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Growth and population dynamic model for the non-zooxanthellate temperate solitary coral *Leptopsammia pruvoti* (Scleractinia, Dendrophylliidae)

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Abstract In corals where complex life history processes decoupling age from size (e.g., fragmentation, fusion, partial colony mortality) are rare or clearly detectable, individual age may be determined from size, and age-based growth and population dynamic models may be applied. One example is the solitary Mediterranean coral *Leptopsammia pruvoti* Lacaze-Duthiers 1897, whose population size and structure, and growth rates were determined at Calafuria (43°28′N and 10°20′E), Ligurian Sea, from December 2007 to June 2009. Growth rate decreased with increasing size. The growth curve derived from field measurements confirmed the one obtained by growth band analysis. The frequency of individuals decreased exponentially with age, indicating a steady state population. Turnover time was 2.3 years. Maximum life span was 13 years. Most reproductive output was from intermediate age classes (6 years), while older individuals (>7 years), although having higher fecundity, were rare and accounted for a minority of population reproductive output. In comparison with other solitary dendrophylliids, *L. pruvoti* life strategy was characterized by a reproduction with *r*-strategy correlates (high fecundity, short embryo incubation, small planula size, fast achievement of sexual maturity), and a rate of demographic renewal occurring halfway along the *r*–*K* continuum (intermediate turnover time and maximum longevity).

Introduction

Demographic analysis of coral populations may reveal the extent to which they are under stress and is especially useful when anthropogenic activities disturb reefs and threaten the viability of coral populations (Grigg 1984; Guzner et al. 2007). In addition, the development of restoration strategies for damaged or degraded coastal areas requires information on population turnover (Chadwick-Furman et al. 2000; Epstein et al. 2001; Goffredo and Chadwick-Furman 2003).

Studies that quantify life history parameters of scleractinian corals are few, partly because of the processes of fragmentation, fusion and partial colony mortality, which cause corals of similar size to be of widely different ages, thus distorting the age-size relationships (Hughes and Jackson 1985; Babcock 1991). The scarce studies on population dynamics of scleractinian corals were reviewed around 35 years ago, describing their growth and survivorship (Connell 1973). Since then, demographic processes have been described for some species in the Southwestern Atlantic (Lins de Barros and Pires 2006), Pacific (Nozawa et al. 2008), Red Sea, Caribbean, Great Barrier Reef, and the Mediterranean (Goffredo et al. 2008 and references therein). The growth of modular individuals can be modeled through the replication, growth and death of the modules (Harper 1977), and studies of modular growth

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have often focused on plasticity of form and the complexity of both individual colony growth and population dynamics of modular organisms (Hughes and Jackson 1985; Hughes 1989; Babcock 1991). Due to this complexity, an analysis of 13 Caribbean coral species used a size-based, rather than age-based, assessment of population structure (Meesters et al. 2001), and recently new size-structured models for coral growth and population dynamics have been proposed (Artzy-Randrup et al. 2007).

In species in which fragmentation or fusion of individuals are rare, and partial mortality can be recognized by anomalies in the regular growth pattern, coral age can be determined (Babcock 1991; Chadwick-Furman et al. 2000). The growth and dynamics of some modular organisms can be examined using age-based models applied to colony morphology (Grigg 1977, 1984; Goffredo and Lasker 2006). In addition, in some solitary corals, age estimates may be easily obtained from externally visible growth bands (Chadwick-Furman et al. 2000; Goffredo and Chadwick-Furman 2003). Growth band analysis has been widely used to determine the age of colonial scleractinian and gorgonian corals (Knuston et al. 1972; Logan and Anderson 1991; Goffredo and Lasker 2006). Thus, growth and population dynamic models based on age can be applied to certain coral species to describe demographic characteristics (Grigg 1984; Ross 1984; Chadwick-Furman et al. 2000; Goffredo and Chadwick-Furman 2003). Recently, an age-based Beverton–Holt model provided an adaptive management approach for regulating an octocoral fishery for bioactive compounds in the Bahamas, avoiding long-term characterization of population dynamics which is rarely feasible (Goffredo and Lasker 2008).

The solitary coral considered in the present study is typical of species where age-based models can be easily applied. *Leptopsammia pruvoti* is an ahermatypic, non-zooxanthellate and solitary scleractinian coral, which is distributed in the Mediterranean basin and along the European Atlantic coast from Portugal to Southern England and Ireland (Zibrowius 1980). It is one of the most common organisms in semi-enclosed rocky habitats, under overhangs, in caverns and small crevices at 0–70 m depth, with mean abundances of $>10^4$ individuals m^{-2}, i.e., >2 kg m^{-2} of $CaCO_3$ biomass (Goffredo et al. 2007). The biometry (skeletal density, corallite length, width and height) of individuals and their abundance are not affected by sea surface temperature and solar radiation along an 850-km latitudinal gradient in western Italian coasts (Goffredo et al. 2007). It is a gonochoric internal brooder (Goffredo et al. 2006). When released, the planulae (695–1,595 μm in length) are ready to settle and swim by ciliary movement for 1–20 days (Goffredo et al. 2005). Evidence of asexual reproduction (either through polyp budding, fission or asexual production of planulae) has not been observed (Goffredo et al. 2006, and references therein). Its genetic structure is characterized by heterozygote deficits at all scales, from patch to populations, with no significant correlation between genetic differentiation and geographic distance (Goffredo et al. 2009). Its yellow color and high abundance make this species attractive to recreational divers, who represent an important income for coastal tourist resorts in the Mediterranean (Mundet and Ribera 2001).

The purpose of this study is to describe the population dynamics of *L. pruvoti* in the Eastern Ligurian Sea, by applying the Beverton and Holt population dynamic model based on age (Beverton and Holt 1957; Chadwick-Furman et al. 2000; Goffredo and Lasker 2008). This report completes the description of life history strategy of this temperate coral in the Mediterranean Sea, together with previous studies on reproductive biology, environmental correlates of demographic characteristics and genetic differentiation (Goffredo et al. 2005, 2006, 2007, 2009). Previously obtained data on size structure and reproduction of this species (Goffredo et al. 2006, 2007) are merged with the present data for estimating population reproductive output and larval mortality. The questions addressed in this study are as follows: (1) Do the growth bands of *L. pruvoti* reflect the growth pattern in the field? (2) What is the growth rate, age structure, mortality rate, turnover time, maximum life span, yield, reproductive output and larval mortality of this species at Calafuria? (3) How is the population abundance, maximum coral size, turnover time, maximum longevity, fecundity, period of embryo incubation, planula size and dispersal mode, individual size and age at sexual maturity of this species compared to other related corals? While growth band analysis integrates information on growth throughout the life of individuals (several years), field growth analysis may be influenced by the particular environmental conditions during the measurement period. Question number 1 is then particularly important to check if the two methods give comparable results (i.e., if the environmental conditions at the time of field measurement reflect the ones in the previous years), given their different accuracy (Campana 2001).

Materials and methods

The study population of *Leptopsammia pruvoti* was located off the coast of Calafuria (10 km south of Livorno, Italy, Eastern Ligurian Sea, NW Mediterranean, 43°28′N, 10°20′E; see Goffredo et al. 2004 for description of study site). The growth rate of 38 individuals of *L. pruvoti*, marked in situ by numbered plastic tags nailed to the rock, at 16-m depth, was measured from December 2007 to June 2009. The length (*L*: maximum diameter of the oral disk) of each marked polyp was measured in situ with calipers (±0.5 mm) every 3 mo for 0.2–1.5 years (average 1 year). The period of measurement varied among individuals because corals that died (8 during the whole study, of different size) were replaced by others of similar size during the study. Corals were sampled at depths known to have high population abundance and at the same depth as that of previous studies on the reproduction, biometry and population abundance of this species (Goffredo et al. 2005, 2006, 2007). Three digital thermometers (i-Button DS1921L-F52, Maxim Integrated Products, Dallas Semiconductors) were placed in the experimental field to record seawater temperature at 2-h intervals during the study period. Thermometers were replaced every 3 mo to download data and avoid problems of encrustation and overgrowth by marine organisms.

To obtain an additional measure of the relationship between polyp size and age, for comparison with that obtained from field measurements of growth rates, the number of annual growth bands on selected individuals was counted by means of computerized tomography (CT, after Logan and Anderson 1991; Goffredo et al. 2004, 2008). Each CT scan was 1 mm thick and had a resolution of 13,000 dpi. Specimens used in CT measurements ($n = 29$) were collected at Calafuria at 16-m depth near the individuals that were marked for in situ growth measurements. Coral length and dry skeletal mass (M) were measured (Goffredo et al. 2007), and age was determined from growth band counts, based on the pattern in temperate and semi-temperate corals of deposition of two bands per year, a high-density band in winter and a low-density band in summer (Peirano et al. 1999; Goffredo et al. 2004, 2008; Goffredo and Lasker 2006, 2008).

Growth rates based on both the size–age data from CT, and the directly observed growth rates, were fit to the Von Bertalanffy function (Von Bertalanffy 1938):

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

where L_t is individual length at age t, L_∞ is asymptotic length (maximum expected length in the population), K is a growth constant and t is individual age. The parameters L_∞ and K were determined by applying the "Gulland and Holt plot" (for field data) and "Ford–Walford plot" (for growth band data) (see Pauly 1984; Sparre et al. 1989 for the exact procedure, and Goffredo and Chadwick-Furman 2003; Goffredo et al. 2004, 2008; Goffredo and Lasker 2006 for examples of application to corals). Only a single growth rate summarizing growth over the entire observation period was used for each coral. All growth rates were normalized to 1 year.

Population size structure was derived from a 128 cm^2 quadrat dataset from Calafuria obtained during previous work (Goffredo et al. 2007), and age structure was determined using the von Bertalanffy age-length function (Eq. 1). The instantaneous rate of mortality (Z) of the population was determined by an analysis of the age-frequency distribution (see Pauly 1984; Sparre et al. 1989; Babcock 1991; Chadwick-Furman et al. 2000; Goffredo and Chadwick-Furman 2003; Goffredo et al. 2004, 2008). This estimation of mortality rate implies a steady state for the population, requiring an age structure characterized by a decreasing "monotonic" pattern with each age class greater than the next, and it has broadly been used for colonial and solitary corals (Grigg 1984; Babcock 1991; Chadwick-Furman et al. 2000; Goffredo and Chadwick-Furman 2003; Goffredo et al. 2004; Goffredo and Lasker 2008). The instantaneous rate of mortality was then used to express the numeric reduction of the corals over time (survivorship curve):

$$N_t = N_0 e^{-Zt} \tag{2}$$

where N_t is the number of individuals at age t, N_0 is the number of individuals at age 0, Z is the instantaneous rate of mortality and t is individual age measured in years. The turnover time, equivalent to the mean life span, was calculated as the reciprocal of Z (see Pauly 1984; Goffredo and Chadwick-Furman 2003; Goffredo et al. 2004). Maximum life span was calculated as the age at which <0.5% of the population was still surviving, based on survival curves (see Sparre et al. 1989; Chadwick-Furman et al. 2000; Goffredo and Chadwick-Furman 2003).

The age-based length growth curve was converted into a dry skeletal mass growth curve using the skeletal length–mass relationship for this species at this site and depth (Goffredo et al. 2007). Using the Beverton and Holt model (Beverton and Holt 1957), an age-specific curve expressing cohort yield in dry skeletal mass was generated using the growth curve of coral dry skeletal mass and the survivorship curve (i.e., cohort yield at age t = individual dry skeletal mass at age t × survivorship at age t; see Grigg 1984; Chadwick-Furman et al. 2000; Goffredo and Chadwick-Furman 2003; Goffredo et al. 2004).

The sex ratio, average fecundity (number of planulae produced per unit body volume) and percent fertile individuals in each age class all were derived from previous work (Goffredo et al. 2006), and planula production in each age class of *L. pruvoti* at Calafuria was estimated (Appendix 1—Electronic supplementary material). Planula production integrated fecundity (b_i), number of individuals (X_i), sex ratio (SR) and fertility (F_i) in each age class, thus planula production = $b_i\ X_i$ SR F_i, all estimated from the population.

Reliability tests for length-age predictions, that is the Cronbach's alpha coefficient (Cronbach 1951) and the Intraclass Correlation Coefficient (Burch 2009), were calculated with SPSS 12.0.

Results

Growth rate and life time growth curve

The length (maximum axis of the oral disk) of *Leptopsammia pruvoti* was chosen as the primary biometrical measurement because it provided the best fit to dry skeletal mass ($r^2 = 0.924$; see Goffredo et al. 2007).

Observed growth rates were obtained over the full size range of *L. pruvoti* individuals (Fig. 1). Growth rate decreased as a function of coral length. On average, individuals of 0–4 mm length grew 1.0 mm year^{-1} (SE = 0.2; $n = 15$), individuals of 4–6 mm length grew 0.7 mm year^{-1} (SE = 0.1; $n = 20$), while individuals of 6–8 mm length grew 0.3 mm year^{-1} (SE = 0.4; $n = 3$). The average growth rate was significantly different among size classes (ANOVA, $P < 0.001$). The growth rates of *L. pruvoti* individuals at Calafuria were also markedly variable within size groups (coefficient of variation within size classes = 70–190%). The negative relationship between growth rate and coral length, although significant ($P = 0.026$), explained only 13.1% of the total variance in growth rates (Fig. 1). According to the Gulland and Holt plot method, the population had a growth constant $K = 0.185$ and a maximum expected length $L_\infty = 8.6$ mm (Fig. 1).

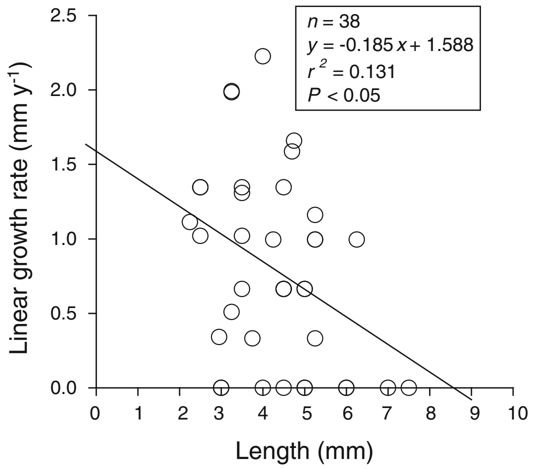

Fig. 1 *Leptopsammia pruvoti*. Variation in linear growth rate from in situ field measurements of individual corals during 0.2–1.5 years on a rocky reef at Calafuria, Eastern Ligurian Sea, at 16-m depth. This plot corresponds to the Gulland and Holt plot for the estimation of von Bertalanffy growth function parameters K and L_∞. Observations are independent; i.e., a separate individual is represented by each data point. Ordinate is size increment per unit time, while abscissa is mean size for the increments in question

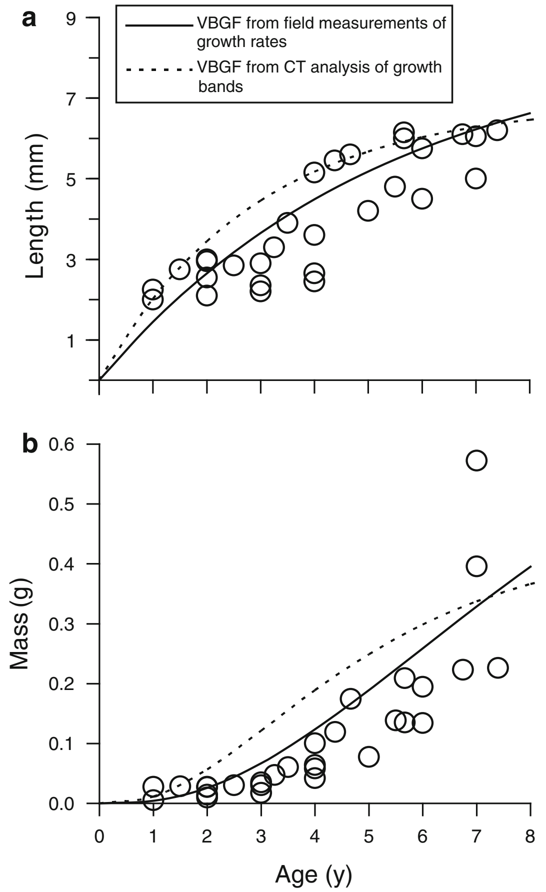

Fig. 2 *Leptopsammia pruvoti*. Age-specific von Bertalanffy growth curves (*VBGFs*) of individuals in Calafuria (Tuscany, Eastern Ligurian Sea), at 16-m depth. Age–size relationship, obtained from application of the von Bertalanffy growth model to linear extension rates measured in the field, is compared to age–size data from CT analysis of skeletal growth bands. **a** Relationship between age and length. **b** Relationship between age and dry skeletal mass. Marked points (*circles*) are lengths and masses of individuals whose age was determined from CT analyses of growth bands. Age-specific growth model curves for length depicted in **a** were converted into mass-growth model curves depicted in **b** by means of the regression $M = 0.001L^{2.894}$, where M is dry skeletal mass and L is length, calculated from a previous work on *L. pruvoti* at the same site and depth (Goffredo et al. 2007)

Using the Ford–Walford plot method for parameter estimation, a von Bertalanffy growth curve was also calculated from the CT data (Figs. 2, 3). The linear regression of the Ford–Walford plot produced the equation $L_{t+1} = 0.707L_t + 2.021$ ($r^2 = 0.986$; $P < 0.01$), from which $L_\infty = 6.9$ mm, $K = 0.347$. The predicted sizes did not differ significantly between the growth curve derived from field measurements and the one derived from CT analysis of growth bands (Fig. 2). Remarkably similar predictions were generated when comparing the predicted sizes for each age class between the two von Bertalanffy growth curves ([reliability tests for length-age predictions (Fig. 2a): Cronbach's alpha coefficient (CAC) = 0.993; intraclass correlation coefficient (ICC) = 0.988 (95% CI = 0.924–0.997). Reliability tests for coral mass-age predictions (Fig. 2b): CAC = 0.979; ICC = 0.953 (95% CI = 0.852–0.986)]). The regressions between observed coral length at known age and predicted length produced overlapping 95% CIs between the two growth curves (Gulland

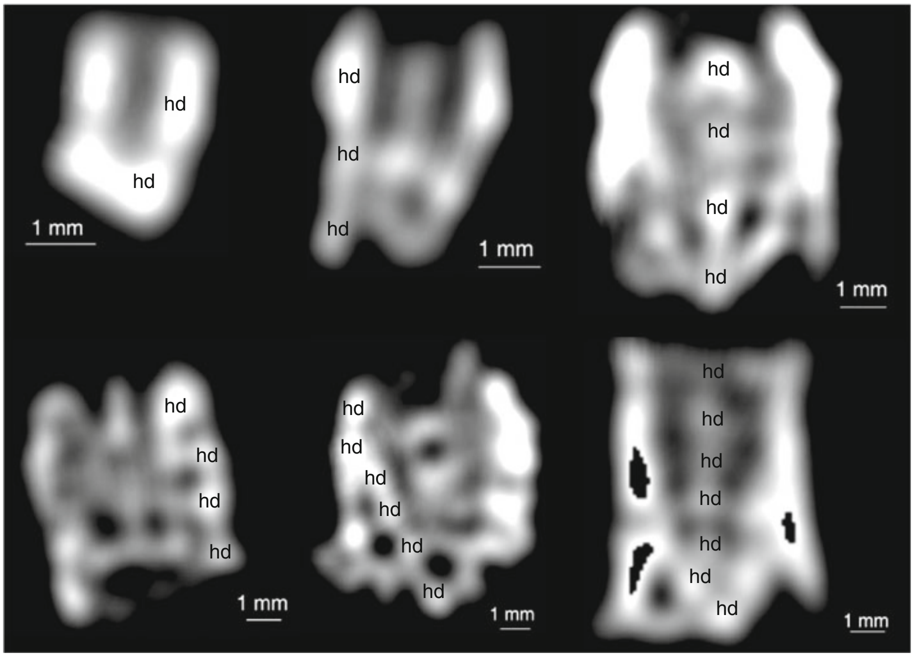

Fig. 3 *Leptopsammia pruvoti*. Computerized tomography (*CT*) scans of corallites collected in Calafuria at 16-m depth. Sagittal CT scan sections are shown (the oral pole is at the top). Each section of annual growth is made up of two bands, a high-density band (*hd*) and a low-density band. Coral age was determined by counting high-density bands. In these samples, 2–7 high-density bands, corresponding to 2–7 years of growth, are visible. Multiple CT views facilitated the identification of *hd* bands. Slab thickness of each tomography scan was 1 mm

and Holt growth curve: slope = 0.745–1.490, intercept = −1.754–1.352; Ford–Walford growth curve: slope = 0.500–1.420, intercept = −0.973–2.865). The regressions between observed coral mass at known age and predicted mass produced overlapping 95% CIs between the two growth curves (Gulland and Holt growth curve: slope = 0.534–1.364, intercept = −0.030–0.102; Ford–Walford growth curve: slope = 0.295–1.476, intercept = −0.013–0.174).

Population age structure and survivorship

The size frequency of individuals observed in the field, when converted to an age-frequency distribution using the above age–size relationship, revealed a population with a majority of young individuals (Fig. 4a). Within the population sample, 51.0% of individuals were <3 years old (<4 mm in length), i.e., under or at the age of sexual maturity, while few individuals (1.0%) fell into the three oldest age classes: 8, 9 and 10 years. Despite their higher numerical proportion, young individuals contributed only 9.1% of biomass, as shown by the gaussian age-specific yield distribution (Fig. 4b). The observed biomass distribution exhibited a peak at 4 years (Fig. 4b). The largest individuals observed were estimated to be 10 years old (7 mm length). The gradual decrease in the number of corals in the older age categories indicates that age structure may be stable (Fig. 4a).

From the above age-frequency distribution, the instantaneous rate of mortality (Z) was estimated using the equation $\ln(N_t) = -0.427t + 4.339$ ($r^2 = 0.839; P < 0.001$), which produced $Z = 0.427$ and $N_0 = 76.6$ (see "Methods" for definition of Z and N_0). The estimated survival curve for members of this population ($N_t = 76.6e^{-0.427t}$ per 128 cm^2 of sampled area) indicated a maximum life span of 13 years (Fig. 4c).

The age-specific curves of growth and survival were used to calculate yield of *L. pruvoti* individuals at Calafuria (Fig. 4b). Calculated yield, which was based on the predicted survivorship and age-specific individual biomass, increased rapidly when the individuals were young, due to their rapid increase in size. Predicted yield was maximal at 4–5 years of age, after which losses due to mortality overtook gains due to individual growth. The age at maximum yield occurred 2–3 years after the age at sexual maturity (Fig. 4b).

Life table

The total number of planulae released during a reproductive season by members of this population was 264,810 larvae m^{-2}. Most reproductive output was by corals 4–8 years of age (Appendix 1—Electronic supplementary material; Fig. 4d). The older year classes, though made up of larger polyps having higher fecundity, represented only a small fraction (6.4%) of the reproductive population, and thus contributed a smaller percentage (24.2%) of total population reproductive output (Appendix 1—Electronic supplementary material; Fig. 4c, d). The ratio between estimated reproductive output and recruit abundance estimated in the same area yielded an average "local" larval mortality of 97.7% (95% CI = 84.4–99.6%;

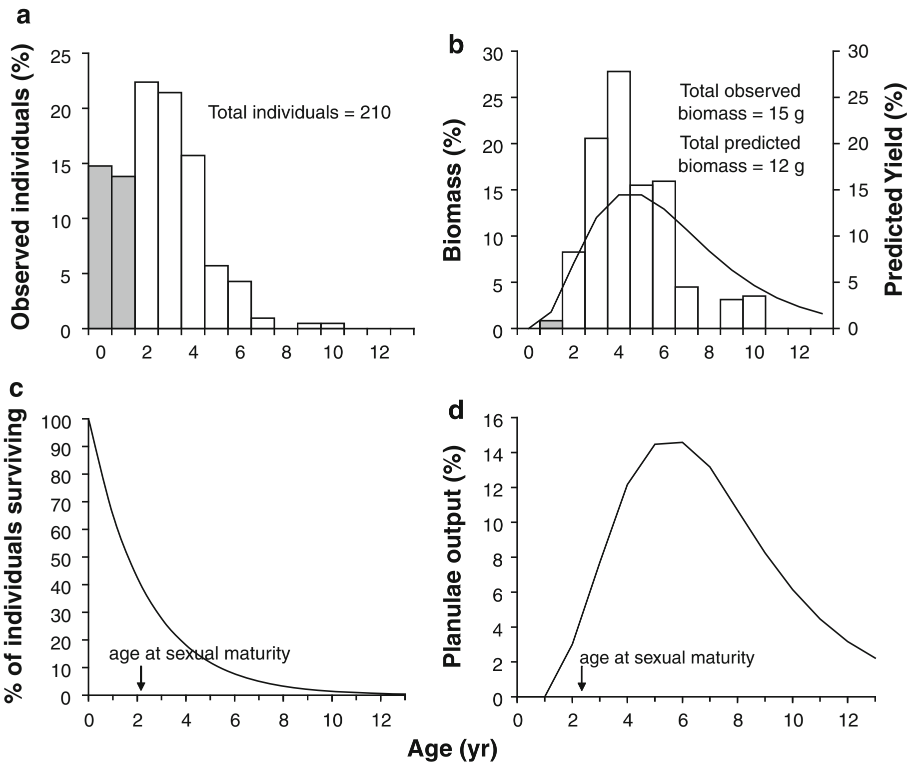

Fig. 4 *Leptopsammia pruvoti.* Age class distribution in terms of number (**a**), observed dry biomass (*bars*) and Beverton–Holt yield curve in dry biomass (**b**) of individuals, survivorship (**c**), and reproductive output (**d**) at Calafuria (eastern Ligurian Sea). Gray bars for number and biomass of individuals denote individuals that have not yet reached reproductive size (Goffredo et al. 2006). The 210 individuals used for observed distributions come from a previous work (Goffredo et al. 2007)

Appendix 1—Electronic supplementary material), with the assumption of localized recruitment.

Discussion

Field measurements of growth rate were highly variable within each size class of *Leptopsammia pruvoti*. It is highly likely that this variation was due to the different time interval of measurement between corals and by the mean seasonal temperature differences, which may span 7 degrees (mean winter/spring temperature = 13.6°C, range = 13–15°C; mean summer/fall temperature = 21.4, range = 19–26°C), coupled with the small sample size for each size class (Table 1). While it is reasonable that these corals vary their growth rate throughout the year, the annual average growth rate appears useful for modeling growth in the sympatric solitary coral *Balanophyllia europaea* (Goffredo et al. 2004). Using corals measured for only one season may cause problems in species with seasonal differences in growth when normalizing growth rates to a year. However, this bias is limited in this study because only a small number of individuals were measured for less than one season (Table 1). Moreover, the coefficient of variation of growth data is not correlated with the duration of measurement ($P > 0.05$). More data points for growth in the field or longer measurement time could have increased the predictive power of the analysis, but the strong confirmation from CT growth data made more field effort unnecessary. In fact, the growth curve obtained by field measurements was remarkably similar to the one obtained by CT scans, which is based on up to 7 years of growth (Fig. 2). This highlights the importance of assessing growth rate using different independent methods.

Size profoundly influences the physiological traits, ecological relationships and evolutionary success of organisms (Brown et al. 2000). Within the mechanical constraints of organism design, the environment may strongly affect the ultimate size an individual attains (Sebens 1987). In free-living corals, a genetic limitation on maximum size may represent an adaptation to avoid sinking in the soft substrata they colonize (Chadwick-Furman and Loya 1992). The individuals of some attached intertidal species tend to be larger in sheltered coves than at wave-exposed sites, likely reflecting the reduced risk of detachment where water movement is limited (Denny et al. 1985). Alternatively, energetic costs can limit growth. Sea anemones occupying the lower intertidal grow larger than those inhabiting the upper intertidal, potentially as a result of increased feeding time and decreased aerial exposure (Sebens 1982). Finally, considerable surplus of energy can be apportioned to physiological functions other than growth, such as sedimentation removal, locomotion, maintenance and competition, when individuals gradually decrease their calcification rates and have upper size limits (Elahi and Edmunds 2007). Many scleractinian corals grow indeterminately, and thus

Table 1 Number of *Leptopsammia pruvoti* polyps in each size class that were measured in the field for the indicated time interval

Size class (mm)	Duration of field measurement (mo)						Total
	0–3	4–6	7–9	10–12	13–15	16–18	
0–3	–	3	3	1	–	–	7
4–6	1	3	3	5	1	15	28
7–9	–	2	–	–	–	1	3
Total	1	8	6	6	1	16	38

theoretically have unlimited body size (i.e., even the largest individuals continue to grow; Hughes and Jackson 1985). Unlimited growth is possible through the production of energetically self-sufficient modules, and also because the energy available for growth or reproduction increases with increasing colony mass (Buddemeier and Kinzie 1976). However, some scleractinian corals reduce their growth rate as they get bigger. Modular scleractinian coral species with size-dependent growth include branching (*Pocillopora* spp.; Grigg and Maragos 1974), massive (*Goniastrea aspera*; Sakai 1998) and free-living colonies (i.e., not attached to a solid substrate in the adult phase, such as *Manicina areolata*; Johnson 1992). Several cases of size-dependent modular growth are also known for octocorals (Cordes et al. 2001; Bastidas et al. 2004; Goffredo and Lasker 2006). Solitary scleractinians with size-dependent growth include free-living polyps (many species of mushroom corals; Yamashiro and Nishihira 1998; Chadwick-Furman et al. 2000; Goffredo and Chadwick-Furman 2003; Knittweis et al. 2009), and attached polyps such as *L. pruvoti* (this study), *B. europaea* (Goffredo et al. 2004), *B. elegans* and *Paracyathus stearnsii* (Gerrodette 1979). In these species, the determinate growth could be due to aging or to a preferential allocation to reproduction of the increased available energy due to larger mass, without investing further energy on somatic growth.

Temperature is strongly linked to coral biometry, physiology and demography (Harriott and Banks 2002) and may significantly affect the maximum size of individuals in populations (Goffredo et al. 2008). The maximum individual coral length predicted here by the von Bertalanffy model ($L_\infty = 6.9$–8.6 mm) was similar to that observed in the field at Calafuria (maximum observed length = 7.3 mm). While the maximum reported length for *L. pruvoti* individuals is 17 mm (Zibrowius 1980), a positive correlation between annual SST in the populations and coral length has recently been observed (Goffredo et al. 2007), with the largest corals (13 mm) measured at Scilla (625 km south of Calafuria and in warmer waters). A strong positive relationship between annual SST and coral size also occurs in *B. europaea*, another sympatric dendrophylliid coral along the west coast of Italy (Goffredo et al. 2007).

The age-frequency distribution of individuals > 2 years old showed an exponential decrease, with the youngest age classes probably under-represented, which is typical for field samples (Grigg 1984; Babcock 1991; Goffredo and Chadwick-Furman 2003; Goffredo et al. 2004; Goffredo and Lasker 2008), and is probably due to the difficulty of seeing the smallest corals (<3 mm long). A population with constant mortality across age classes and where the number of recruits equals the total number of deaths in all age classes is characterized by a negative exponential decrease in frequency of individuals in each age class and is considered in steady state (Wetherall et al. 1987). Thus, the observed gradual decrease in the number of corals in successive age classes indicates a population in steady state, in that no age cohorts were missing or over-represented, as would be the case if a major disturbance event had recently altered recruitment patterns (Grigg 1977, 1984; Chadwick-Furman et al. 2000; Goffredo and Chadwick-Furman 2003; Goffredo et al. 2004; Santangelo et al. 2007; Goffredo and Lasker 2008). In a theoretical population at steady state, the coefficient of correlation of the semi-log regression from which the instantaneous rate of mortality (Z) is estimated has a value $r = -1.000$ (Pauly 1984). In *L. pruvoti*, this was $r = -0.916$, a value similar to those calculated for other coral populations reported to occur in a steady state ($r = -0.851$ to -0.993; Grigg 1984; Ross 1984; Chadwick-Furman et al. 2000; Goffredo and Chadwick-Furman 2003; Goffredo et al. 2004; Goffredo and Lasker 2008), indicating that our assumption of steady state for calculating the instantaneous rate of mortality was reasonable. According to population dynamic models, the instantaneous rate of mortality equals the inverse of the mean life span of the individuals in a population (turnover time), and hence is equal to their turnover rate (Pauly 1984; Chadwick-Furman et al. 2000; Goffredo and Chadwick-Furman 2003; Goffredo et al. 2004). The turnover time for *L. pruvoti* at Calafuria was 2.3 years (calculated as the reciprocal of Z; 95% CI = 1.7–3.6 years). These estimates appear reasonable and closely reflect field observations.

Cohort yield of *L. pruvoti* reached its maximum earlier than *B. europaea* at the same locality (age at maximum yield: for *L. pruvoti* 4–5 years, this study; for *B. europaea* 6–7 years, Goffredo et al. 2004). The age-based cohort yield curve depends on individual rates of mortality and growth. *Leptopsammia pruvoti* was characterized by higher growth and mortality rates compared to *B. europaea*, both contributing to the early peak of cohort biomass (*L. pruvoti*: $K = 0.185$–0.347, $Z = 0.427$, this study; *B. europaea*: $K = 0.111$–0.126, $Z = 0.275$; Goffredo et al. 2004). In other solitary scleractinian corals, the age at maximum cohort yield ranges from 5 years in *Fungia scutaria* to 20 years in *Heliofungia actiniformis* (Chadwick-Furman et al. 2000; Goffredo and Chadwick-Furman 2003; Knittweis et al. 2009).

The estimates of population reproductive parameters (Goffredo et al. 2005, 2006) enabled us to construct a static life history table that summarizes the main demographic parameters in this population. Most of the population reproductive output came from individuals of 4–8 years old (65% of planula production), while the age classes with larger individuals with higher fecundity were too infrequent to make a large contribution to reproduction, and therefore accounted for only a small portion of the overall reproductive output. On the contrary, in species with decreasing mortality with increasing size, like colonial corals, the largest colonies contribute the most to the reproductive output.

The ratio between larval output and recruit abundance, estimated in the same population, yielded a local larval mortality rate of about 98%, assuming local recruitment. Even though population genetic structure data indicate that local recruitment is likely in *L. pruvoti* (Goffredo et al. 2009), larval dispersal may affect our estimates of local larval mortality. Self-recruitment (settlement at the natal site) in marine species appears to be more frequent than previously suspected, and thus populations may be less open than originally thought (Levin 2006). Our estimated local larval mortality for *L. pruvoti* was higher than that reported for the brooding red octocoral *Corallium rubrum* at the same site (Santangelo et al. 2004), and similar to that reported for the brooding octocorals *Muricea californica* and *M. fruticosa* in California (Grigg 1977). For marine populations, the number of eggs or larvae required to produce one reproductive offspring that survives the larval and early juvenile stage is poorly known (Botsford et al. 2009). In *L. pruvoti*, according to the life history table, the percent of individuals reaching sexual maturity was 43% (95% CI = 31–58%) and the number of larvae needed for one recruit was 44 (95% CI = 6–234), thus 104 larvae (95% CI = 10–754) were required to produce one reproductive individual.

The average population abundance of *L. pruvoti* is markedly higher than that of other solitary dendrophylliid corals for which population dynamics and reproductive biology have been reported, namely *B. europaea*, endemic to the Mediterranean Sea, and *B. elegans* off North Western America (Appendix 2—Electronic supplementary material). The higher abundance of *L. pruvoti* is most likely due to localized recruitment of a fraction of the azooxanthellate brooded larvae, which attach to the vault of crevices near the parent polyps, causing a high rate of local inbreeding through mating between close relatives (Goffredo et al. 2009). Even *B. elegans* has a higher population abundance compared to *B. europaea* (Appendix 2—Electronic supplementary material), which is most likely due to the low dispersal of the azooxanthellate benthic larvae, which attach to the bottom < 0.5 m from the parent polyp (Gerrodette 1981; Fadlallah and Pearse 1982; Fadlallah 1983). On the other hand, the low population abundance of *B. europaea* may be caused by high dispersal of the zooxanthellate larvae, which have neutral buoyancy and exhibit swimming and pelagic behavior (Richmond 1987; Goffredo and Zaccanti 2004; Goffredo et al. 2004). It should be noted that the dispersal capabilities of the larvae of the three species may be strongly influenced by their behavior rather than by the symbiotic condition, since not all zooxanthellate larvae have higher dispersal than azooxanthellate ones (Ben-David-Zaslow and Benayahu 1998).

Life history theory predicts that organisms develop different life history strategies (as a result of trade-offs among reproduction, growth and survival; Stearns 1989; Roff 1992) to maximize their fitness under different environmental conditions and selective pressures (Pianka 1970; Stearns 1976, 1989). Concerning reproductive strategies, the classic *r*/*K*-selection theory (Pianka 1970) has often been used to categorize organisms: *r*-strategists (also called opportunistic species) are characterized by high fecundity, high mortality rates, small size, short generation time and high dispersal potential; whereas *K*-strategists usually have the opposite characteristics. The original theory has been reviewed and updated in the last 40 years (Stearns 1976, 1989; Roff 1992), and information on the evolution of life history traits in scleractinians has been recently reviewed (Baird et al. 2009). The *r*/*K* correlates are still widely used to describe life history strategies and are particularly useful for groups where life history strategies have rarely been studied. It appears there are dendrophylliid solitary corals that have evolved mixed life strategies (Appendix 2—Electronic supplementary material). *B. elegans* has demographic renewal with *r*-characteristics and reproduction with *K*-characteristics; *B. europaea* has a *K*-demographic renewal strategy and reproduction with intermediate characteristics; *L. pruvoti* has an *r*-reproductive strategy and demographic renewal with intermediate characteristics (Appendix 2—Electronic supplementary material). However, this comparison should be viewed cautiously, since the life histories of the three species have been studied at only one site, and differences may exist between populations subject to different environmental conditions or selective pressures.

This study completes the description of the main life strategy characteristics of the temperate *L. pruvoti* in the Calafuria population, together with previous studies on its reproductive biology and biometry. Further studies of this species are needed to reveal possible differences in the life history traits among populations in different environmental conditions.

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