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Sexual reproduction of the solitary sunset cup coral *Leptopsammia pruvoti* (Scleractinia, Dendrophylliidae) in the Mediterranean. 2. Quantitative aspects of the annual reproductive cycle

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Abstract There are few data on the reproductive biology of coral species living in temperate zones, particularly in the Mediterranean Sea. *Leptopsammia pruvoti* is a solitary coral that is commonly found in sea caves and under overhangs throughout the Mediterranean basin and along European coasts from Portugal to southern England. In this paper, we describe its annual reproductive cycle in the eastern Ligurian Sea near the city of Leghorn (Tuscany, Italy). Polyps were sexually mature at 3 mm in length (maximum diameter of the oral disc), were dioecious with a sex ratio of 1:1, and brooded their larvae. The maturation of spermaries took 12 months and oocytes 24 months. The rate of gonad development increased significantly from November to January, fertilization occurred from January to April and planulation during May and June. Seasonal variations in water temperature and photoperiod may have played an important role in regulating reproductive events. The amount of energy devoted to male gametogenesis (quantified by gonad index) was significantly higher in the sex separated species *L. pruvoti* than in the hermaphroditic dendrophylliid *Balanophyllia europaea*, whose reproduction has been studied in a previous work. We hypothesize that this difference is due to the contrasting sexuality or fertilization biology of these two species (cross-fertilization in the sex separated *L. pruvoti* versus possibly self-fertilization in the hermaphroditic *B. europaea*). Greater male sexual allocation in reproductive strategies characterized by dioecism or cross-fertilization when compared to those characterized by hermaphroditism or self-fertilization is common in plant

mating systems. In relation to other solitary dendrophylliids, *L. pruvoti* presents an 'r'-reproductive strategy.

Introduction

Understanding reproductive biology, including patterns of fecundity, sex ratio, and seasonal cycles in reproduction, is fundamental to the comprehension of the population dynamics of marine organisms. Gamete production also is a key component of fitness. Data on the age and/or size at sexual maturity as well as on the sex ratio are essential for the study of the demography of marine invertebrates (Harvell and Grosberg 1988; Beiring and Lasker 2000). Sexual maturity, which depends on the size and age of the organism, is determined by a balance between the growth rate and risk of mortality. Variations in age and size at the time the organism first reproduces, and the sex ratio, influence population growth rates (Harvell and Grosberg 1988; Dobson 1998; Fujiwara and Caswell 2001). These variations are important as they may represent the beginning of evolutionary divergences (Richmond and Hunter 1990). When there is an increase in fitness, small differences in reproductive strategies among populations may result in speciations (Moran 1992; Stearns 1992).

Until the 1970s, available data on reproduction in scleractinians was primarily based on studies conducted on farmed populations, or on sporadic field observations (Fadlallah 1983a; Richmond and Hunter 1990). More recently, research has focused on colonial species living in tropical and sub-tropical climates (Fadlallah 1983a; Willis et al. 1985; Babcock et al. 1986; Szmant 1986; Harrison and Wallace 1990; Richmond and Hunter 1990; Richmond 1997; Lam 2000; Heltzel and Babcock 2002; Neves and Pires 2002). Very few data are available on the reproductive biology of solitary coral species living in temperate zones (Szmant-Froelich et al. 1980; Tranter et al. 1982; Stoddart and Black 1985; Ward 1992; Beauchamp 1993). Particularly for the Mediterranean

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Sea, the little information we have comes from a modest number of observations recorded over a century ago by Lacaze-Duthiers (1873, 1897) on the solitary species *Caryophyllia smithi*, *Balanophyllia regia*, and *Leptopsammia pruvoti* and on the colonial species *Astroides calycularis* and *Cladopsammia rolandi*, and from some recent studies conducted by our laboratory on the solitary corals *Balanophyllia europaea* and *Leptopsammia pruvoti* (Goffredo and Telò 1998; Goffredo and Zaccanti 2004; Goffredo et al. 2000, 2002, 2004a, b, 2005).

In scleractinians, the most common sexual condition is hermaphroditism; gonochorism occurs in 25% of the species studied (Fadlallah 1983a; Harrison and Wallace 1990; Richmond and Hunter 1990; Hall and Hughes 1996; Richmond 1997). Harrison (1985) suggests that sexual condition is a constant trait at higher taxonomic groupings. The annual cycle of gametogenesis usually culminates with a short period in which gametes are released into the environment where external fertilization occurs (Oliver et al. 1988; Harrison and Wallace 1990; Richmond and Hunter 1990). It is important that gamete development and release be synchronous in order to maximize fertilization rate and reproductive success, since the rapid dilution of gametes in the aquatic environment lowers the probability of fertile encounters (Harrison and Wallace 1990). Regulation of the reproductive cycle has been correlated to several environmental factors (Harrison et al. 1984; Babcock et al. 1986; Harrison and Wallace 1990; Penland et al. 2004). While some authors propose that the main factors regulating the annual reproductive cycle of corals are seasonal variation in photoperiod and water temperature (Giese and Pearse 1974; Babcock et al. 1986; Oliver et al. 1988; Harrison and Wallace 1990; Richmond and Hunter 1990; Soong 1991; Penland et al. 2004), others suggest that these variations may not affect the regulation of reproductive events (Beauchamp 1993; Babcock et al. 1994; Fan and Dai 1995). The period of germ cell release into the environment varies from site to site (Harrison and Wallace 1990; Richmond and Hunter 1990), and comparing the different periods among regions offers yet another angle of study that could help us understand species responses to different environmental conditions (Oliver et al. 1988; Harrison and Wallace 1990; Babcock et al. 1994; Fan and Dai 1995). These conditions could also influence reproduction by acting as long-term agents exerting selective pressure on the sexuality of populations (Giese and Pearse 1974; Bacci 1975; Rossi 1975; Loya 1976; Van Moorsel 1983; Szmant 1986; Tomascik and Sander 1987; Shaw 1989; Fautin 1992; Ward 1992; Fan and Dai 1995; Acosta and Zea 1997).

Harrison (1985) defines Dendrophylliidae, the family to which *L. pruvoti* belongs, as a gonochoric taxon. Dendrophylliidae is a cosmopolitan family comprising of 148 extant species divided into 19 genera. The genus *Leptopsammia* is made up of ten species of solitary, azooxanthellate corals living in various parts of the globe: one, *L. columna*, lives in the Indian Ocean; four, *L. crassa*, *L. poculum*, *L. queenslandiae*, and *L. stokesi-*

ana, live in the western Pacific Ocean; another, *L. trinitatis*, lives in the western Atlantic Ocean; and the last four, *L. chevalieri*, *L. formosa*, *L. Britannica*, and *L. pruvoti*, live in the eastern Atlantic (Avian et al. 1995; Cairns 1999; Cairns et al. 1999; Veron 2000). According to some authors, the genera *Leptopsammia* and *Balanophyllia* are so closely related that the two taxa may be considered synonymous (Fadlallah 1983a; Heltzel and Babcock 2002). In accordance with Cairns et al. (1999), authors of the most recently compiled list of scleractinian extant species, we also consider *Leptopsammia* and *Balanophyllia* as two distinct taxa.

L. pruvoti is geographically distributed throughout the Mediterranean basin and along European coasts from Portugal to southern England. It is one of the most commonly found organisms in sea caves and under overhangs in waters ranging in depth from the surface to 70 m (Zibrowius 1980). In the Mediterranean, at depths of 15–21 m, this species has a population density of 4,000 to 17,000 individuals per square meter (S. Goffredo, personal observations).

In this paper, we describe the annual reproductive cycle of *L. pruvoti* in Calafuria, located in the eastern Ligurian Sea near the city of Leghorn, Italy. Data are presented on the size of individuals at sexual maturity, sex ratio, fecundity, and seasonal patterns of gonadal development and planulation.

Materials and methods

Scuba divers collected polyps of *Leptopsammia pruvoti* Lacaze-Duthiers (1897) at Calafuria (Leghorn; 43°28.4'N, 10°20'E) during monthly trips from July 2001 to September 2002 at a depth of 15.0–16.5 m. For a more detailed description of the topography and habitat of the sampling area, see Goffredo et al. (2004a). The average interval between samplings was 30 days (SE = 2). Water temperature was measured directly in the field at the depth and time of sampling using a mercury thermometer. Astronomical almanacs were used to calculate photoperiods.

During each sampling period, 12 individuals were collected across the entire size range of the population (1–8 mm maximum diameter of the oral disc; S. Goffredo, personal observations). Biometric analyses were performed in the field where we measured length (*L*, maximum diameter of the oral disc), width (*l*, minimum diameter of the oral disc), and height (*h*, oral–aboral diameter of the polyp), while volume (*V*) was calculated using the formula $V = h(L/2)(l/2)\pi$; after Goffredo and Telò (1998). Specimens were then fixed in Bouin solution and transferred to the laboratory for histological analyses. After decalcification in EDTA for approximately 4 h, and dehydration in a graded alcohol series, the polyps were embedded in paraffin and serial transverse sections were cut at 7 μ m from the oral to the aboral poles. Tissues were then stained with Mayer's hematoxylin and eosin.

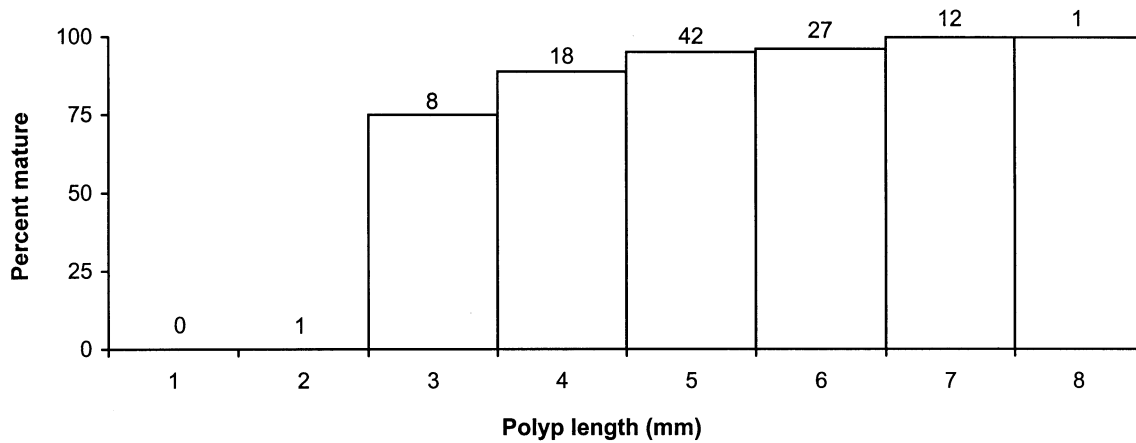


Fig. 1 *Leptopsammia pruvoti*. Percentage of sexually mature individuals per size class collected at Calafuria, to the south of Leghorn, Italy. Value above bars indicate the number of polyps sampled (total $N=109$)

Cytometric readings were taken with a LEICA Q5001 W image analyzer. We measured the maximum and minimum diameters of the spermaries and oocytes in nucleated sections. The size of each reproductive element was determined as the average of the two diameters. Spermaries were classified into five morphologically identified developmental stages (after Rinkevich and Loya 1979; Szmantz-Froelich et al. 1980; Fadlallah and Pearse 1982a, b; Stoddart and Black 1985; Beauchamp 1993; Kruger and Schleyer 1998; Kramarsky-Winter and Loya 1998; Glynn et al. 2000; Goffredo et al. 2002). We noted the presence and developmental stages of embryos found in the coelenteron of female polyps (Goffredo and Telò 1998; Goffredo et al. 2005). The size of the embryos was calculated as the average of the maximum and minimum diameters.

Oocytes and spermaries were ellipsoidal in shape and their volume was estimated using the formula $V_0 = (4/3)\pi(D/2)(d/2)^2$, where V_0 = volume of oocyte or spermary, D = maximum diameter, and d = minimum diameter. Gonadal volume was calculated as the sum of the volume of each oocyte or spermary. The index of gonadal development was expressed as the percentage of body volume taken up by the gonads (Hall and Hughes 1996; Goffredo et al. 2002).

Fecundity was expressed as the number of mature oocytes produced per polyp per reproductive season. We used the following formula to calculate the number of mature oocytes: fecundity = $(A \times B)/C$, where A is the length of the "ovary" (based on the number of sections in which oocytes were present), B is the observed frequency of mature oocytes, C is the size of the mature oocytes (after Kruger and Schleyer 1998; Goffredo et al. 2002).

Results

Sexuality and reproductive mode

Leptopsammia pruvoti was gonochoric and ovoviparous (=planula brooder). The sexually mature polyps we

examined either had only spermaries (56 male individuals; $L_{(mm)}=5.0$, $SE=0.15$) or only oocytes (45 female individuals; $L_{(mm)}=4.9$, $SE=0.15$). Sex ratio was 1:1, the chi-square test, $\chi^2=1.20$, $df=1$, $P>0.25$ was calculated for all the sexually mature individuals we examined. We found incubated embryos in the coelenteron of females collected from March to May 2002. Size at sexual maturity was $L_{(mm)}=3$ (Fig. 1). According to biometric analyses (S. Goffredo, personal observations), a polyp in this category has $l_{(mm)}=2-3$, $h_{(mm)}=2-3$, $V_{(mm)}^3=8-18$.

Distribution of gametogenetic processes along the oral-aboral axis in gonochoric individuals

Gonad distribution along the polyps' oral-aboral axis was significantly different in males and females (Fig. 2). While spermary size in males had no correlation to the distance from the oral pole, in females, the size of the oocytes had a positive correlation. Furthermore, the average distance of spermaries from the oral pole was significantly lesser than that for oocytes (Student's t -test, $t=7.277$, $df=11,788$, $P<0.001$; Fig. 2).

Annual reproductive cycle

Gonadal size increased sixfold in males and threefold in females during autumn and winter, from November to January, the months during which the photoperiod is the shortest of the year and the water temperature is the coldest (Fig. 3). In females, we found two distinct stocks of oocytes, composed of small cells (from 20 to 340 μm) or large cells (from 340 to 680 μm). In males, we observed an acceleration in spermatogenesis with the appearance of mature spermaries (Fig. 4).

Fertilization took place from January to April, during which both photoperiod and water temperature were increasing (Fig. 3). In males, we observed the emptying of spermaries, and in females, the disappearance of large

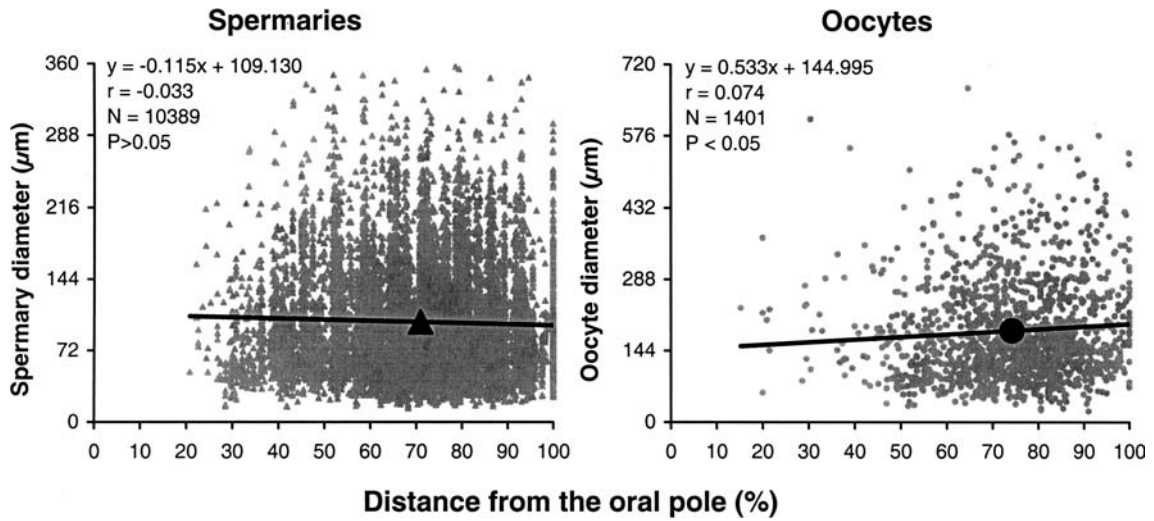


Fig. 2 *Leptopsammia pruvoti*. Distribution according to size along the oral–aboral axis of spermaries in male polyps, and oocytes in female polyps. The distance from the oral pole is expressed as a percentage: 0% = at oral pole level and 100% = at aboral pole level. *Filled triangle* The point at which the mean spermary distance

(71.00%, SE=0.15) and mean spermary size (100.99 μm , SE = 0.53) intersect. *Filled circle* The point at which mean oocyte distance (74.21%, SE=0.39) and mean oocytes size (184.55 μm , SE=2.76) intersect. Note that the value ranges on the ordinate axes are different

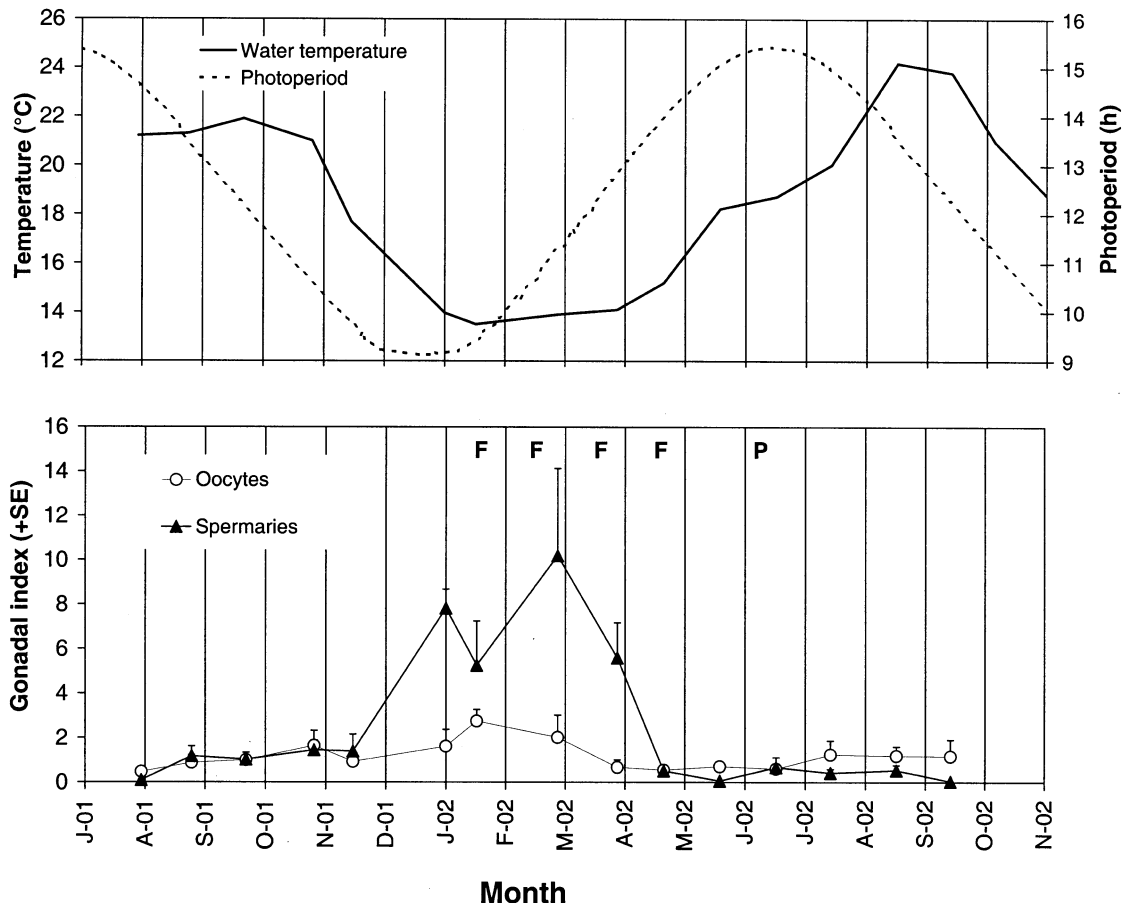


Fig. 3 *Leptopsammia pruvoti*. Variations in gonadal development, water temperature, and photoperiod from July 2001 to September 2002. The mean length of male polyps examined was 5.0 mm

(SE=0.15; N=56), and of female polyps examined was 4.9 mm (SE=0.15; N=45). *F* period of fertilization, *P* period of planulation

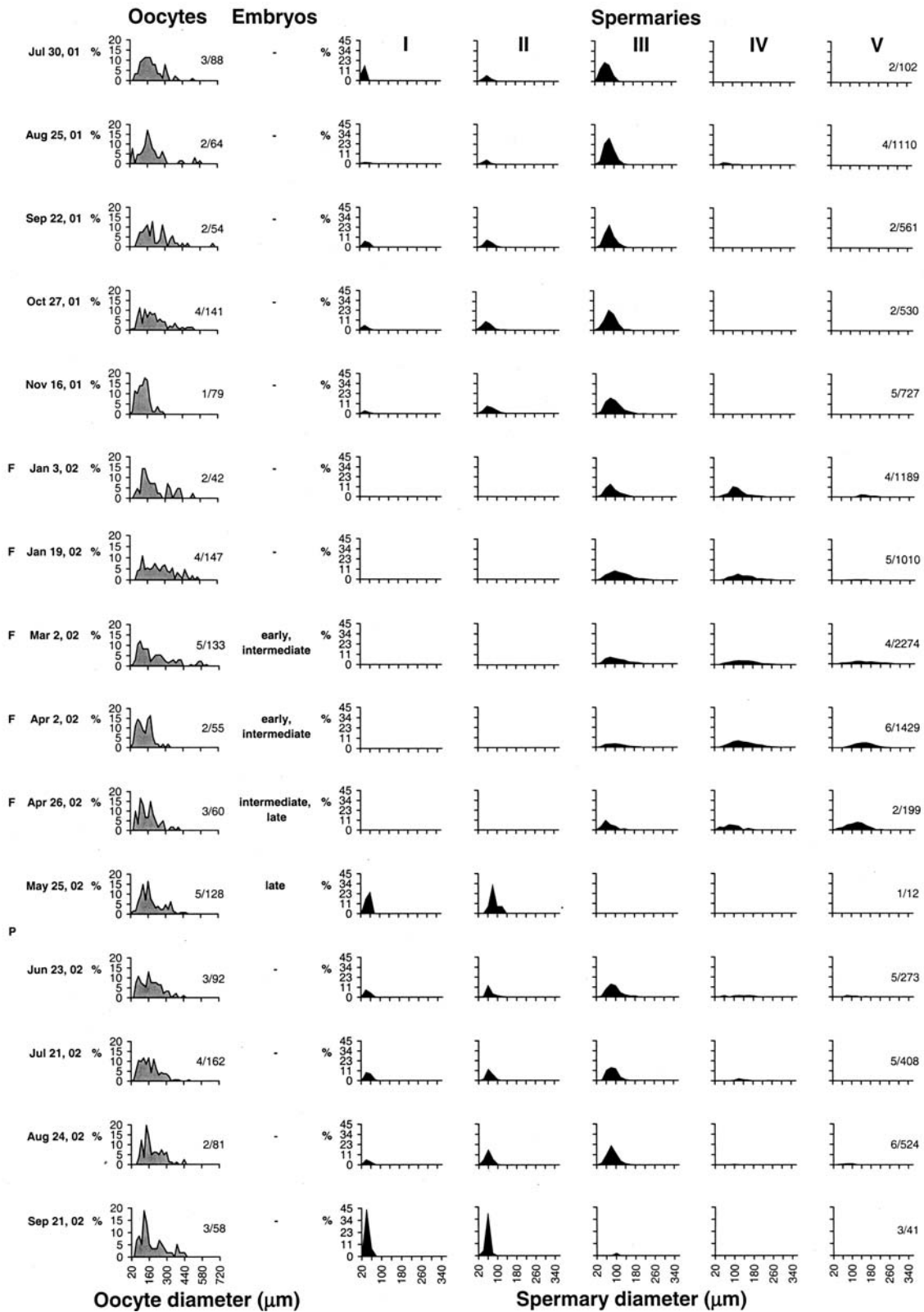


Fig. 4 *Leptosammia pruvoti*. Size–frequency distribution of oocytes and of the five stages of spermary maturation in monthly samples collected at Calafuria from July 2001 to September 2002. The mean length of male polyps examined was 5.0 mm (SE=0.15; $N=56$), and of female polyps was 4.9 mm (SE=0.15; $N=45$).

Values reported indicate the number of polyps/the total number of oocytes or spermaries measured per monthly sample. The *middle column* illustrates the presence and stage of development of embryos found in the coelenteric cavity of females. *F* fertilization period, *P* planulation period

Table 1 Characteristics of the reproductive biology of the three species of solitary scleractinian corals belonging to the family Dendrophylliidae whose annual reproductive cycle is known

	<i>L. pruvoti</i>	<i>B. europaea</i>	<i>B. elegans</i>
Sexual condition	Gonochoric	Hermaphroditic	Gonochoric
Individual size at sexual maturity [fraction of maximum size (observed size)]	32% (3 mm)	38% (8 mm)	56% (6 mm)
Maximal polyp size (oral disc maximum diameter, mm)	8	21	10
Fecundity (mature oocytes/100 mm ³ polyp)	36–105	8–14	2–6
Embryonic incubation period (months)	1–4	4–5	14–15
Planulae size (oral–aboral axis, μ m)	1,145	2,150	4,000

Data sources: this paper and Goffredo et al. (2005) for *Leptopsammia pruvoti*; Goffredo et al. (2002, 2004a) and Goffredo and Zaccanti (2004) for *Balanophyllia europaea*; Fadlallah and Pearse (1982a) and Beauchamp (1993) for *Balanophyllia elegans*

oocytes from the mesenteries and the subsequent appearance of embryos in the coelenteric cavity (Figs. 3, 4).

During the months immediately following the period of fertilization (April–May), we observed the growth of the oocyte stock that remained after the reproductive event, the recruitment of new oocytes, and incubated embryos in females, while we observed the development of early stages of spermary maturation in males (Fig. 4).

Planulation took place during the months of May and June, the period in which days are approaching their maximum yearly length (Fig. 3). The coelenteric cavity no longer contained mature embryos (Fig. 4).

Size of mature oocytes and fecundity

Mature oocytes ranged in size from 340 to 680 μ m (Fig. 4). We found an average of 20.2, SE = 5.0 mature oocytes in average-sized females of $L_{(mm)} = 4.4$, SE = 0.2 ($l_{(mm)} = 4.1$, SE = 0.2; $h_{(mm)} = 3.7$, SE = 0.3; $V^3_{(mm)} = 56.3$, SE = 7.6; $N = 17$ polyps collected during the period of maximum annual gonadal development, Fig. 3).

Discussion

Sexuality and reproductive mode

The reproductive cycle of a species of the scleractinian genus *Leptopsammia* is described for the first time in this paper. The sexual condition and reproductive mode we found in *L. pruvoti* are the same as those observed by Lacaze-Duthiers (1897), and as expected in the Dendrophylliidae, a taxon in which gonochorism and planulae brooding are the most prevalent reproductive characteristics (Fadlallah 1983a; Harrison 1985; Goffredo et al. 2000, 2005). Following Szmant (1986), in gonochoric species of coral, the incubation of embryos should yield a sex ratio that favors females. This deviation does not appear to occur in *L. pruvoti* or in *Balanophyllia elegans*, another dendrophylliid coral living along North America's western coast (Fadlallah and Pearse 1982a). The 1:1 sex ratio we observed leads us to

hypothesize that mating is random, and that the genetic structure of the population follows the Hardy–Weinberg equilibrium (Maynard-Smith 1978). We are currently conducting genetic studies in our laboratory on the population structure of *L. pruvoti*.

The size of *L. pruvoti* individuals at sexual maturity compared with other solitary dendrophylliids whose reproductive cycle is known (Table 1) indicates that reproductive activity begins early in this species, at 3 mm polyp length.

Oral–aboral distribution of gametogenic processes

We observed a different distribution of reproductive elements along the oral–aboral axis in gonochoric polyps of *L. pruvoti* than we have observed for hermaphroditic polyps of *B. europaea* (Goffredo et al. 2002). In the latter, mature spermaries tend to be distributed towards the oral pole, while mature oocytes are distributed towards the aboral pole. We have hypothesized that this type of arrangement may decrease encounters among opposite sex gametes produced by the same individual thus serving as a “statistical barrier” to self-fertilization. In *L. pruvoti*, the absence of a differential spermary distribution along the oral–aboral axis in males could be related to this species' gonochorism, which ensures the physical separation of male and female gametogenic processes in separate individuals, and in turn assures cross-fertilization.

The reproductive cycle

The size frequency distribution of spermaries observed during monthly samples suggests that spermatogenesis in *L. pruvoti* follows an annual cycle, and that male germ cells take 12 months to mature. In the case of females, oocyte distribution indicates that female germ cells take approximately 24 months to mature, because of the fact that two oocyte stocks were present. Similar gametogenic cycles have been documented for the two other species of solitary corals belonging to the family Dendrophylliidae whose reproductive cycles have been observed in detail:

B. europaea in the Mediterranean Sea (Goffredo and Telò 1998; Goffredo et al. 2002), and *B. elegans* along the western coast of North America (Fadlallah and Pearse 1982a; Beauchamp 1993). A longer maturation period for female germ cells is typical of gametogenesis in anthozoans (Benayahu et al. 1990; Harrison and Wallace 1990; Richmond and Hunter 1990; Coma et al. 1995; Acosta and Zea 1997; Fan and Dai 1995, 1998; Kra-mar-sky-Winter and Loya 1998; Goffredo et al. 2002).

We observed that the reproductive phase (gonadal development, fertilization, planulation) in the annual cycle of *L. pruvoti* takes place from November to June. As the period from June to November was one of reproductive quiescence, these summer–autumnal months may represent a trophic phase, during which polyps invest in somatic growth. During the summer zooplankton abundance in most parts of the Mediterranean Sea is at its annual peak, increasing food intake by sit-and-wait predators like cnidarian polyps (Rodriguez 1983; Fonda-Umani 1992; Siokou-Frangou 1996; Chomsky et al. 2004). We suggest that reproductive events in this species occur in relation to seasonal variations in water temperature and photoperiod, as has been suggested for other anthozoans (Richmond and Hunter 1990; Soong 1991; Clayton and Collins 1992; Coma et al. 1995; Steiner 1995; Tanner 1996; Glynn et al. 2000). In winter, the fact that photoperiod and water temperature reach their annual lows may act as a signal that triggers the start of gonadal development. The subsequent increase in photoperiod and water temperature, during the winter and spring, could trigger the release of sperm and fertilization of eggs. Similarly, maximal photoperiod, occurring at the summer solstice, could trigger the start of planulation. Different interpretations have been given to the role played by photoperiod and water temperature in the regulation of the annual reproductive cycle in other dendrophylliids. For example, in *B. europaea* it has been suggested that both these factors play an important role in regulating major reproductive events (Goffredo et al. 2002), while in *B. elegans* it has been suggested that the reproductive cycle is regulated by water temperature alone, and that it is in no way affected by the photoperiod (Fadlallah and Pearse 1982a; Beauchamp 1993). It is necessary that future experimental studies on populations raised in the laboratory be performed in order to better understand the role played by environmental factors in regulating reproductive events in these scleractinians.

In *L. pruvoti*, we found the body volume occupied by male gonads to be 3.7 times greater than that held by female gonads. The estimated ratio of mature spermatozoa to mature oocytes is $1.04 \times 10^9:1$. In the simultaneous hermaphroditic species *B. europaea*, the body volume used by male gonads is the same as that of female gonads, with a ratio of mature spermatozoa to mature oocytes of $1.97 \times 10^8:1$ (Goffredo et al. 2000, 2002). From these figures, we can deduce that the proportion of energy devoted to male gametogenesis is significantly higher in *L. pruvoti* than in *B. europaea*.

This difference could be related to the contrasting sexuality or fertilization biology of these two species. Cross-fertilization likely takes place in the case of the gonochoric *L. pruvoti*, while in the hermaphroditic *B. europaea* fertilization could be autogamous (Goffredo et al. 2004b). Greater male sexual allocation in reproductive strategies characterized by dioecism or cross-fertilization when compared to those characterized by hermaphroditism or self-fertilization is common in plants (Cruden 1977; Charnov 1982; Mione and Anderson 1992; Jürgens et al. 2002).

In this study, information on the annual reproductive cycle was collected over a 15-month period and therefore inter-annual variation was not examined. However, similar stages in the reproductive cycle were observed in the period from July to September in both years examined (2001 and 2002).

Reproductive Strategies

Reproductive strategies of solitary dendrophylliids in which the reproductive cycle has been observed (Table 1) seem to cover the entire range of the r–K life history strategy continuum (Pianka 1970). When we compare the two gonochoric species, *L. pruvoti* and *B. elegans*, we find that the former reaches sexual maturity early, has a higher level of fecundity, has a shorter embryonic incubation period and smaller size planulae representing an r–reproductive strategy, while *B. elegans* reaches sexual maturity later, is less fecund, has a longer embryonic incubation period and larger size planulae representing a K–reproductive strategy. The reproductive strategy of the hermaphrodite *B. europaea*, whose reproductive characteristics lie somewhere between the above-mentioned gonochoric species characteristics, is placed half-way along the r–K continuum.

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