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REPORT

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Growth and population dynamics model of the Mediterranean solitary coral *Balanophyllia europaea* (Scleractinia, Dendrophylliidae)

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Abstract Complex life history processes of corals, such as fission, fusion, and partial mortality of colonies, that decouple coral age from size, are rare or clearly detectable in corals that produce distinct colonial or solitary forms. In some of these corals, individual age may be determined from size, and standard age-based growth and population dynamics models may be applied. We determined population size and structure and measured growth rates of *Balanophyllia europaea* individuals at Calafuria in the eastern Ligurian Sea. We then applied demographic models to these data. Growth rate decreased with increasing coral size. The age–size curve derived from field measurements of growth rates fits that obtained from the computerized tomography analysis of skeletal growth bands. The frequency of individuals in each age class decreased exponentially with age, indicating a population in a steady state. The survival curve showed a turnover time of 3.6 years and a maximum life span of 20 years. This is nearly three times the turnover time and maximum life span recorded for *Balanophyllia elegans* living off the western coasts of North America, the only congeneric species whose population dynamics has been studied. The Beverton and Holt population model may be useful for comparative analyses of demographic traits and for resource management of solitary or compact, upright growth forms that rarely fragment. This paper completes the description of the main life-strategy characteristics of the Mediterranean endemic coral *B. europaea*, together with our previous studies on the reproductive biology of this species. This constitutes a major advance in the understanding of the biology and ecology of Mediterranean scleractinian corals, and represents the most complete description of a coral from this geographic area to date that we are aware of.

Keywords Dendrophylliidae · Solitary coral · Growth model · Population ecology · Mediterranean Sea · Reef management

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Introduction

Demographic parameters reveal relationships between organisms and their environment, and contribute to the assessment of habitat stability (Grigg 1975; Bak and Meesters1998; Meesters et al. 2001). In addition, information on population turnover may contribute to techniques for the restoration of damaged or degraded coastal areas (Connell1973; Rinkevich1995; Chadwick-Furman et al. 2000; Goffredo and Chadwick-Furman 2003).

Scattered information is available on the population dynamics of scleractinian corals. Connell (1973) reviewed the modest amount of data that had been collected in the previous 30 years, and described parameters such as growth and survivorship. Since then, demographic processes have been described for some coral species in the Red Sea (Loya 1976a, 1976b; Goffredo 1995; Chadwick-Furman et al. 2000; Goffredo and Chadwick-Furman 2003), northeastern Pacific (Gerrodette 1979a; Fadlallah 1983), Caribbean Sea (Hughes and Jackson 1985; Johnson 1992; Meesters et al. 2001), Great Barrier Reef, Australia (Babcock 1988, 1991), and in the Mediterranean Sea (Goffredo 1999). The paucity of information on population dynamics in most species of scleractinian corals may be attributed in part to a distortion of age–size relationships in this group, resulting from processes of fragmentation, fusion, and partial colony mortality (Hughes and Jackson 1985; Hughes and Connell 1987; Babcock 1991; Hughes et al. 1992). These phenomena, characteristic of clonal modular organisms (Hughes 1989), prevent the application of traditional growth and population dynamics models based on organism age and create highly complex demographic patterns (Hughes and Jackson 1985). Due to these complexities, a recent analysis of 13 Caribbean coral species used a size-based, rather than age-based, assessment of population structure (Meesters et al. 2001). However, in species in which individuals rarely fragment or fuse, and partial mortality is discernable by anomalies in the regular growth pattern, it is possible to determine coral age (Chadwick-Furman et al. 2000). Corals that form discrete, upright branching colonies that rarely fragment in certain environments, such as *Pocillopora* and *Stylophora*, are suitable for this analysis (Grigg 1984). In addition, in some solitary corals, age estimates may be easily obtained from growth bands that are visible externally (Abe 1940; Chadwick-Furman et al. 2000; Goffredo and Chadwick-Furman 2003). Growth-band analysis has been used more widely to determine the age of colonial scleractinian and gorgonian corals (Knuston et al. 1972; Buddemeir and Maragos 1974; Grigg 1974; Logan and Anderson 1991; Mistri and Ceccherelli 1993; Mitchell et al. 1993). Thus growth and population dynamics models based on age can be applied to certain growth forms of scleractinian corals to describe demographic characteristics (Nisbet and Gurney 1982; Grigg 1984; Ross 1984; Bak and Meesters 1998; Chadwick-Furman et al. 2000; Goffredo and Chadwick-Furman 2003).

Balanophyllia europaea is a solitary, ahermatypic, zooxanthellate scleractinian coral that lives on rocky substratum and is endemic to the Mediterranean Sea (Zibrowius 1980,1983; Schumacher and Zibrowius 1985; Aleem and Aleem 1992; Veron 2000). Owing to its symbiosis with zooxanthellae, depth distribution appears restricted in this species; it is found between 0 m and a maximum of 50 m depth (Zibrowius 1980), though congeneric azooxanthellate corals have been reported at depths of up to 1,100 m (Cairns 1977). The reproductive biology of this species is characterized by simultaneous hermaphroditism and brooding (Goffredo and Telò 1998). *B. europaea* is the only species in the genus *Balanophyllia* and one of the few in the family Dendrophylliidae that exhibit hermaphroditism (Harrison 1985; Goffredo et al. 2000). During the annual cycle of sexual reproduction, fertilization takes place from March to June and planulation in August and September (Goffredo et al. 2002).

We describe the population dynamics of *B. europaea* in the eastern Ligurian Sea, applying Beverton and Holt's population dynamics model based on age (Beverton and Holt 1957; Chadwick-Furman et al. 2000; Goffredo and Chadwick-Furman 2003). This paper completes the description of the life strategy of this Mediterranean endemic coral together with previous studies on the reproductive biology of this species (Goffredo and Telò1998; Goffredo et al. 2000, 2002; Goffredo and Zaccanti in press).

Materials and methods

The studied population of *Balanophyllia europaea* was located off the coast of Calafuria (10 km south of Leghorn city, Tuscany region, Italy, eastern Ligurian Sea (NW Mediterranean), 43°28.4′N, 10°20′E). From April to October 1997, five transects were surveyed to collect data on population structure and bathymetric distribution of *B. europaea* (after Gerrodette 1979a; Mistri and Ceccherelli 1994; Goffredo and Chadwick-Furman 2000). Using an underwater compass, we set transects perpendicular to the coastline towards the open sea. Transect length was determined using a metered rope. Along each transect starting at a depth of 13 m, we monitored a series of 23 quadrats, each 1 m^2. Distance between quadrats was 2 m. Within each quadrat, we recorded the depth and the size of all *B. europaea* polyps. We measured polyp length (L: oral disc axis parallel to stomodaeum) and width (W: oral disc axis perpendicular to stomodaeum) (after Chadwick-Furman et al. 2000; Goffredo and Chadwick-Furman 2003). Regular spacing of quadrats and transects may be biased if laid over a population with a natural regular spacing. However, this should not have occurred in this case since the distributional pattern of *B. europaea* individuals is disaggregated (random) (Goffredo and Zaccanti in press).

During each dive, a mercury thermometer was used to measure water temperature in the field at a depth of 6 m. We also placed two digital thermometers (DS 1921L.F5, Dallas Semiconductors) at the same depth in the center of our research area to record water temperature readings every 4 h during the period under study. Photoperiod was calculated from astronomical almanacs.

In April 1998, we collected 75 polyps at a depth of 6 m (depth of maximum population density) and performed biometric analyses on them. Polyps were dried at 400 °C for 24 h and then height (h) (oral–aboral axis), dry skeletal mass (M), length, and width were measured (after Goffredo and Telò1998; Chadwick-Furman et al. 2000; Goffredo and Chadwick-Furman 2003; Goffredo et al. 2002).

Furthermore, we recorded the growth rates of 62 individuals of *B. europaea*, marked in situ by a numbered plastic tag nailed to the rock, at a depth of 6 m from December 1999 to April 2002. Length and width were measured in situ every 3 months for 0.3–2.3 years. The period of measurement varied between individuals, because corals that died were replaced by others of similar size during the study. The choice of the depth of maximum abundance for the determination of growth rates may bias the growth rate towards fast growth. This could underestimate the age of a coral of a given size, but the bias should not affect most individuals, since most of the population biomass (62%) is concentrated at 5–7 m (Goffredo 1999).

To obtain an objective relationship between polyp size and age, for comparison with that obtained by field measurement of growth rates, we counted the number of annual growth bands by means of computerized tomography (CT) technology (after Dodge1980; Kenter 1989; Logan and Anderson 1991; Bosscher 1993). Specimens used in the CT measurements were collected at Calafuria, at a depth of 6 m near the marked individuals. Age was determined from the growth-band counts based on the observation that temperate zooxanthellate corals deposit two bands per year, a high density band in winter and a low density band in summer (Peirano et al. 1999). Growth bands were counted on corals up to 15 mm in length (75% of the maximum coral size in this population). Individuals larger than this had growth bands too close to be distinguished by CT scans.

Growth was fit to the von Bertalanffy function (von Bertalanffy 1938):

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

where L_t is individual length at age t, L_∞ is asymptotic length (maximum expected length), K is a growth constant, and t is individual age. The parameters L_∞ and K were determined via application of "Gulland and Holt plot" and "Ford-Walford plot" traditional methods (Ford1933; Walford1946; Gulland and Holt 1959 and see the manuals of Pauly 1984 and Sparre et al. 1989, and for the exact procedure Sebens1983 and Mitchell et al. 1993 and Chadwick-Furman et al. 2000 for examples of application to corals).

Population size structure was derived from surveying the transects, and population age structure was then determined using the above length-age function. The instantaneous rate of mortality (Z) was determined by an analysis of the age frequency distribution (after Grigg 1984; Ross 1984; Pauly 1984; Sparre et al. 1989; Babcock 1991; Chadwick-Furman et al. 2000; Goffredo and Chadwick-Furman 2003). The method consists of a plot of the natural logarithm of the numbers (frequency) in each age class (N_t) against their corresponding age (t), or

$$\ln N_t = at + b,$$

Z being estimated from the slope a, with sign changed; the intercept b is equal to the natural logarithm of the number of individuals at age zero (N_0). The most important limitation of this method to estimate mortality rate is the assumption of the steady state of the population. The instantaneous rate of mortality was then used to express the numeric reduction of the corals over time (i.e., survivorship curve):

$$N_t = N_0 e^{-Zt}$$

Maximum individual lifespan was calculated as the age at which <0.5% of the population was still surviving, based on survival curves (after Sparre et al. 1989).

According to the Beverton and Holt (1957) model, an age-specific curve expressing cohort yield in skeletal mass was generated using the growth curve of skeletal mass and the survival curve of the individuals (i.e., cohort yield = individual mass at age t×percent survival at age t; after Grigg 1984; Ross 1984; Chadwick-Furman et al. 2000; Goffredo and Chadwick-Furman 2003). Based on the rates of growth and mortality for a population, the model predicts that a cohort of organisms will gain weight until a point (i.e., age/size) is reached where growth gains are overtaken by mortality losses. Maximum production by the cohort occurs at the point where losses due to mortality equal gains from growth. As the cohort ages and reaches a point of maximum longevity, production declines to zero.

Results

Description of habitat and population distribution

The seabed at Calafuria is initially rocky and drops rapidly from the coastline to a depth of 15 m, at which point it becomes sandy and slopes slightly but steadily until it hits a rocky vertical wall approximately 200–250 m from the coastline. The rocky wall starts at a depth of 16 m and ends at 45 m in a flat sand and mud bottom.

Balanophyllia europaea occurred on rocky substrata from 2 to 12 m deep with an average density of 16 individuals m^{-2} (SE = 3). Population density reached a peak of 113 individuals m^{-2} (SE = 33) at a depth of 6 m (Fig. 1).

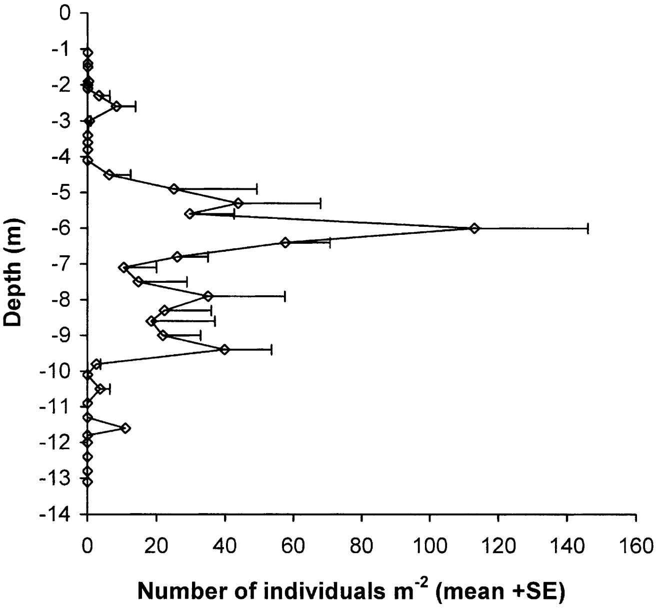

Fig. 1 Variation in the abundance of *Balanophyllia europaea* individuals according to depth on a rocky reef at Calafuria, eastern Ligurian Sea

The water temperature at 6-m depth varied seasonally by approximately 10 °C; the lowest temperatures occurred between January and March with an average of 13.7 °C (range = 13.0–15.5 °C), and the highest temperatures were in August with an average of 23.3 °C (range = 19.5–27 °C). The average annual temperature was 18.1 °C. Summer and winter photoperiods had a 6-h difference, with the longest daylength being 15 h, and the shortest, 9 h.

Individual growth patterns

The length of *B. europaea* was chosen as the primary biometrical measurement because it provided the best fit to dry skeletal mass. The mass-length plot produced the equation $M\ (\mathrm{g}) = 0.0018L(\mathrm{mm})^{2.537}$ ($r = 0.930$; $p < 0.01$). *B. europaea* growth was characterized by an inverse exponential relationship between individual length and width:length ratio, this ratio changing with coral growth (Fig. 2A). This changing proportion indicated allometric growth, with oral disc length increasing more rapidly than width, resulting in an oval body shape. Individual height and length had a linear relationship, with a constant ratio as the coral grew, indicating isometric growth (Fig. 2B).

Growth rate and lifetime growth curve

The growth rate of individuals of *B. europaea* decreased linearly with increasing coral size (Fig. 3). According to the Gulland and Holt plot method for the estimation of von Bertalanffy growth function parameters, the rate of this decrease is the growth constant K, which is the slope of the linear regression, with sign reversed. The population of *B. europaea* had $K = 0.111$ (0.058–0.163, 95% confidence interval (CI); Fig. 3). The maximum expected coral length (L_∞) corresponds to the coral length where the growth regression intercepts the x-axis (Fig. 3), which for *B. europaea* at Calafuria $L_\infty = 2.362$ (intercept)/0.111 (−slope) = 21.279 mm (16.365–26.505, 95% CI).

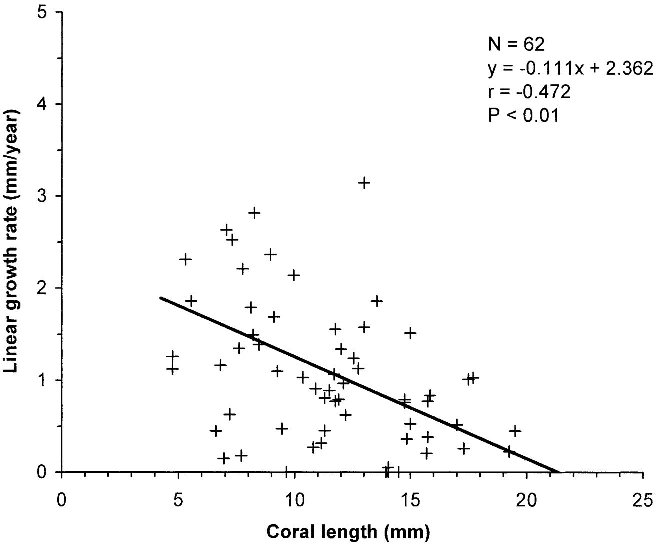

Fig. 3 Variation in linear growth rate among individuals of *Balanophyllia europaea*. From in situ field measurements of individual corals during 0.3–2.3 years on a rocky reef at Calafuria, eastern Ligurian Sea. This plot corresponds to the Gulland and Holt plot for the estimation of von Bertalanffy Growth function parameters K and L_∞. The observations are independent of one another; i.e., a single coral contributes one point. The ordinate is size increment per unit time $[(L_2 - L_1)/(t_2 - t_1)]$, and the abscissa are mean size for the increments in question $[(L_1 + L_2)/2]$

For corals < 10–11 years in age (< 14–15 mm in length), the von Bertalanffy growth curve derived from field measurements of growth rates produced a similar age–size relationship as that obtained from the CT analysis of skeletal growth bands; after this 10–11 year age, coral growth was so slow that bands became indistinguishable and hence the CT analysis unusable (Fig. 4, Fig. 5). Using the Ford-Walford plot method for parameter estimation, we also calculated a von Bertalanffy growth curve from the CT data (Fig. 4). A Ford-Walford plot factors out differences in growth that are age-dependent by plotting size (coral length, L) at age $t+1$ on the ordinate versus size at age t on the abscissa. The linear regression of this plot produced the equation $L_{t+1}(\mathrm{mm}) = 0.882L_t(\mathrm{mm}) +$

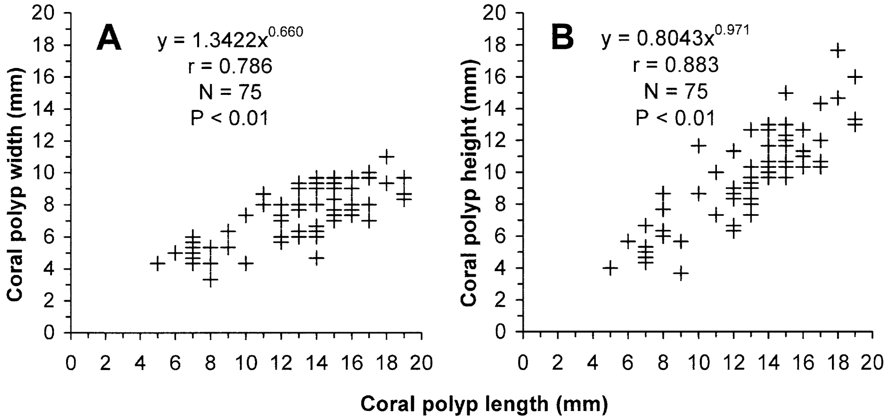

Fig. 2A, B Dependence of biometric parameters on individual length in the solitary coral *Balanophyllia europaea*. **A** Width. The confidence interval (CI) of the exponent of the nonlinear regression does not contain 1 (0.54–0.83, 95% CI), indicating allometric growth, with oral disc length increasing more rapidly than width. **B** Height. The confidence interval of the exponent of the nonlinear regression contains 1 (0.86–1.155, 95% CI), indicating coral polyp height and length have isometric growth

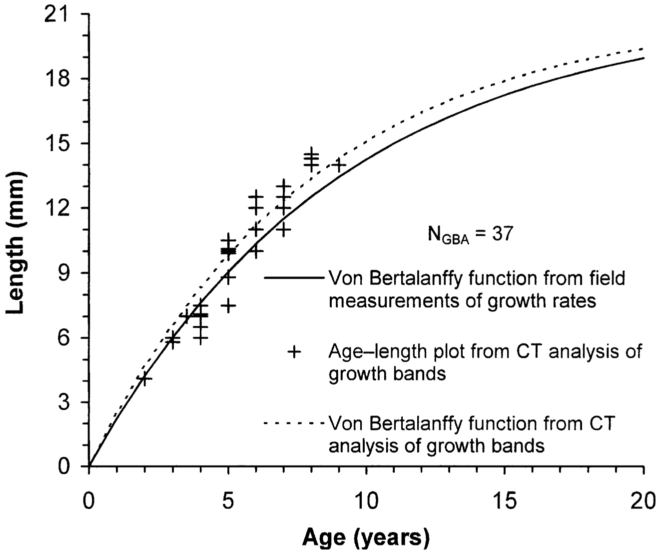

Fig. 4 Age-specific growth curves of individuals of the solitary coral *Balanophyllia europaea* at Calafuria (eastern Ligurian Sea). The age-length relationship, obtained from application of the von Bertalanffy growth model to linear extension rates measured in the field, is compared with age-length data from CT analysis of growth bands. N_{GBA} Number of corals examined for growth band analysis (37)

2.494 ($r = 0.978$; $p < 0.01$), from which L_∞ = intercept/(1−slope) = 21.136 mm (17.820–26.250, 95% CI), $K = -\ln$ (slope) = 0.126 (0.080–0.145, 95% CI). The confidence intervals of the CT function parameters fell within the confidence intervals of the function parameters from field growth rate measurements, indicating no significant differences between the two growth curves (Fig. 4).

According to the von Bertalanffy growth model, young individuals of *B. europaea* (1–2 years old) grew relatively rapidly (2.00–2.49 mm year^{-1}), but, as they aged their growth rate decreased (0.91–1.04 mm year^{-1} at 8–9 years old), and by the time they were 19–20 years old, grew at 0.23–0.30 mm year^{-1} (Fig. 4).

Population age structure and survivorship

The size-frequency of individuals observed in the field population, when converted to an age-frequency distribution using the above age–size relationship, revealed a population dominated by young individuals (Fig. 6A). Of the population sample, 50% was < 5 years old (< 9–10 mm in individual length), i.e., under or at the age of sexual maturity. The largest individuals observed were estimated to be 20 years old (= 19 mm length). The gradual diminution in number of corals in the older age categories suggests that age structure is relatively stable.

From the above age-frequency distribution, we estimated the instantaneous rate of mortality (Z). The youngest age classes (0–1 years) were excluded from the mortality-rate analysis because they are known to be under-represented in field samples (Grigg 1976, 1984; Babcock 1991; Chadwick-Furman et al. 2000; Goffredo and Chadwick-Furman 2003). In our case, the under-representation of young corals is probably a consequence of the difficulty in seeing corals of this size (< 2–3 mm in length). The plot of the natural logarithm of the numbers of individuals (frequency) in each age class (N_t) against their corresponding age (t), produced the equation $\ln N_t = -0.275t(\text{years}) + 6.690$ ($r = 0.967$; $p < 0.01$). From this equation $Z = -(-0.275) = 0.275$ and $N_0 = e^{6.690} = 804.3$. The estimated survival curve for members of this population ($N_t = 804.3e^{-0.275t}$) indicated the maximum life span to be 20 years (Fig. 6B).

Population yield

The above data were used to calculate yield, in terms of skeletal mass per recruit, of *B. europaea* individuals at Calafuria (Fig. 6B). Cohort yield increased rapidly when the polyps were young, due to their rapid increases in size. Yield was maximal at 6–7 years of age, after which losses due to mortality overtook gains due to individual growth. The age at maximum yield occurred 2–4 years after the polyps reached sexual maturity (Fig. 6B).

Discussion

The population dynamics of *Balanophyllia europaea* at Calafuria revealed in this study, in combination with previous works on the species' reproductive biology (Goffredo and Telò 1998; Goffredo et al. 2000,2002; Goffredo and Zaccanti in press), have yielded a description of the main life strategy characteristics of this endemic, Mediterranean Sea, solitary coral. This constitutes a major advance in our understanding of the biology and ecology of Mediterranean scleractinian corals, and is the most complete description of a coral of this geographic area to date.

Depth distribution

The depth distribution of *B. europaea* at Calafuria was strictly limited; corals were not found below a depth of 12 m. This contrasts with previous studies, where the maximum known depth was 50 m (Ziborwius1980). Because *B. europaea* is zooxanthellate (Zibrowius1980, 1983), its bathymetric distribution is limited by light availability, while azooxanthellate congeners can live at depths of more than 1,000 m (Cairns1977). The very shallow depth distribution found in this study may be attributed to turbidity in this area that reduces light penetration (personal observations). In the nearby islands of the Tuscan archipelago (Elba and Capraia, for example), which are characterized by more transparent water because of the absence of continental terrigenous contributions, individuals of *B. europaea* have been found at depths of up to 30 m (personal observations).

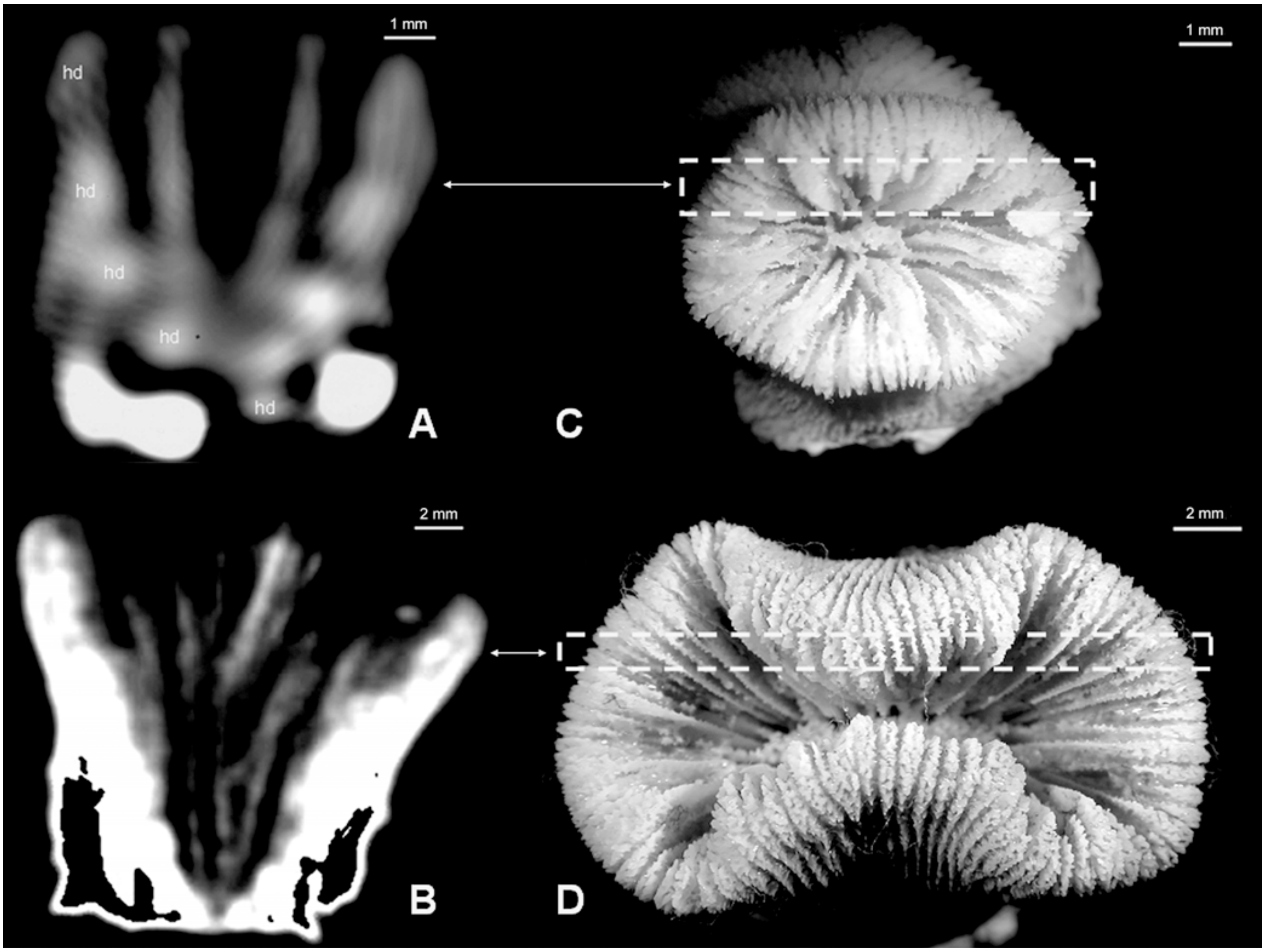

Fig. 5A–D Computerized tomography (CT) scans of *Balanophyllia europaea* corallites collected at Calafuria. Saggital CT scan sections are shown in **A** and **B** (the oral pole is at the *top*). *hd* High density band. Multiple CT views facilitated the identification of hd bands. The slab thickness of the tomography scan was 1 mm. **A** Age determination by counting the skeletal growth bands was possible in corallites up to 15 mm in length. In this sample (8 mm in length), five high-density bands, corresponding to 5 years of growth, are visible. **B** Age determination in individuals larger than 15 mm in length was not obtained by counting the skeletal growth bands because the growth bands are too close and no longer distinguishable by CT scans. In this sample (19 mm in length), determining age on the basis of an accurate band count is clearly not possible. **C, D** The original corallite is shown, in which is indicated where the saggital CT scan section was taken

Biometry

B. europaea oral disc length and width follow an allometric growth pattern leading to a change in polyp shape during its lifetime. Sexually immature polyps are round (with a width: length ratio = 1 at 1 year of age). Polyps gradually acquire a more oval shape, which becomes increasingly pronounced with age (width: length ratios of 0.75 at 3 years of age and 0.50 at 15–18 years of age). This allometric growth is the product of less active skeletal secretion along the width than along the length axis of the oral disc, and results in (lengths being equal) a smaller oral disc surface area than in individuals with isometric growth. The relatively small surface area of oval or elongate corals may favor the removal of sediments and the acquisition of food in unstable habitats (Foster et al. 1988; Hoeksema 1991).

Growth rate and models

Many scleractinian corals are known to grow indeterminately, and thus theoretically to have unlimited body size (reviewed in Hughes and Jackson 1985; Bak and Meesters 1998). However, some corals reduce their growth rate as they age. Scleractinian corals with size-dependent growth include species with branching colonies (*Pocillopora* spp.; Stephenson and Stephenson 1933; Grigg and Maragos1974), massive colonies (*Goniastrea* spp.; Motoda 1940; Sakai 1998), free-living colonies (*Manicina areolata*; Johnson 1992), free living solitary polyps (many species of mushroom corals; Stephenson and Stephenson 1933; Goffredo 1995; Yamashiro and Nishihira 1998; Chadwick-Furman et al. 2000; Goffredo and Chadwick-Furman 2003), and attached solitary polyps such as *B. europaea* (this study), *B. elegans,* and

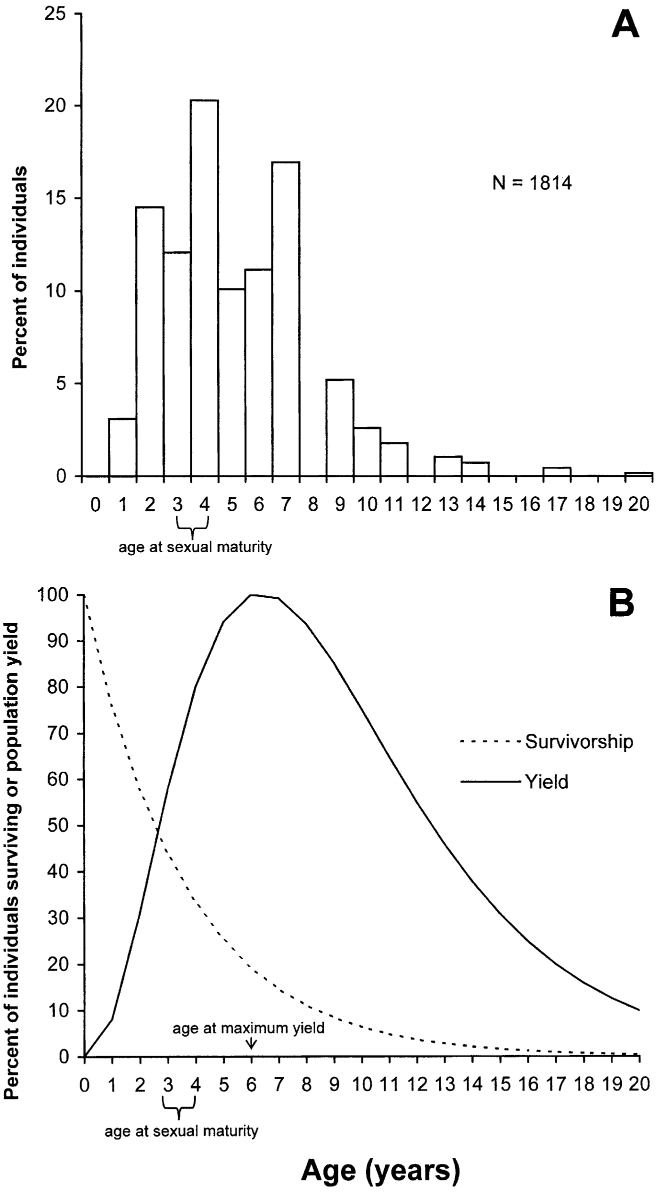

Fig. 6A, B Population age structure (**A**), and (B) survivorship curve and population yield (**B**) in dry skeletal mass of the solitary coral *Balanophyllia europaea* at Calafuria (eastern Ligurian Sea). Age at sexual maturity is from Goffredo et al. (2002). *N* Sample size

Paracyathus stearnsii (Gerrodette 1979a). In free-living corals, which often colonize soft substrata, a genetic limitation on maximum size may represent an adaptation to avoid sinking (Chadwick-Furman and Loya 1992). Among attached corals, other constraints may influence maximal size, such as the biomechanics of a skeleton with highly branched architecture, or the physiology of a solitary polyp with a single mouth.

The maximum individual length predicted by the von Bertalanffy model ($L_\infty = 21$ mm) is similar to that observed in the field population sampled at Calafuria (maximum observed length is 19 mm). Zibrowius (1980) gave 24 mm as the maximum length for *B. europaea* individuals, although larger individuals, up to 28 mm in length, are common in depths ranging from 0 to 30 m in the Straits of Messina about 625 km south of Calafuria (G. Neto, personal communication). The smaller size of the Calafuria individuals compared to those found at Messina and observations by Zibrowius (1980) could be attributed both to latitudinal characteristics of the annual daylength cycle and water temperature, and to mechanical limitations of the colonized environment (see Denny et al. 1985). A negative relationship between growth rate and latitude was shown for scleractinians in the genus *Porites* (Isdale1983; Lough and Barnes 2000; Grigg 1981, 1997) and in the family Fungiidae (Goffredo and Chadwick-Furman 2003). Alternatively, the Calafuria coast is often hit by storms, which expose the coral population to intense wave action. Organisms growing in strong wave action environments are generally smaller than organisms living in deeper or calmer waters (Harger 1970, 1972; Paine 1976; Adey 1978; Smith and Harrison 1977; Vosburgh 1977).

Population dynamics

The age structure of the examined population showed an exponential decrease in the frequency of individuals with age. This structure 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 (Coe1956; Grigg 1977, 1984; Santangelo et al. 1993; Chadwick-Furman et al. 2000; Goffredo and Chadwick-Furman 2003). Other coral populations reported to occur in a steady state are those of the scleractinian *Pocillopora verrucosa* (Grigg 1984; Ross 1984), of scleractinian mushroom corals (Chadwick-Furman et al. 2000; Goffredo and Chadwick-Furman 2003), the gorgonians *Muricea californica* (Grigg 1977) and *Lophogorgia ceratophyta* (Mistri 1995), and the commercially important *Corallium rubrum* (Santangelo et al. 1993), *C. secundum* and *Anthipathes dichotoma* (Grigg 1984).

In a theoretical population in steady state, the coefficient of correlation of the semi-log regression from which the instantaneous rate of mortality (Z) is estimated has a value $r = -1.000$ (see Beverton and Holt 1956; Robson and Chapman 1961; Pauly 1984 for reviews on this method). In *B. europaea*, this coefficient of correlation was $r = -0.967$. This value is close to the best value of those calculated for other coral populations reported to occur in a steady state (r values reported for other coral populations with a stationary age distribution range from −0.851 to −0.993; Grigg 1984; Ross 1984; Chadwick-Furman et al. 2000; Goffredo and Chadwick-Furman 2003). This indicates that the steady-state assumption that we made in order to calculate the instantaneous rate of mortality is not unreasonable. According to population dynamics models, the instantaneous rate of mortality equals the inverse of the mean lifespan of the individuals in a population (turnover time), and hence is equal to their turnover rate, or
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annual production:biomass ratio (P/B) (Pauly 1984; Clasing et al. 1994; Chadwick-Furman et al. 2000; Goffredo and Chadwick-Furman 2003). The turnover time for *B. europaea* at Calafuria was 3.6 years (calculated as the reciprocal of *Z*). Our estimates of the mortality rate and maximum life span for *B. europaea* appear to be reasonable, in that values derived from the survival curve closely reflect field observations.

We did not observe any 0-year-old and relatively few 1-year-old individuals of *B. europaea* at Calafuria. Probably, newly settled individuals are under-represented because of the difficulty in locating them, due to their small size (< 2–3 mm in individual length). Young of other coral species are known to be under-represented in field samples (as mentioned in Results), and the youngest age classes of corals are usually excluded from population dynamic analyses to overcome this difficulty (Grigg 1984; Babcock 1991).

Life strategies in the genus *Balanophyllia*

The average population density of *B. europaea* in Calafuria (16 individuals m^{-2}) is markedly lower than the only other *Balanophyllia* species for which population dynamics and reproductive biology are reported, namely *Balanophyllia elegans* off western North America (Table 1). *B. elegans* occurs from the Island of Vancouver (50°N) to Baja California (29°N) (Gerrodette 1979b). At the center of its geographic range, between a depth 6 and 13 m, the average population density is 563 individuals m^{-2} (Fadlallah1983), while at its northern limit, at a depth of 15 m the average population density is 136 individuals m^{-2} (Bruno and Witman1996). The higher population density of *B. elegans* is most likely due to the low dispersion capability of the azooxanthellate benthic larvae which attach to the bottom less than 0.5 m from the parent polyp (Gerrodette1981; Fadlallah and Pearse1982; Fadalallah1983). On the other hand, the low population density of *B. europaea* may be caused by the high dispersion capability of the larvae, which are zooxanthellate and have neutral buoyancy, with a prevalently swimming and pelagic behavior (Goffredo and Zaccanti in press). Symbiont zooxanthellae contribute to the energy requirement of larvae during dispersion and this may increases the dispersion capability (Richmond 1987, 1989; Ben-David-Zaslow and Benayahu 1998; Goffredo and Zaccanti in press).

Pianka (1970) visualized an *r*–*K* continuum, with any particular organism occupying a position along it. The *r*-endpoint represents the quantitative strategy, while the *K*-endpoint represents the qualitative strategy (see Table 1 in Pianka 1970 for a summary of the correlates of the *r*- and *K*-selected extremes). The comparison of the biological characteristics of the two congeneric species *B. europaea* and *B. elegans*, which is presented in Table 1 of this paper, reveals that the two species have evolved opposite life strategies, which are not identifiable with the endpoints of the *r*–*K* continuum. Rather, the two strategies appear mixed; *B. europaea* shows *K* characteristics for demography and *r* characteristics for reproduction, while on the contrary, *B. elegans* has a demography with *r* characteristics and a reproduction with *K* characteristics.

Application to the management of exploited populations

We propose that the Beverton and Holt population dynamics model, which expresses a cohort's biomass curve in relation to age, could be applied more widely to the management of exploited populations of certain scleractinian corals. This model has been previously applied to the study and/or management of populations of precious corals in Hawaii (Grigg 1976, 1984) and in the Mediterranean (Caddy 1993), as well as to populations of reef-building stony corals in the Philippines (Ross 1984) and in the Red Sea (Chadwick-Furman et al. 2000, Goffredo and Chadwick-Furman 2003). By estimating the minimum size at which individuals may

Table 1 Life-history characteristics of two species of the genus *Balanophyllia*. Data for *B. europaea* are from Goffredo and Telò (1998), Goffredo (1999), Goffredo et al. (2000, 2002), Goffredo and Zaccanti (in press), and this paper. Data for *B. elegans* are from Gerrodette (1979a, 1979b, 1981), Fadlallah and Pearse (1982), Fadlallah (1983), and Beauchamp (1993)

	Balanophyllia europaea	*Balanophyllia elegans*
Trophic strategy	Zooxanthellate coral	Azooxanthellate coral
Demography	Large coral size (maximum length = 21 mm)	Small coral size (maximum length < 10 mm)
	Long time of turnover (3.6 years)	Short time of turnover (1.3 years)
	Long longevity (maximum = 20 years)	Short longevity (maximum = 7 years)
	Low population density (mean = 16 individuals/m^2)	High population density (mean = 563 individuals/m^2)
Reproductive biology	Hermaphroditism	Gonochorism
	High fecundity (14 mature oocytes/100 mm^3polyp volume)	Low fecundity (6 mature oocytes/100 mm^3polyp volume)
	Short period of embryo incubation (4–5 months)	Long period of embryo incubation (14–15 months)
	Small planulae size (mean oral-aboral diameter = 2,150 μm)	Large planulae size (mean oral-aboral diameter = 4,000 μm)
	Pelagic dispersion of planulae	Benthic dispersion of planulae

be removed sustainably from populations (i.e., the size at maximum yield), a wider use of this model could contribute to techniques for the transplantation of corals from "pristine" reef habitats to damaged areas in need of restoration (Rinkevich 1995; Edwards and Clark 1998; Epstein et al. 1999).

The approach used in this study, the Beverton Holt model, to examine the population dynamics of a solitary temperate coral may have wider applications to other scleractinians. Due to the increasing exploitation of corals on a global scale for the jewelry and handicraft industries and for live displays in aquariums, sustainable management programs are urgently needed for the commercial harvesting of coral populations (Rinkevich 1995; Bentley1998; Hatcher1999). Broader application of the Beverton and Holt model to suitable coral species would reduce over-harvesting and rapid depletion of stony coral populations in economies that depend upon this natural resource, and may contribute to the recovery of damaged and degraded reefs.

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