

Growth, population dynamics, and reproductive output model of the non-zooxanthellate temperate solitary coral *Caryophyllia inornata* (Scleractinia, Caryophylliidae)

Erik Caroselli,¹ Francesco Ricci,¹ Viviana Brambilla,¹ Chiara Marchini,¹ Giada Tortorelli,¹ Valentina Airi,¹ Guido Mattioli,² Oren Levy,³ Giuseppe Falini,⁴ Zvy Dubinsky,³ Stefano Goffredo^{1*}

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

²Operative Unit of Radiology and Diagnostics by Images, Hospital of Porretta Terme, Local Health Enterprise of Bologna, Porretta Terme, Italy

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

⁴Department of Chemistry “Giacomo Ciamician”, University of Bologna, Bologna, Italy

Abstract

Coral age can be strictly related to size, but processes like fragmentation, fusion, and partial colony mortality can decouple this relationship. When these phenomena are negligible, such as in solitary corals, age-based growth and population dynamics models can be used. In this study, the population size, structure, and growth rates of the temperate solitary coral *Caryophyllia inornata* were assessed at Elba Island (north-western Mediterranean Sea). Growth rate of this species decreased exponentially with age. The two growth curves estimated by field measurements and by growth band analysis provided homogeneous relationships between size and age. The decreasing number of individuals with age indicated a steady state population, with a turnover time of 4 yr and a maximum life span of 22 yr. Maximum biomass yield and most reproductive output was by individuals of 8–15 yr age classes. The life strategy was characterized by high fecundity, continuous embryo production, high larval output, and high larval mortality.

Investigations of scleractinian population dynamics began about 45 yr ago (Connell 1973). Since then, the knowledge has been extended through studies performed all around the world (e.g., Grigg 1977; Chadwick-Furman et al. 2000; Lins de Barros and Pires 2006; Nozawa et al. 2008; Caroselli et al. 2016a).

The demography of coral populations may reveal their health status and provide information to assess habitat stability and suitability (Grigg 1977; Meesters et al. 2001; Guzner et al. 2007; Caroselli et al. 2012b). Knowledge about population turnover and age of maximum biomass yield can be useful for reef restoration and conservation actions (Hughes 1984; Hughes and Connell 1987; Chadwick-Furman et al. 2000; Epstein et al. 2001; Goffredo and Lasker 2008; Vardi et al. 2012; Hernandez-Delgado et al. 2014). Demographic data obtained through growth and population dynamics models can benefit from reproductive data, which

are useful to assess the life strategy, reproductive success and colonization potential of corals (Santangelo et al. 2004; Goffredo et al. 2008, 2010). Furthermore, demographic traits may help to understand the complex relationships between organisms and their environment (Grigg 1984; Chadwick-Furman et al. 2000; Meesters et al. 2001; Goffredo et al. 2010; Caroselli et al. 2012b). Scleractinian species are sensitive to environmental conditions (Lough and Barnes 2000; Goffredo et al. 2008; Rodolfo-Metalpa et al. 2008; Caroselli et al. 2015) such as temperature (Goffredo et al. 2007, 2008; Kružić et al. 2012), light (Rodolfo-Metalpa et al. 2008), water flow (Purser et al. 2010), nutrients (Muscatine et al. 1989; Orejas et al. 2011), waves (Lasker 1990), substrate slope and structure (Vertino et al. 2010), and pH (Goffredo et al. 2014; Fantazzini et al. 2015).

The skeletons of some gorgonians and many colonial and solitary scleractinians record one high density and one low density growth band each year, which can be used to determine their age (Dodge et al. 1974; Chadwick-Furman et al. 2000; Goffredo and Lasker 2008; Goffredo et al. 2008, 2010; Caroselli et al. 2012b, 2016a). The assessment of individual age is useful for analyses of linear growth rate (Dodge et al.

*Correspondence: s.goffredo@unibo.it

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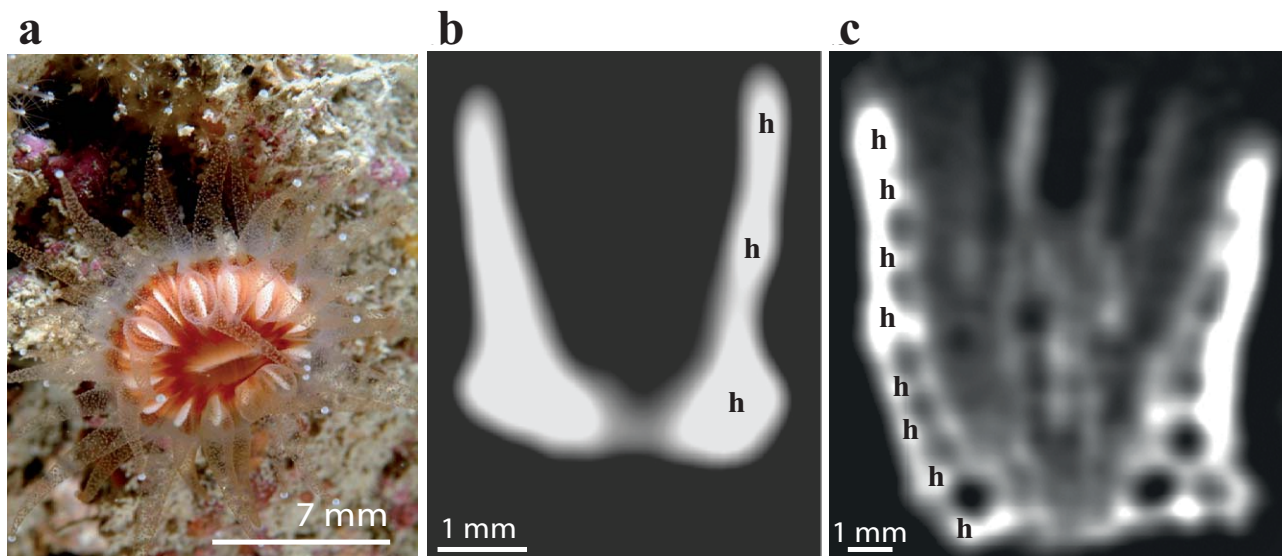


Fig. 1. *Caryophyllia inornata*. (a) Living specimen, (b) computerized tomography (CT) scan of a juvenile coral (3 yr); (c) CT scan of a mature coral (8 yr). h: high-density bands.

1974; Hudson 1981; Peirano et al. 1999), net calcification rate (Tanzil et al. 2009; Carricart-Ganivet et al. 2012; Caroselli et al. 2016b), and population dynamics (Grigg 1984; Chadwick-Furman et al. 2000; Goffredo et al. 2010; Caroselli et al. 2012b, 2016a). By integrating the above information with environmental data (Carricart-Ganivet 2004; Goffredo et al. 2008, 2009; Caroselli et al. 2012a, 2016a), it is possible to project future trends of coral populations in relation to environmental change (Cooper et al. 2008; Cantin et al. 2010; Caroselli et al. 2015, 2016b).

To apply some population dynamic models, an age-size relationship is needed (Beverton and Holt 1956; Madin et al. 2012). In certain forms of solitary and colonial corals this relationship can be determined by comparing their size and annual skeletal growth bands, which may be counted through computerized tomography (CT) scans (Grigg 1984; Chadwick-Furman et al. 2000; Goffredo et al. 2004, 2008, 2010; Goffredo and Lasker 2008; Lough 2008; Caroselli et al. 2012b, 2016a,b). Other solitary corals have external growth bands, which can be counted to estimate their age (Chadwick-Furman et al. 2000; Goffredo and Chadwick-Furman 2003). In species where processes that decouple individual age and size (i.e., fragmentation, fusion or partial colony mortality) do not occur, age-based growth and population dynamics models can be used (Hughes and Jackson 1985; Babcock 1991; Madin et al. 2012).

The present study focused on the non-zooxanthellate solitary scleractinian *Caryophyllia inornata* (Duncan, 1878), which lives in the Mediterranean Sea and North-Eastern Atlantic Ocean, from the United Kingdom to the Azores Islands, up to 100 m depth (Zibrowius 1980). *C. inornata* lives on shaded hard substrata such as walls and vaults of

caves, crevices and sometimes the shaded portion of wrecks (Zibrowius 1980; Caroselli et al. 2015). The polyps of this species are gonochoric and brooding. Females, males, and sexually inactive polyps unusually and continuously produce apparently agamic embryos (Goffredo et al. 2012a; Marchini et al. 2015). The growth, net calcification rate, and demography of this species seem unaffected by temperature in the Mediterranean Sea, while populations are less stable and present deficits of young individuals with increasing solar radiation, possibly in relation to the associated decrease in plankton availability (Caroselli et al. 2015, 2016a,b).

This study aimed to: (1) assess if the growth bands of *C. inornata* are representative of field growth patterns; (2) assess the sexual reproductive output and larval mortality of this species at Elba Island; (3) compare the life history traits of this species with other co-located corals.

Materials

Field measurements

The studied population of *C. inornata* (Fig. 1a) was located at Elba Island (Italy, Tyrrhenian Sea, NW Mediterranean, 42°45' N, 10°24' E). Twenty individuals of *C. inornata* of different size (covering the whole range of observed coral size) were haphazardly selected and marked in situ by numbered plastic tags glued to the substratum (under the wings of a sunken plane wreck). Their growth rate was measured from December 2010 to November 2012. The length (L : maximum axis of oral disk) of each marked polyp was measured in situ with calipers (± 0.5 mm) every 8 months for 0.7–2 yr (Table 1). Length was selected as the primary biometric parameter because it has the best fit to dry skeletal mass (Caroselli et al. 2015) and is used in all previous studies on this species

Table 1. Number of *Caryophyllia inornata* polyps in each size class that were measured in the field for the indicated time interval.

Size class (mm)	Duration of field measurement (months)			Total
	7–9	16–18	22–24	
0–4	1	1	1	3
4–8	4	1	6	11
8–12	1	/	5	6
Total	6	2	12	20

(Goffredo et al. 2012a; Caroselli et al. 2015, 2016a,b; Marchini et al. 2015). The period of measurements varied among individuals because some specimens died and were replaced (total loss = 10 individuals of different size). Each dead specimen was replaced with the closest coral of similar size. For each coral, an average growth rate representing the growth during the entire observation period was estimated. Growth rates were normalized to 1 yr.

Temperature (°C) at the sampling depth was recorded during the entire experimental period by three digital thermometers (i-Button, DS1921G-F5#, Maxim Integrated Products, Dallas Semiconductors) placed at the experimental site, which recorded seawater temperature every 2 h. Thermometers were replaced every 8 months to avoid problems of encrustation and overgrowth by marine organisms.

Coral collection

Samples were collected on 14th May 2009 in the same site of field measurement. All samples present (241 specimens) in four haphazardly placed quadrats of 0.01 m² each, arranged in a line crossing both wing tips of the plane wreck and at ~3 m distance, were collected at 13 m depth, where high population abundance is reported (Caroselli et al. 2015) and where previous studies on the reproduction of *C. inornata* have been performed (Goffredo et al. 2012a; Marchini et al. 2015).

Sample analysis

Coral tissue was totally removed by immersing the samples in a 10% solution of commercial bleach for 3 d (Caroselli et al. 2011). Specimens were dried in an oven 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), which is under investigation using these samples in diffractometric analyses (Goffredo et al. 2012b). The biometric measurements of polyp length (L : maximum axis of the oral disc) were performed with a Vernier caliper (Metrica, Milano, Italy). The dry skeletal mass (M) was measured with a digital precision balance.

A subset of 38 specimens of different size was randomly selected from the 241 collected corals, and each sample was dated by counting the growth bands on scans obtained by CT (Fig. 1b,c). This is based on the fact that some scleractinians (e.g., temperate corals) record in their skeletons one low-density band in summer and one high-density band in winter (Dodge et al. 1974; Goffredo et al. 2004, 2008, 2010; Peirano et al. 2005; Caroselli et al. 2012b, 2016a,b).

Growth and population dynamics

Growth rates were directly measured in the field, assessed by CT scan analysis and were fitted to the von Bertalanffy growth function (von Bertalanffy 1938):

$$L_t = L_\infty \cdot (1 - e^{-kt}) \quad (1)$$

Where: L_t = individual length at age t ; L_∞ = asymptotic length (maximum expected length in the population); k = growth constant (higher for a faster growth, smaller for a slower one); t = individual age. The parameters L_∞ and k from field measurements were determined by applying the “Gulland and Holt plot” (Pauly 1984; Sparre et al. 1989; Goffredo et al. 2004, 2010). For the samples dated through CT scans, L_∞ and k , including their confidence interval, were calculated by a least squares method using the software MATLAB R2012a (Caroselli et al. 2016a), whose fitting properties are higher (Sparre and Venema 1998) than traditional methods (e.g., Pauly 1984).

The obtained von Bertalanffy age-length function (Eq. 1) was used to estimate the age of collected samples for which CT scans were not performed, in order to reconstruct the population age structure. The regression analysis of population age-frequency distribution allows us to estimate the number of individuals at age zero (N_0), the population structure stability (R^2), and the instantaneous rate of mortality (Z). The turnover time (i.e., mean life span) was obtained as Z^{-1} (Pauly 1984; Goffredo and Chadwick-Furman 2003; Goffredo et al. 2004, 2010; Caroselli et al. 2012a). The survivorship curve, expressing the reduction in coral number over time, was calculated by the equation:

$$N_t = N_0 e^{-Zt} \quad (2)$$

where N_t is the number of individuals at age t , and t is the individual age measured in years. Based on the survival curve, maximum life span was defined as the age at which <0.5% of the population was still surviving (Sparre et al. 1989; Goffredo and Chadwick-Furman 2003; Goffredo et al. 2004, 2010; Caroselli et al. 2012a, 2016b).

The dry skeletal mass growth curve was estimated by applying to Eq. 1 the relationship between length and mass derived from a previous study on the biometry of *C. inornata* (Caroselli et al. 2015):

$$M = 0.001L^{2.915} \quad (3)$$

The Beverton and Holt model (Beverton and Holt 1956) provides coral dry skeletal mass for each cohort yield (i.e., cohort yield = dry skeletal mass \times survivorship; see Grigg 1984; Chadwick-Furman et al. 2000; Goffredo and Chadwick-Furman 2003; Goffredo et al. 2004, 2010). Thus, the age at maximum biomass was determined to assess the threshold after which population biomass losses due to mortality prevail on biomass gains due to growth.

Reproductive parameters

The reproductive parameters were estimated only for females, assuming that each mature oocyte will result in a larva (planula), as in previous analyses on other Mediterranean species (Goffredo et al. 2010; Gizzi et al. 2014). Even though male and sexually inactive individuals of this species display an unusual embryo production (Goffredo et al. 2012a; Marchini et al. 2015), they were excluded by the analysis because the timing of their embryogenetic cycle is unknown.

Sex ratio, size at sexual maturity, average fecundity (number of planulae per unit polyp volume), and percentage of mature polyps in each age class were derived from previous studies (Marchini et al. 2015). The number of planulae of sexual origin released by each age class of females (biXi) was estimated by multiplying: fecundity (bi), number of individuals (Xi), female sex ratio (SR), and percentage of mature polyps (Fi).

Statistical analysis

To test the significance of growth rate differences among size classes, the non-parametric Kruskal–Wallis test was run (Kruskal and Wallis 1952) because data were not normally distributed. The test was computed using IBM SPSS Statistics 22.

Results

Growth rate and lifetime growth curve

Polyp growth rates measured in the field were plotted against polyp length according to the Gulland and Holt plot method (Fig. 2; Pauly 1984; Sparre et al. 1989). Growth rate decreased with age as a function of coral length (annual growth rate = $-0.156 \times L + 1.654$). Field measurements indicated that on average, individuals of 0–4 mm in length grew 0.9 mm yr^{-1} (SE = 0.4; $n = 3$), 4–8 mm individuals grew 0.7 mm yr^{-1} (SE = 0.2; $n = 11$) and 8–12 mm individuals dropped to 0.2 mm yr^{-1} (SE = 0.1; $n = 6$). Length explained 37.5% of growth rate variance (Fig. 2) and growth rates were significantly different among size classes (Kruskal Wallis test, $df = 2$, $p < 0.05$). Within size classes, individual growth rates were markedly variable (coefficient of variation = 0.7–1.8). The population growth parameters estimated by field measurements were a growth constant $k = 0.156$ (95% CI = 0.056–0.256) and an asymptotic length $L_\infty = 10.6 \text{ mm}$ (95%

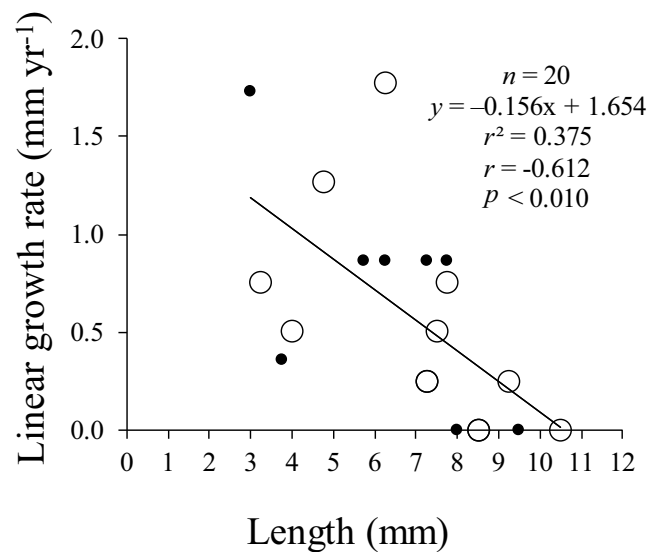


Fig. 2. *Caryophyllia inornata*. Variation in polyp linear growth rate from field measurements, corresponding to the Gulland and Holt plot used to estimate the parameters K and L_∞ of the von Bertalanffy growth function. Each data point represents a separate individual. White circles indicate the 12 corals that were measured for 2 full years (only 10 are visible because two pairs of points are overlapped). Black circles indicate the eight corals that were not measured for a full year or 2 full years. The indicated values and equation were calculated using the whole dataset of 20 samples.

CI = 9.2–16.8). Using only the 12 corals that were measured for 22–24 months, remarkably similar growth parameters were obtained, which fell well within the CI of those derived using the whole dataset of 20 corals ($k = 0.144$; $L_\infty = 10.7 \text{ mm}$).

The population growth parameters derived by CT scans were a growth constant $k = 0.042$ (95% CI = 0.017–0.066) and an asymptotic length $L_\infty = 22.5 \text{ mm}$ (95% CI = 12.1–32.9; Fig. 3). Thus, the von Bertalanffy growth functions obtained by field measurements and by CT scans provided similar predicted sizes per ages, since the confidence intervals of their k and L_∞ were overlapped. By applying Eq. 3 to the age-length growth curve by CT scans, a mass-length growth curve was obtained (Fig. 3), with an estimated asymptotic individual mass in the population of $M_\infty = 8.7 \text{ g}$.

Population age structure and survivorship

Converting from a size-frequency to an age-frequency distribution, the observed population mainly was dominated by young individuals (Fig. 4a). Sixty one percent of individuals belonged to age classes that had not reached sexual maturity, which was at 8 yr and corresponded to $\sim 6.1 \text{ mm}$ (Marchini et al. 2015). Despite the majority of individuals falling into immature age classes, population biomass was concentrated in sexually mature age classes (Fig. 4b). In fact, the percentage of biomass up to 8 yr old was only 18%, while observed biomass was maximum at 12 yr (Fig. 4b). The

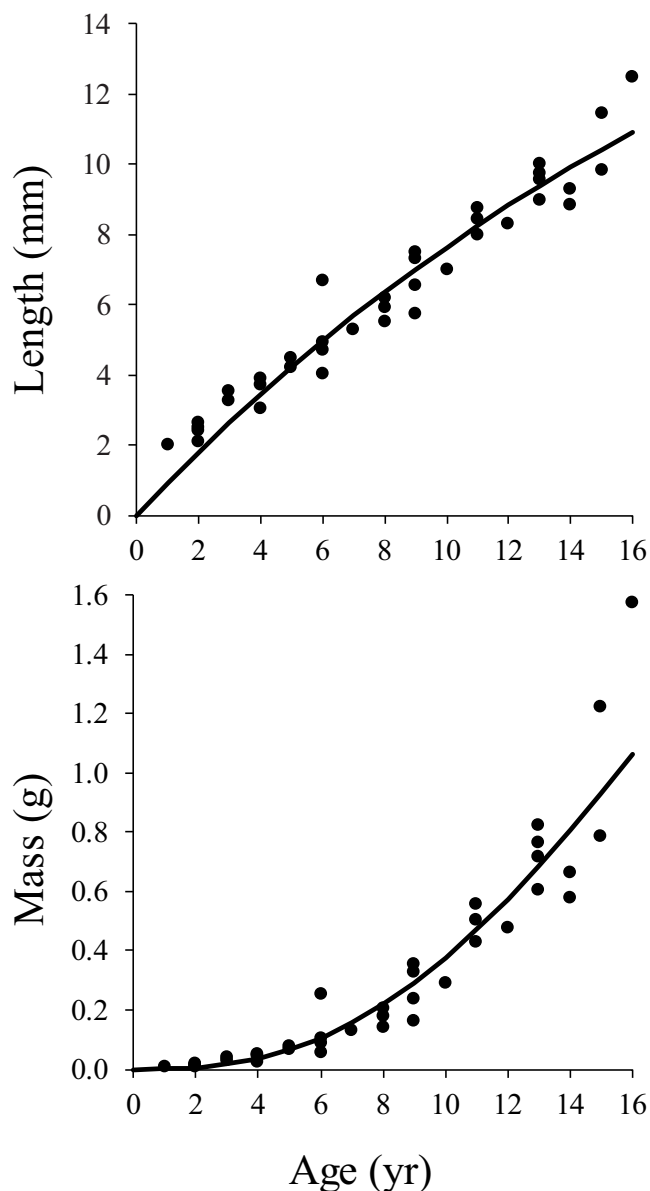


Fig. 3. *Caryophyllia inornata*. Age-length von Bertalanffy growth curve of individuals and age-specific growth curve of individual skeletal mass. Dots are length and mass data of individuals dated through CT scans.

largest observed individual was 12.5 mm in length and was estimated as 19 yr old.

The observed age-frequency distribution allowed us to estimate population parameters and provided the instantaneous rate of mortality ($Z = 0.241 \text{ yr}^{-1}$) and population structure stability ($df = 11$, $R^2 = 0.777$, $p < 0.001$). Maximum life span was 22 yr, based on the estimated survival curve derived by Eq. 2 (Fig. 4c).

The age-specific growth and survival curves were used to estimate the theoretical biomass distribution of *C. inornata* individuals at Elba Island. The estimated biomass

distribution was maximum at 10 yr (Fig. 4b). At older ages, losses of biomass due to mortality overtook the gains due to individual growth.

Life table

Based on the population reconstructed through the Beverton and Holt model (Beverton and Holt 1956), female polyps released 9.58×10^6 larvae m^{-2} during 1 yr (Supporting Information Table 1). Fifteen percent (95% CI = 7–29%) of the population reached the age of sexual maturity. Most reproductive output (74%) came from corals 8–15 yr old (Supporting Information Table 1). Older polyps (> 15 yr) represented only a small fraction (12%) of the reproductive population, and thus contributed a smaller percentage (26%) to reproductive output. Assuming local recruitment, larval mortality of sexually originated planulae released by female polyps was estimated as 99.97% (95% CI = 99.58–99.996%; Supporting Information Table 1). The number of planulae needed for 1 recruit was 3188 (95% CI = 239–23033), and for 1 reproductive polyp was 21921 (95% CI = 3269–79593; Supporting Information Table 1).

Discussion

The study site at Elba Island is characterized by remarkable thermal differences among seasons. Mean seasonal temperature at the sampling depth spans 5.6°C (mean winter/spring temperature = 14.3°C, 11.8°C to 18.7°C; mean summer/fall temperature 19.9°C, 15.6°C to 22.8°C). Therefore, for a reliable analysis, field measurements were performed throughout the year to include the whole range of differential seasonal growth rates. The measurement of annual growth rate is necessary to determine the applicability of von Bertalanffy growth model, which requires a negative exponential growth rate with increasing age (von Bertalanffy 1938; Pauly 1984; Sparre et al. 1989). Decreasing growth rate with age observed in the solitary coral *C. inornata* is similar to the growth pattern of other co-located solitary scleractinians in the Mediterranean Sea, such as *Balanophyllia europaea* (Goffredo et al. 2004, 2008) and *Leptopsammia pruvoti* (Goffredo et al. 2010; Caroselli et al. 2012b). Differential growth due to seasonal variations could be problematic when growth rate is normalized to 1 yr. However, only a few polyps were measured for less than 1 yr, thus this bias is limited in this study (Table 1). Moreover, the values of k and L_∞ obtained using the whole dataset were remarkably similar to those obtained using only the corals that were monitored for 22–24 months, thus indicating that the biases spread over different seasons and tend to balance each other. The wide variation in individual growth rate likely was due in part to the small sample size, which was only $n = 3$ for the smallest size class (0–4 mm), and was not large for all size classes put together ($n = 20$; Fig. 2). More accurate growth rates would be obtained if a study with a larger sample size were conducted. In *C. inornata*, the reliability of growth analysis

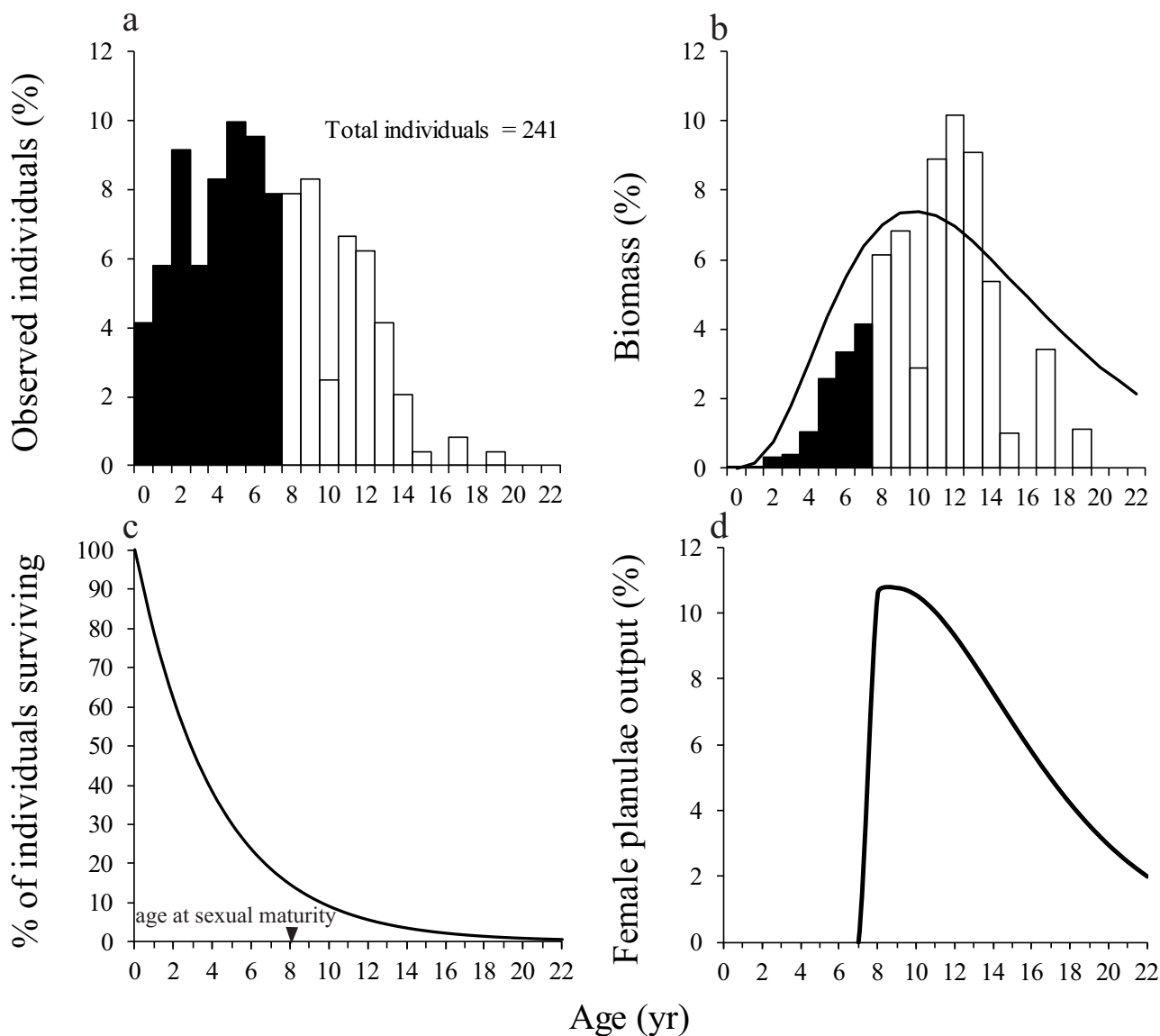


Fig. 4. *Caryophyllia inornata*. (a) Age class distribution in terms of number of individuals. Total sampled area = 0.04 m². (b) Observed dry mass (bars) and dry biomass curve (line). (c) Survivorship. (d) Female planulae output. Black bars indicate sexually immature age classes (Marchini et al. 2015).

through CT scans was confirmed by field measurements, because the two derived growth curves were highly similar and provided comparable predicted size and mass at a certain age. Also this result is in line with all other solitary Mediterranean corals for which field and CT growth curves were compared (Goffredo et al. 2004, 2010), confirming that CT scans are useful to assess coral growth without costly field measurements for a long time. The decreasing growth rate with age in *C. inornata* is an example of determinate growth (Sebens 1987), which is typical of some colonial octocorals (Goffredo and Lasker 2008), colonial scleractinians (Grigg and Maragos 1974; Johnson 1992; Sakai 1998),

and solitary scleractinian corals (Gerrodette 1979; Yamashiro and Nishira 1998; Chadwick-Furman et al. 2000; Goffredo et al. 2008, 2010; Knittweis et al. 2009; Hamel et al. 2010; Caroselli et al. 2012b, 2016a,b). Determinate growth is a genetically controlled feature affected by environmental conditions (Sebens 1987), allowing the coral to allocate energetic resources to processes other than growth, such as reproduction. An unusual behavior occurs in the first years of sexual maturity (> 8 yr) of this population: growth decreased but continued at a remarkable rate, until it dropped to a very low rate in polyps > 10 yr. Thus, even though sexually mature corals still invest energetic resources

to increase their size, the reproduction effort is enough to sustain the population, whose 82% of biomass (39% of individuals) is represented by sexually mature individuals.

A theoretical population in steady state (i.e., no age cohort missing or over-represented in response to disturbance events; Grigg 1984) age explains 100% of the variance of age class frequency and the R^2 of the natural logarithm of the number of individuals against their corresponding age is equal to unity. Populations that deviate from steady state will have reduced R^2 values (Sparre et al. 1989; Goffredo et al. 2004; Caroselli et al. 2012b, 2016a). The stability value for the Elba population of *C. inornata* ($R^2 = 0.777$) is within the range of other populations of solitary corals for which a steady state has been assumed, such as *B. europaea* ($R^2 = 0.935$, Goffredo et al. 2004) and *L. pruvoti* ($R^2 = 0.839$; Goffredo et al. 2010) in the NW Mediterranean and mushroom corals in the Red Sea ($R^2 = 0.725$ – 0.986 ; Goffredo and Chadwick-Furman 2003). The Elba population is thus characterized by exceptionally high abundance (Caroselli et al. 2015) and high population structure stability. With increasing age, the age classes after 5 yr (corresponding to ~ 4 mm in length) showed an exponential decrease in their frequency (Fig. 4a). Age classes < 5 yr were under-represented, which is typical for field sampling due to the difficulty in observing the smallest corals during diving (Grigg 1984; Babcock 1991; Goffredo and Chadwick-Furman 2003; Goffredo et al. 2008; Caroselli et al. 2012b, 2016a,b).

Past studies on the unusual reproductive biology of *C. inornata* (i.e., both sexual reproduction and continuous production of apparently agamic embryos in females, males, and sexually inactive individuals; Goffredo et al. 2012a; Marchini et al. 2015) enabled us to reconstruct a life table summarizing the principal demographic and reproductive parameters of this population. The estimated number of released planulae ($9.58 \times 10^6 \text{ m}^{-2} \text{ yr}^{-1}$) was higher than for other co-located solitary corals (i.e., *L. pruvoti* and *B. europaea* at Calafuria, Italy; Goffredo et al. 2010; Gizzi et al. 2014). This result might depend on the life strategy of this species, characterized by high reproductive potential (Supporting Information Table 1; Marchini et al. 2015). Assuming local recruitment and given the ratio between larval output and recruit abundance, a larval mortality of 99.97% was estimated. This value is likely underestimated, because some recruits in the population may result from embryos asexually produced by male and sexually inactive polyps. Only 1 in 3188 released planulae successfully settled, and 21921 planulae were required to obtain 1 reproductive individual. Other Mediterranean coral species whose recruitment has been studied are the scleractinians *L. pruvoti* (Goffredo et al. 2010), *B. europaea* (Gizzi et al. 2014), and the octocoral *Corallium rubrum* (Santangelo et al. 2004), all with lower larval mortality compared to *C. inornata* (97.7%, 98.6%, and 94.6%, respectively). The four species are co-located, colonize hard substrates, and share part of their depth

distribution. However, while *B. europaea* is zooxanthellate and lives in open habitats, *C. inornata*, *L. pruvoti*, and *C. rubrum* dwell in the dark and are frequently found in the same coralligenous crevices and caves where their bathymetric distribution overlaps (10–60 m depth, Zibrowius 1980; Teixido et al. 2011).

Most reproductive output was by individuals of 8–15 yr (74% planulae production; Fig. 4d), which belong to the age classes of maximum biomass (observed peak of biomass at 12 yr, estimated peak of biomass at 10 yr; Fig. 4b). This means that in the population, the same age classes were characterized by high reproductive output and maximum biomass production (Fig. 4b–d), while usually the energetic trade-off between growth and reproduction results in an age of maximum reproductive output that is older than the biomass peak. For instance, *L. pruvoti* reaches the biomass peak at 4 yr and most reproductive output is by corals 4–8 yr of age (Goffredo et al. 2010). Similarly, *B. europaea* reaches the biomass peak at 6 yr and most reproductive output is at 7 yr (Goffredo et al. 2004; Gizzi et al. 2014). Coincidence between age classes of maximum biomass and higher reproductive output might be due to the environmental conditions that characterize this site (i.e., absence of trophic competitors and artificial substratum), which could be optimal for *C. inornata* survival. The Elba Island population is the most abundant among those investigated (Caroselli et al. 2015). Moreover, southern populations show a lack of young individuals (possibly due to lower energetic resources from zooplankton, which is less abundant) while northern ones show lack of old individuals when compared with Elba (Caroselli et al. 2016b). The lack of old individuals in northern populations may be due to recent mass mortality events of benthic suspension feeders in the NW Mediterranean, caused by warming-enhanced stratification of seawater coupled with lower zooplankton availability in summer, which consequently decrease available energy for affected taxa (Coma et al. 2009).

It must be noted that the population sampled in this study was located on an artificial substratum and no other trophic competitors were present, resulting in an exceptional abundance relative to populations on natural substratum (Caroselli et al. 2015). Larval production and recruit number are expected to be lower on natural substrata, thus any comparison with other species requires caution. The planulae high mortality rate could be due to a reproductive strategy based on high production of inefficient larvae. To estimate the actual rate of self-recruitment (settlement at natal site), population genetics studies are needed and currently lacking. However, self-recruitment is likely, because the high larval mortality of *C. inornata* might be offset by planulae being heterotrophic and brooding (i.e., quickly settling; Jackson 1986; Harrison and Wallace 1990; Goffredo and Zaccanti 2004; Baird et al. 2009).

This study extended the knowledge about *C. inornata*. The analysis of its ecological role and comparison with co-located species was possible by merging data about reproduction (Goffredo et al. 2012a; Marchini et al. 2015) with models of growth and population dynamics (von Bertalanffy 1938; Pauly 1984; Sparre et al. 1989). In summary, results indicate that: (1) skeletal growth bands of *C. inornata* reflect field growth patterns; (2) sexual reproductive output was 9.58×10^6 planulae $m^{-2} yr^{-1}$ with an estimated larval mortality of 99.97%; (3) the obtained value of larval mortality is higher than in other co-located scleractinians and octocorals for which similar analyses were performed. The investigated site at Elba Island seems characterized by optimal environmental condition for this species, as suggested by remarkable abundance and high planulae output. High reproductive potential may be a characteristic of *C. inornata* that provides an advantage during interspecific spatial competition. Further analysis of the embryogenesis, larval features, and genetic structure of populations of this species could clarify the dispersal potential and rate of self-recruitment.

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Conflict of Interest

None declared.

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