediterranean Sea in 2003 (Rodolfo-Metalpa et al. 2006) may have changed the abundance of northern populations and may have biased the analysis.

The demography of *C. inornata* populations showed the same tolerance to temperature recorded for the non-zooxanthellate solitary scleractinian *L. pruvoti* studied at the same sites (Goffredo et al. 2010; Caroselli et al. 2012). Even though *C. inornata* shares several biological features and a tolerance to temperature with *L. pruvoti*, at least at these sites, the trend of demographic parameters with SR differs between the two species. The deficit of immature *C. inornata* polyps with increasing SR may be related to reduced plankton availability, but it contrasts with the lack of trend with SR variations along the latitudinal gradient for *L. pruvoti* (Caroselli et al. 2012). The different responses of the two species and their different range of population density values (*C. inornata* has an abundance up to ten times lower than *L. pruvoti*) (Goffredo et al. 2007; Caroselli et al. 2015b) could be explained if *C. inornata* had a more specialist diet than *L. pruvoti*, resulting in lower availability of resources when zooplankton abundance is depleted. Unfortunately, the feeding strategies of the two species have not yet been investigated, and further analyses are needed to verify this hypothesis.

In conclusion, this research shows that the growth rate of *C. inornata* is homogeneous along a Mediterranean latitudinal gradient covering 2.4 °C of DT variation and 52 W m^{-2} of SR variation. In this latitudinal range, while population dynamics parameters are uncoupled with DT, they are strongly related to variation in SR, with populations becoming progressively less stable and with fewer young individuals with increasing SR (southward). The implications of SR for demography are attributed to indirect effects of zooplankton availability. Previous studies on Mediterranean solitary corals hypothesized that zooxanthellate species were more sensitive to high temperatures than non-zooxanthellate species. This work suggests that this may be the case for DT, but that non-zooxanthellate species may be negatively affected in their demography by the indirect effects of SR.

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