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# Sexual reproduction of the solitary sunset cup coral *Leptopsammia pruvoti* (Scleractinia: Dendrophylliidae) in the Mediterranean.

## 1. Morphological aspects of gametogenesis and ontogenesis

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**Abstract** Information on the reproduction in scleractinian solitary corals and in those living in temperate zones is notably scant. *Leptopsammia pruvoti* is a solitary coral living in the Mediterranean Sea and along Atlantic coasts from Portugal to southern England. This coral lives in shaded habitats, from the surface to 70 m in depth, reaching population densities of  $>17,000$  individuals  $m^{-2}$ . In this paper, we discuss the morphological aspects of sexual reproduction in this species. In a separate paper, we report the quantitative data on the annual reproductive cycle and make an interspecific comparison of reproductive traits among Dendrophylliidae aimed at defining different reproductive strategies. The present study on *L. pruvoti* is the first in-depth investigation of the reproductive biology of a species of this genus. As expected for a member of the family Dendrophylliidae, *L. pruvoti* is a gonochoric and brooding coral. The gastrodermal tissue of the gametogenic mesenteries we examined was swollen and granular, which led us to hypothesize that interstitial cells could have a trophic function favoring gametogenesis. Undifferentiated germ cells arose in the gastrodermis and subsequently migrated to the mesoglea, where they completed gametogenesis. During spermary development, spermary diameter increased from a minimum of 14  $\mu m$  during the immature stages to a maximum of 410  $\mu m$  during the mature stages. As oogenesis progressed, we observed a gradual reduction in the nucleus to cytoplasm ratio due to the steady synthesis of yolk. During the final stages of oogenesis, after having migrated to the extreme periphery of the oocyte and having firmly adhered to the oolemma, the nucleus be-

came indented, assuming a sickle or dome shape. We can hypothesize that the nucleus' migration and change of shape may have to do with facilitating fertilization and determining the future embryonic axis. During oogenesis, oocyte diameter increased from a minimum of 20  $\mu m$  during the immature stage to a maximum of 680  $\mu m$  when mature. Embryogenesis took place in the coelenteron. We did not see any evidence that even hinted at the formation of a blastocoel; embryonic development proceeded via stereoblastulae with superficial cleavage. Gastrulation took place by delamination. Early and late embryos had diameters of 204–724  $\mu m$  and 290–736  $\mu m$ , respectively. When released, the larvae had completed ontogenesis and swam by a ciliary movement with the aboral pole at the anterior, their shape varied from spherical to cylindrical (in the latter the oral–aboral axis measured 695–1,595  $\mu m$  and the transversal one measured 267–633  $\mu m$ ).

### Introduction

Sexual reproduction, which entails the dispersal of genetically unique larval recruits, plays a crucial role in the life cycle and guarantees the survival and evolution of the community (Harrison and Wallace 1990; Hughes et al. 1992). Information on sexual reproduction is essential to understanding genetic structure and population connectivity and their effects on population dynamics, as well as to understanding the resistance and resilience of populations vis à vis natural and anthropogenic disturbances (Connell and Keough 1985). Basic data includes sexuality (hermaphroditic or gonochoric), reproductive mode (broadcasting or brooding), embryonic and larval development.

Studies to date on sexual reproduction in scleractinians have been almost exclusively on tropical and subtropical colonial corals (Fadlallah 1983a; Harrison et al. 1984; Shlesinger and Loya 1985; Szmant 1986; Harrison

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and Wallace 1990; Richmond and Hunter 1990; Richmond 1997). In most cases, reproduction is characterized by hermaphroditism and broadcasting, and by an annual gametogenic cycle that ends with a short period during which germ cells are released into the environment. Temperature, photoperiod, tides and lunar phases seem to play a role in synchronizing gametogenic processes.

We do not have much information on temperate scleractinians (Beauchamp 1993; Harii et al. 2001; Heltzel and Babcock 2002). Aside from recent work by Goffredo et al. (2002, and references therein), studies from the Mediterranean basin date back to the 19th century, to the work of Lacaze-Duthiers (1873, 1897). Finally, as noted by Heltzel and Babcock (2002), most studies focus on colonial corals, leaving a lack of knowledge on solitary species. Given the importance of reproduction and recruitment to survival recovery following disturbances, and for the broader conservation and management of scleractinian species, widening our knowledge would help us to construct a database that would allow comparisons of different life-strategy adaptations in scleractinians, as well as between solitary and colonial organisms in general (Harrison and Wallace 1990).

Dendrophylliidae is a cosmopolitan taxon of colonial or solitary corals, comprising 148 extant species divided into 19 genera (Avian et al. 1995; Cairns 1999; Cairns et al. 1999). There are seven species of Dendrophylliidae living in the Mediterranean today, subdivided into five genera, two of which, *Balanophyllia* and *Leptopsammia*, are solitary. Systematics of these two genera is not clear, some authors consider them to be synonymous (*Balanophyllia* = *Leptopsammia* in Vaughan and Wells 1943; Wells 1956; Fadlallah 1983a; Heltzel and Babcock 2002), while others argue that they are two separate taxa (Zibrowius 1980; Cairns et al. 1999). We agree with Cairns et al. (1999) and their most recent list of extant species of Scleractinia, in which *Leptopsammia* and *Balanophyllia* are recorded as two distinct taxa.

According to Cairns et al. (1999), the genus *Leptopsammia* comprises ten species, geographically distributed in the Atlantic, Indian and central-western Pacific Oceans. There is only one species, *Leptopsammia pruvoti* Lacaze-Duthiers, 1897, living in the Mediterranean (Avian et al. 1995). *L. pruvoti* has also been reported along Atlantic coasts from Portugal to southern England. Along the species' distributional area, the mean annual sea surface temperature ranges from 12°C, in southern England, to 19°C, in the Mediterranean. This species tends to live in shaded habitats, under overhangs and in grottos, at depths ranging from the surface to 70 m (Zibrowius 1980). The species reaches an average population density of 4,000–17,000 individuals m<sup>-2</sup> at depths ranging between 15 and 21 m (authors' personal observations). There is not much information on the biology of this species. The only data available concerning reproduction dates back > 100 years (Lacaze-Duthiers 1897) from samples collected in the Golfe du

Lion, near Marseilles. The author reported sex-separated individuals and embryonic development within the coelenteron of females.

We are currently studying sexual reproduction in *L. pruvoti* living in the eastern Ligurian Sea near Leghorn. We are conducting morphological, cyto-histometric and quantitative studies on the gametogenesis, embryonic development and larval stages of these organisms, as well as genetic and population dynamics studies (manuscripts in preparation). The studies being conducted on *L. pruvoti* are part of a broader research framework that we have developed to fill the gaps in our knowledge of the biology of Mediterranean scleractinians (Goffredo and Telò 1998; Goffredo et al. 2000, 2002, 2004a, 2004b; Goffredo and Zaccanti 2004). In this paper we describe morphological aspects of spermatogenesis, oogenesis, embryogenesis and larval development in *L. pruvoti*. In a separate paper, we will report on quantitative data regarding the annual reproductive cycle, including the size of individuals at sexual maturity, sex ratio, the cyto-histometric analyses of gametogenesis, a comparison of gonadal development with environmental parameters, seasonality in sexual development and planulation, and fecundity.

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## Materials and methods

Polyps of *Leptopsammia pruvoti* were collected at Calafuria (Leghorn; 43°28.4'N; 10°20'E) in 18 monthly samplings from July 2001 to December 2002. Divers took samples at depths of 15–17 m (see Goffredo et al. 2004a for a description of the habitat and topography of the sampling area).

We made sure that the samples, made up of 12 specimens each, included the entire size range of the population (1–8 mm maximum diameter of the oral disc). Biometric analyses were performed in the field; 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) were measured. Volume ( $V$ ) was calculated using the formula:

$$V = h * (L/2) * (l/2) * \pi \quad (1)$$

(after Goffredo et al. 2002).

Specimens were then fixed and transferred to the laboratories for histological analysis. After decalcification and dehydration, the polyps were embedded in paraffin and serial transverse sections were cut at 7- $\mu$ m intervals from the oral to the aboral poles.

Histological observations of gametogenesis and embryogenesis were made under a light microscope. Cyto-histological readings were made with a LEICA Q5001 W image analyzer. We measured the maximum and minimum diameters of the spermaries and of the oocytes in nucleated sections. The size of each reproductive element was determined as the average of the two diameters. In accordance with earlier studies on

gametogenesis in scleractinians by Beauchamp (1993), Kramarsky-Winter and Loya (1998), Kruger and Schleyer (1998), Glynn et al. (2000) and Goffredo et al. (2002), the spermaries were classified in five developmental stages.

A binocular microscope was used for morphological observations of live larvae released by specimens collected from the sea during the month of March, 2003.

## Results

### Sexual condition and reproductive mode

For this study, we performed histological analysis on 52 specimens, collected in the 14 samplings carried out from 30 July 2001 to 24 August 2002. We found the species *Leptopsammia pruvoti* (Fig. 1) to be sex separated. All specimens examined had either male or female germ cells (Figs. 2, 3); none had both types. We did not observe sexual dimorphism, nor were there significant differences in average body size between males and females (length: males = 5.1 mm, SE = 0.2,  $N = 26$ , females = 5.0 mm, SE = 0.2,  $N = 25$ , student's  $t$ -test  $P > 0.5$ ; volume: males = 74.7 mm<sup>3</sup>, SE = 8.2,  $N = 26$ , females = 70.1 mm<sup>3</sup>, SE = 6.8,  $N = 25$ , student's  $t$ -test  $P > 0.5$ ). Only one specimen collected in May and smaller than the average size of the others did not have differentiated germ cells; we considered it to be sexually immature. Some females had embryos in the coelenteron, indicating a brooding reproductive mode (Fig. 4).

### Spermaries and oocytes

The gastrodermal tissue lining the mesenteries with clearly visible gametocytes was swollen and had a granular appearance (Figs. 2A, B, 3A, B).

The spermaries (Fig. 2) were made up of groups of germ cells, located in the mesentery, and delineated by

the mesogleal envelope. We identified five developmental stages:

Stage I—Undifferentiated germ cells arose in the gastrodermis and then migrated towards the mesoglea of the mesentery where they regrouped forming the spermary. The spermary was made up of an early aggregation of three to ten spermatogonia (Fig. 2A). Spermaries had a diameter of 36  $\mu\text{m}$  (SE = 0.7,  $N = 299$ ) and seemed to grow larger as they incorporated additional spermatogonia.

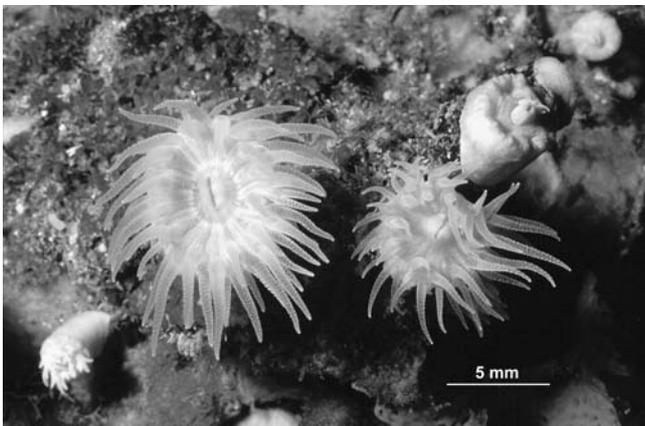
Stage II—the spermary was made up of a group of spermatocytes undergoing meiosis (Fig. 2B). The mesogleal layer enveloping the spermary had not yet formed a wall. Spermary diameter was 58  $\mu\text{m}$  (SE = 0.8,  $N = 647$ ).

Stage III—the spermary, made up of a group of spermatocytes undergoing meiosis, was delineated by a clearly differentiated wall formed by the mesoglea (Fig. 2C). Spermary diameter was 86  $\mu\text{m}$  (SE = 0.6,  $N = 4,134$ ).

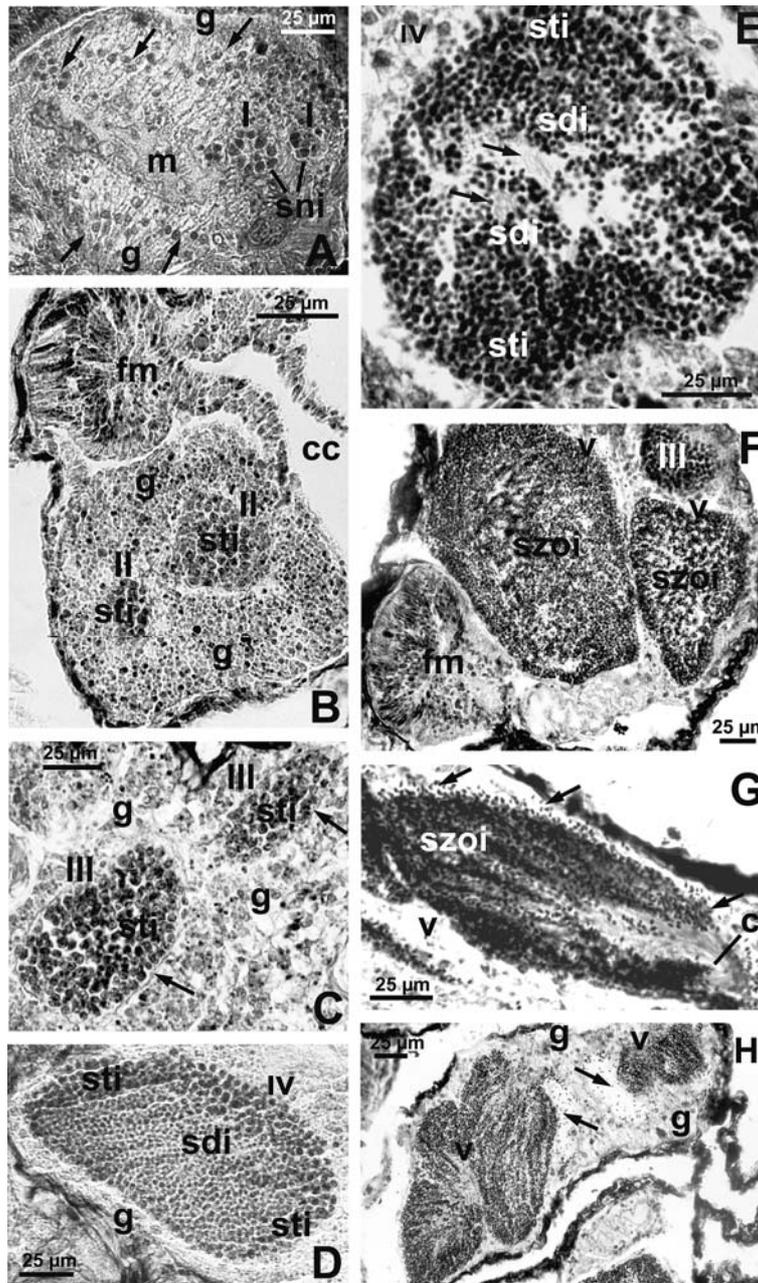
Stage IV—the spermary showed a centripetal maturation gradient in that less mature and larger germ cells (spermatocytes) were located on the periphery of the spermary, while more mature and smaller ones (spermatids) were located in the center (Fig. 2D, E). Spermatid tails were projecting towards the spermary's central cavity (Fig. 2E). Spermary diameter was 127  $\mu\text{m}$  (SE = 1.6,  $N = 1,468$ ).

Stage V—the spermary was made up of a mass of spermatozoa with their tails projecting in the same direction (an arrangement known as a "bouquet"; Fadlallah and Pearse 1982; Glynn et al. 1991, 1996, 2000; Fan and Dai 1998; Neves and Pires 2002; Fig. 2F–H). At the time of fertilization, the spermatozoa were released into the coelenteron (Fig. 2G, H); the spent spermary left an empty cavity in the mesentery (Fig. 2H). Spermary diameter was 130  $\mu\text{m}$  (SE = 2.3,  $N = 563$ ).

The oocytes were oval-shaped and located in the mesenteries (Fig. 3). The early stages of oogenesis were visible in the mesentery's gastrodermal layers (Fig. 3A). Early oocytes had a diameter ranging from 20 to 34  $\mu\text{m}$ , a centrally located spherical nucleus, a high ratio of nucleus to cytoplasm and a homogeneous cytoplasm. The intermediate stages of oogenesis developed in the mesoglea of the mesenteries (Fig. 3B, C). Intermediate stage oocytes were enveloped by the mesogleal layer and had a diameter ranging from 30 to 345  $\mu\text{m}$ . The nucleus was spherical, and yolk had begun to accumulate, causing a reduction in the ratio of nucleus to cytoplasm. In the late stages of oogenesis, the oocytes were still located in the mesenteries and enveloped by the mesogleal layer, with a diameter ranging from 340 to 680  $\mu\text{m}$  (Fig. 3D–F). During the late stages, yolk synthesis and differentiation were completed. The nucleus



**Fig. 1** *Leptopsammia pruvoti*. Specimens photographed at Calafuria (Leghorn; 43°28.4'N; 10°20'E) at 16 m depth



had also migrated to the cell's periphery, and adhering closely to the cell membrane it changed shape, becoming indented and concave (Fig. 3E, F). During oogenesis, the nucleolus was always positioned on the periphery of the nucleus (Fig. 3A–C, F).

#### Embryos and larvae

While the oocytes were found inside the mesenteries, embryos were located in the coelenteron (Fig. 4). Early-stage embryos were stereoblastulae (they were solid and lacked blastocoels). A cleaved superficial layer was visible surrounding a central yolk mass (Fig. 4A, B). Stereoblastulae had diameters ranging from 204 to

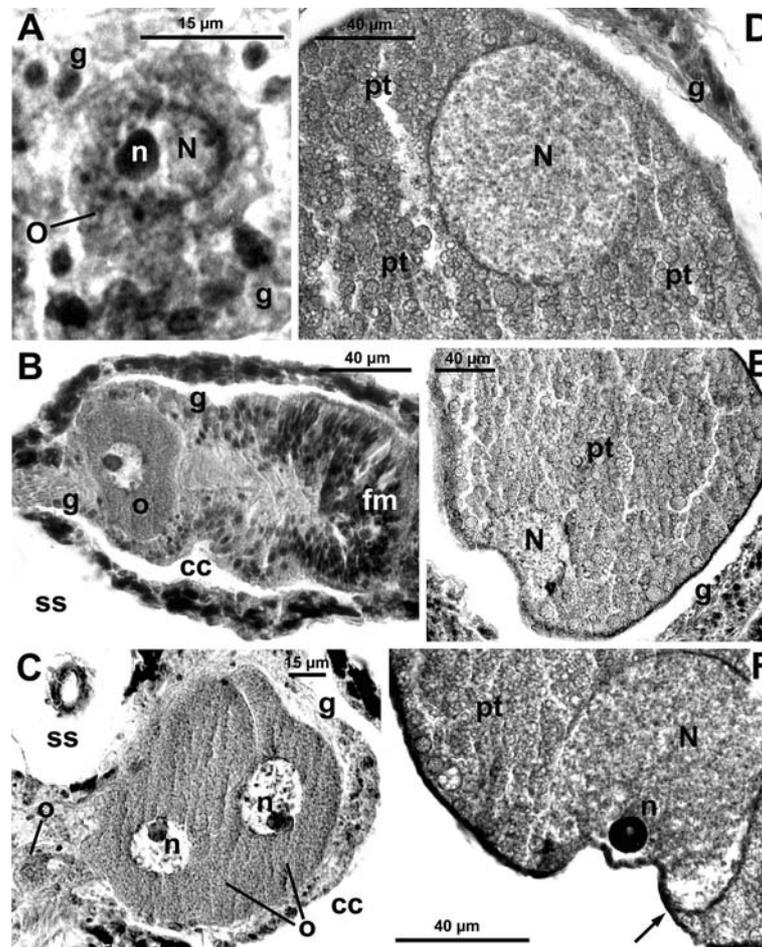
724  $\mu\text{m}$ . During the intermediate stage, called stereogastrula because there was no archenteron, gastrulation by delamination took place (Fig. 4C, D). The ectoderm layer was clearly differentiated and appeared separated from the endodermal mass by a clearly defined mesogleal layer. At this stage of development, the ectoderm was made up of a columnar epithelium, in which differentiated cnidocytes were visible (Fig. 4D). Stereogastrulae had diameters ranging from 204 to 601  $\mu\text{m}$ . At late stage, the stereogastrulae had developed a stomodeum and mesenteries (Fig. 4E–G). The differentiation of the stomodeum began with the proliferation of ectoderm cells and their invagination towards the center of the embryo (Fig. 4E, F). Mesentery differentiation started with the invagination of the mesogleal layer

**Fig. 2A–H** *Leptopsammia pruvoti*. Spermary developmental stages. **A** Early stage. Undifferentiated germ cells are lined up in the mesenteries' gastrodermal layers (*arrows*). Spermaries are formed by the migration of undifferentiated germ cells that move from the gastrodermis and cluster in the mesoglea. Stage I is made up of a group of spermatogonia. **B** Stage II: the spermary is made up of a group of spermatocytes undergoing meiosis. Note how the gastrodermis is swollen and granular. **C** Stage III: the spermary, containing spermatocytes undergoing meiosis, is delineated by a wall that has arisen from the mesoglea (*arrows*). **D** Stage IV: the spermary presents an external layer of spermatocytes and an internal mass of spermatids. **E** Stage IV: spermatocytes are visible on the spermary's periphery, while spermatids with their tails facing the central cavity are visible on the inside (*arrows*). **F** Stage V: the spermary is made up of a mass of spermatozoa. **G** Stage V: shortly before leaving the spermary, mature spermatozoa form "bouquets", with their tails all facing in the same direction. Some spermatozoa are leaving the spermary (*arrows*). **H** Stage V: some spent spermaries (*arrows*) are visible next to the mature spermaries still in the process of releasing spermatozoa (*c* spermatozoa tails; *cc* coelenteric cavity; *fm* mesenterial filament; *g* gastrodermis; *m* mesoglea; *sdi* spermatids; *sni* spermatogonia; *sti* spermatocytes; *szo*i spermatozoa; *I, II, III, IV, V* spermary developmental stage, see "Results")

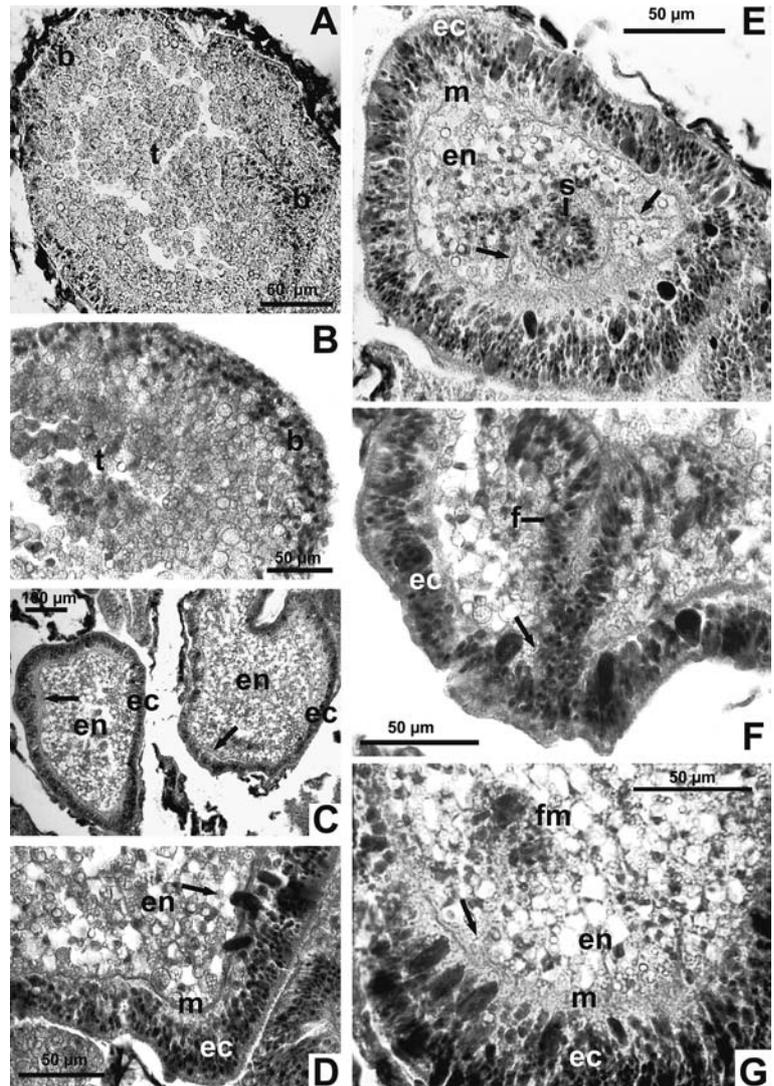
towards the center of the embryo, followed by the formation of the mesenterial filament via the apposition of endoderm cells to the mesentery's free edge (Fig. 4G). Late stereogastrulae had diameters ranging from 290 to 736  $\mu\text{m}$ .

When released, larvae had completed ontogenesis (differentiated mouth and pharynx, the gastrovascular cavity was divided into compartments by mesenteric septa; Fig. 5). The normally pear-shaped larvae were able to contract and become more spherical or to stretch out

**Fig. 3A–F** *Leptopsammia pruvoti*. Oogenesis. **A** Early stage. Previtellogenic oocyte located in the gastrodermis of a mesentery is characterized by a high nucleus to cytoplasm ratio. Note the granular texture of the gastrodermis surrounding the oocyte, this is due to the high number of granules or cellular nuclei inside the unstained cells. **B** Intermediate stage. Vitellogenic nuclei located in one of the mesenteries. Note the gastrodermis' granular texture, due to granules or cellular nuclei. **C** Intermediate stage. Two vitellogenic oocytes located in one of the mesenteries. The ratio nucleus to cytoplasm has diminished. Spherical nuclei with a single nucleolus are still located in the center of the cells. The cytoplasm has a homogeneous appearance. A small early oocyte is visible in the section. **D** Late stage. The ooplasm has started to differentiate, yolk plates are now present. The spherical nucleus has started to migrate towards the cell's periphery. **E** Late stage. The nucleus has become concave and is now located on the cell's periphery where it has begun to adhere to an invagination of the plasma membrane. The ooplasm is full of yolk plates. **F** Late stage. Detail of the nucleus in a mature oocyte. The nuclear membrane is strongly adherent to the cellular membrane (*arrow*). The nucleolus is located close to the bottom of the plasma membrane invagination (*cc* coelenteric cavity; *g* gastrodermis; *fm* mesenterial filament; *O* oocyte; *N* nucleus; *n* nucleolus; *pt* yolk plates; *ss* skeletal septum)



**Fig. 4A–G** *Leptopsammia pruvoti*. Embryonic development. **A** Stereoblastula (early stage) located in the coelenteron. **B** Detail of the stereoblastula. The cleaved superficial layer surrounds the central yolk mass. **C** Stereogastrula (intermediate stage). At this stage of development, the ectoderm is clearly distinct from the endoderm. The two layers are divided by the mesoglea (arrows). **D** Detail of the periphery of the stereogastrula; the three embryonic layers—endoderm, mesoglea and ectoderm—are evident. There are some cnidocytes (arrow) in the ectoderm. **E** Late stereogastrula, showing the stomodeal invagination; mesentery differentiation has begun (arrows). **F** Detail of the late stereogastrula. Ectodermal cells have begun to multiply, forming an invagination at the embryo's oral pole (arrow); the stomodeum has begun to differentiate. **G** Detail of the late stereogastrula in which a mesentery has begun to differentiate. The first phase of mesentery differentiation is in the introflection of the mesoglea (arrow). At the mesentery's free end, a mesenterial filament has formed by apposition of endodermal cells (*b* blastoderm; *ec* ectoderm; *en* endoderm; *f* pharynx; *fm* mesenterial filament; *m* mesoglea; *s* stomodeal invagination; *t* yolk)



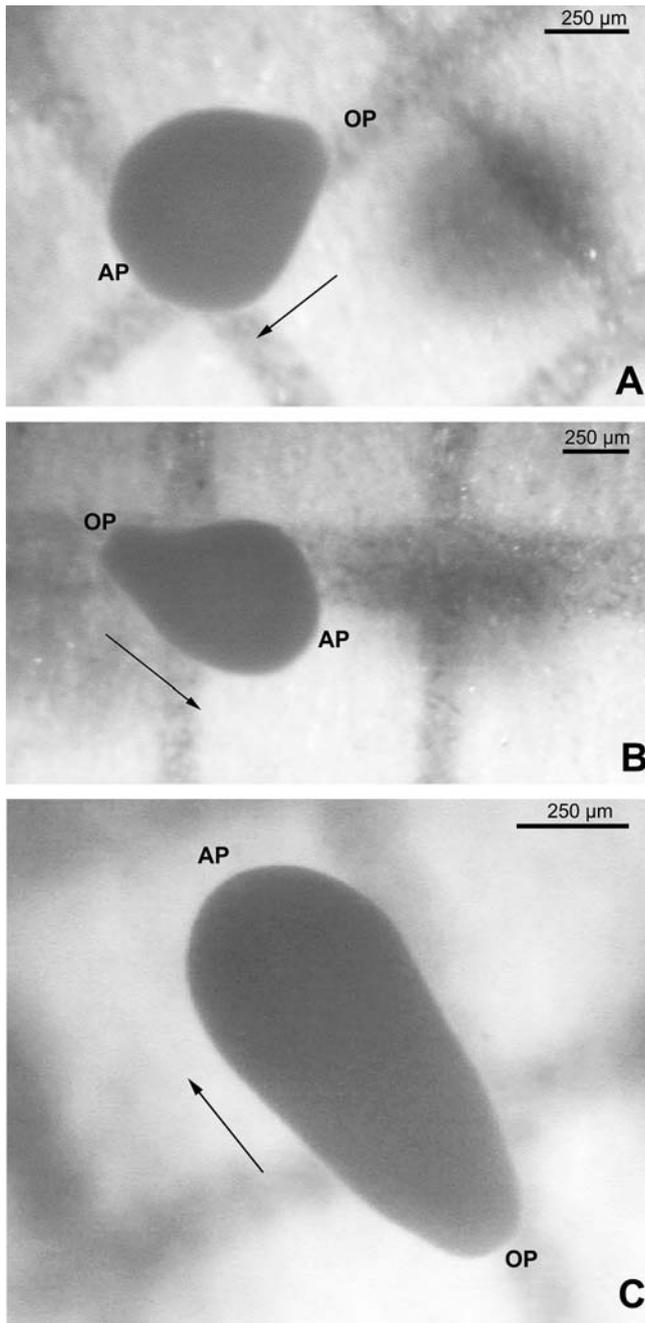
and become more cylindrical (Fig. 5A–C). When elongated and cylindrical in shape, their maximum diameters (oral–aboral axis) ranged from 695 to 1,595 µm and their minimum diameters (transversal axis) from 267 to 633 µm. Motion was achieved via ciliary movement with the aboral pole leading (Fig. 5A–C). The orange-yellow color is similar to that of adult polyps.

## Discussion and conclusions

Examination of the literature reveals that our study of *Leptopsammia pruvoti* is the first in-depth investigation of the reproductive biology in a species of this genus. In this paper, we present the morphological aspects of gametogenesis and ontogenesis. Quantitative and ecological aspects of the annual sexual reproductive cycle will be presented in a separate paper.

The gonochorism and brooding found in the organisms studied support the sexuality and reproductive mode one expects to find in Dendrophylliidae, since

hermaphroditism (found in 27% of the species studied) and broadcasting (found in 39%) are minority reproductive conditions in this taxon (Table 1). According to several authors, while sexual condition (gonochorism vs. hermaphroditism) in scleractinians tends to be phylogenetically correlated and therefore constant through genera and families, reproductive mode (brooding vs. broadcasting) tends to be adaptive and therefore variable (Stimson 1978; Szmant 1986; Harrison 1985; Richmond and Hunter 1990; Ward 1992; Shlesinger et al. 1998; Fautin 2002). In fact, existing data on Dendrophylliidae suggest that there is a greater variability in reproductive mode than in sexual condition (Table 1). Further studies are needed to ascertain the validity of the reproductive pattern that emerges in Dendrophylliidae, i.e. gonochorism associated with brooding, which is contrary to the pattern found in most scleractinians, i.e. hermaphroditism associated with broadcasting (Szmant 1986; Harrison and Wallace 1990; Richmond and Hunter 1990; Soong 1991; Richmond 1997; Shlesinger et al. 1998; Fautin 2002).



**Fig. 5A–C** *Leptopsammia pruvoti*. Larval phase. **A** A contracted, spherical-shaped natant planula. The *arrow* indicates the direction of movement. **B** A partially contracted natant, pear-shaped planula. The *arrow* indicates the direction of movement. **C** An elongated cylindrically shaped natant planula. The *arrow* indicates the direction of movement (*AP* aboral pole; *OP* oral pole)

Although accessory or nutritive cells have not generally been reported during scleractinian gametogenesis (Fadlallah 1983a), the swollen and granular appearance of gastrodermal tissue observed in the mesenteries could have a trophic role supporting gametogenesis. This trophic function may be operated by interstitial cells. Similar scenarios have been described for other scleractinians (see Glynn et al. 1996, and references therein).

Morphological investigations at the ultrastructural level could yield more information on the possible trophic role played by the granular masses in gametogenesis.

Basic histological descriptions of spermary development generally match those of other scleractinians of this and other families with the same or different reproductive traits. For example, aspects of male gonadal development matching those of *L. pruvoti* have been described, among Dendrophylliidae, in the gonochoric and broadcasting *Heteropsammia aequicostatus* and *Heteropsammia cochlea* (Harriott 1983), in the gonochoric and brooding *Balanophyllia elegans* (Fadlallah and Pearse 1982; Beauchamp 1993) and in the hermaphroditic and brooding *Balanophyllia europaea* (Goffredo et al. 2002), as well as in members of other families: in the gonochoric and broadcasting *Fungiacyathus marenzelleri* (Fungiacyathidae; Waller et al. 2002), in the gonochoric and brooding *Monomyces rubrum* (Flabellidae; Heltzel and Babcock 2002), in the hermaphroditic and broadcasting *Mussismilia hispida* (Mussidae; Neves and Pires 2002) and in the hermaphroditic and brooding genus *Madracis* (Pocilloporidae; Vermeij et al. 2004).

While histological aspects of male gonadogenesis remain substantially constant in scleractinians, female gonadal development varies in late-stage oogenesis with respect to fertilization and development (Harrison 1988; Fautin et al. 1989; Soong 1991). Brooding species generally produce a relatively small number of rather large-sized oocytes containing substantial deutoplasmatic reserves (Fadlallah 1983a; Richmond and Hunter 1990; Shlesinger et al. 1998). Oogenesis in *L. pruvoti* seems to follow this pattern. Moreover, during the final phases of oogenesis, a singular process of nuclear differentiation takes place. The occurrence of this process is not clear in female scleractinian gametogenesis. After migrating to the cell's periphery, as normally occurs during oogenesis in scleractinians, and more generally in anthozoans (Szmant-Froelich et al. 1985), the nucleus: (1) adheres closely to the cell membrane and (2) undergoes deformation, becoming notably concave and indented; at this point, the nucleolus is located next to the base of the indentation. A similar situation, in which the nucleus affixes itself in this manner to the oolemma and becomes indented taking on a sickle, dome or “U” shape, has been observed in mature oocytes of other scleractinians across taxonomic classifications, sexual conditions and reproductive modes: in *Favia fragum* (hermaphroditic and brooding, Faviidae; Szmant-Froelich et al. 1985), in *Porites porites* (gonochoric and brooding, Poritidae; Tomascik and Sander 1987), in *Pocillopora damicornis* and *Pocillopora elegans* (hermaphroditic and broadcasting, Pocilloporidae; Glynn et al. 1991), in species of the genus *Pavona* and in *Gardineroseris planulata* (hermaphroditic and broadcasting, Agariciidae; Glynn et al. 1996, 2000), in *Balanophyllia europaea* (hermaphroditic and brooding, Dendrophylliidae; Goffredo et al. 2002) and in *Monomyces rubrum* (gonochoric and brooding, Flabellidae; Heltzel and Babcock 2002). Szmant-Froelich et al.

**Table 1** Reproductive traits found in the literature on Dendrophyllidae corals (*h* hermaphroditic; *g* gonochoric; – unknown; *b* brooder; *bs* broadcast spawner)

Species	Sexual condition	Reproductive mode	Source
<i>Astroides calycularis</i>	h	b	Lacaze-Duthiers 1873; Fadlallah 1983a
<i>Balanophyllia elegans</i>	g	b	Fadlallah 1981; Fadlallah and Pearse 1982; Fadlallah 1983b; Beauchamp 1993
<i>Balanophyllia europaea</i>	h	b	Goffredo and Telò 1998; Goffredo et al. 2000, 2002
<i>Balanophyllia regia</i>	–	b	Lacaze-Duthiers 1897; Yonge 1932; Lyons 1973; Kinchington 1981; Fadlallah 1983a
<i>Balanophyllia</i> sp.	–	b	Abe 1937; Fadlallah 1983a; Richmond and Hunter 1990
<i>Cladpsammia rolandi</i>	h	b	Lacaze-Duthiers 1897; Fadlallah 1983a
<i>Dendrophyllia manni</i>	–	b	Edmondson 1929, 1946; Fadlallah 1983a; Richmond and Hunter 1990
<i>Dendrophyllia</i> sp.	g	b	Babcock et al. 1986; Richmond and Hunter 1990
<i>Heteropsammia aequicostatus</i>	g	bs	Harriott 1983; Richmond and Hunter 1990
<i>Heteropsammia cochlea</i>	g	bs	Harriott 1983; Richmond and Hunter 1990
<i>Leptopsammia pruvoti</i>	g	b	Lacaze-Duthiers 1897; present work
<i>Rhizopsammia minuta</i>	–	b	Abe 1939; Fadlallah 1983a
<i>Stephanophyllia formosissima</i>	–	b	Moseley 1881; Fadlallah 1983a
<i>Tubastrea aurea</i>	–	b	Edmondson 1929, 1946; Fadlallah 1983a
<i>Tubastrea coccinea</i>	–	b	Edmondson 1929, 1946; Richmond and Hunter 1990
<i>Tubastrea faulkneri</i>	g	b	Babcock et al. 1986; Richmond and Hunter 1990
<i>Turbinaria bifrons</i>	–	bs	Babcock et al. 1994
<i>Turbinaria frondens</i>	g	bs	Willis et al. 1985; Richmond and Hunter 1990
<i>Turbinaria frondens</i>	–	bs	Babcock et al. 1994
<i>Turbinaria mesenterina</i>	–	bs	Babcock et al. 1994
<i>Turbinaria peltata</i>	–	bs	Babcock et al. 1994
<i>Turbinaria radicalis</i>	–	bs	Babcock et al. 1994
<i>Turbinaria reniformis</i>	g	bs	Willis et al. 1985; Richmond and Hunter 1990; Babcock et al. 1994

(1985) suggest that the indentation of the nucleus serves to facilitate fertilization. These authors suggest, particularly in brooding species, gametes of opposite sexes unite when the oocyte is still in the mesentery and that the mesenterial gastrodermis adjacent to the indentation of the nucleus represents a site of easy penetration for the spermatozoa. Since we found mature oocytes exclusively inside the mesenteries and never observed them in the coelentric cavity, we can hypothesize that the union of gametes could occur when the oocytes are still in the mesentery. From histological evidence and fertilization experiments, Heltzel and Babcock (2002) also deduced that in *Monomyces rubrum* (a brooding species in which mature oocytes have an indented nucleus) oocytes remain inside the mesentery's mesogleal layer until they are fertilized, and only then do they enter the polyp's gastrovascular cavity. Another possible explanation is that these cellular processes may be oogenic

phases involved in determining the embryo's future oral–aboral axis (Van Buskirk and Schüpbach 1999; Lei and Warrior 2000; Riechmann and Ephrussi 2001).

There is no evidence of formation of a blastocoel during embryogenesis, embryonic development proceeds via stereoblastulae, and subsequent gastrulation occurs by delamination rather than invagination. This is the case for other brooding scleractinians as well, whose embryology has been studied in detail: *Favia fragum* (Szmant-Froelich et al. 1985), *Balanophyllia europaea* (Goffredo and Telò 1998), *Pocillopora damicornis* (Diah Permata et al. 2000) and *Monomyces rubrum* (Heltzel and Babcock 2002). Authors have suggested that gastrulation occurs by delamination, even in the brooding *Balanophyllia elegans* (Fadlallah and Pearse 1982). Similarly, in many brooding octocorals, development progresses by means of solid stereoblastulae (see Table 2). Thus, generally in scleractinians and octoco-

**Table 2** Brooding octocorals in which development progresses by means of solid stereoblastulae

Species	Order	Brooding mode	Source
<i>Parerythropodium fulvum</i>	Alcyonacea	Embryos are brooded in a layer of mucous on the surface of the colonies	Benayahu and Loya 1983, Benayahu 1989
<i>fulvum</i> and <i>Clavularia hamra</i>			
<i>Heliopora coerulea</i>	Helioporacea	Brooding begins in the coelenteron and ends on the surface of the colonies	Babcock 1990
<i>Xenia umbellata</i>	Alcyonacea	Brooding takes place in the coelenteron	Benayahu et al. 1990
<i>Xenia macrospiculata</i>	Alcyonacea	Brooding takes place on the colony's surface in invaginations in the epiderm	Achituv et al. 1992
<i>Anthelia glauca</i>	Alcyonacea	Embryos are brooded in pharyngeal pouches	Kruger et al. 1998
<i>Pseudopterogorgia elisabethae</i>	Gorgonacea	Embryos are brooded in a layer of mucous on the surface of the colonies	Gutiérrez-Rodríguez and Lasker 2004

rals, the type of embryogenesis normally associated with brooding appears to be by means of stereoblastulae. On the contrary, data from 24 scleractinians (Szmant-Froelich et al. 1980; Babcock and Heyward 1986; Shlesinger and Loya 1991; Hirose et al. 2000) plus the pennatulacean octocoral *Ptilosarcus guernei* (Chia and Crawford 1973) suggest that embryogenesis associated with broadcasting occurs by means of coeloblastulae. There are, however, some known exceptions to this pattern: coeloblastulae form in the scleractinian *Manicina areolata* both in conditions of broadcasting and brooding (Wilson 1888), the broadcasting scleractinian *Fungia scutaria* produces stereoblastulae (Krupp 1983), as does the broadcasting alcyonacean octocoral *Dendronephthya hemprichi* (Dahan and Benayahu 1998). Babcock (1990) and Heltzel and Babcock (2002) hypothesize that different embryonic formations may be correlated to the availability of physical space during ontogenic processes. These authors suggest that the restricted amount of space for developing embryos in brooding organisms constrains the formation of a solid blastula, while external fertilization and embryonic development in broadcasting organisms allows ontogenesis to take place via a hollow blastula. Further studies are needed, especially on embryogenesis in broadcasting octocorals, for which there are few and conflicting data, to verify the relationship between the pattern of embryogenesis and the reproductive mode that seems to be indicated in scleractinians and octocorals.

As was expected for a brooding species of coral (Harrison and Wallace 1990; Richmond and Hunter 1990), larval ontogenesis was complete at the time of planulation; released larvae had a clearly formed and differentiated mouth and pharynx, with the coelenteron clearly compartmentalized by mesenteries. The planula's plastic and changeable shape, varying from contracted spherical- to partially contracted pear- to an elongated cylindrical-shape, is a trait common to anthozoan larvae (see Chia and Crawford 1973 for pennatulacean planulae; Benayahu 1989 for alcyonacean planulae; Hand and Uhlinger 1992 for actiniarian planulae; Gutiérrez-Rodríguez and Lasker 2004 for gorgonacean planulae; Goffredo and Zaccanti 2004 for scleractinian planulae). Another frequently observed trait was the ciliary movements that larvae used for propulsion with the aboral pole leading (see Atoda 1951; Hartnoll 1977; Goffredo and Zaccanti 2004). The larvae we measured were smaller when compared to the larvae of other solitary brooding corals of the same family (oral-aboral axis of planulae ranged from 695 to 1,595  $\mu\text{m}$  in *L. pruvoti*; compared to 2,150  $\mu\text{m}$  in *Balanophyllia europaea*, Goffredo and Zaccanti 2004; and 4,000  $\mu\text{m}$  in *Balanophyllia legans*, Fadlallah and Pearse 1982). The positions on the r-K (maximum population increase-maximum competitive ability) continuum (Pianka 1970) of the different reproductive strategies associated with planula size will be presented in a separate paper. In that same paper we will also present data on fecundity and

incubation time for embryos fundamental to the inter-specific comparison of reproductive traits.

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