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Hermaphroditism and brooding in the solitary coral balanophyllia Europaea (Cnidaria, anthozoa, scleractinia)

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ABSTRACT

Simultaneous hermaphroditism and brooding were observed in the solitary coral *Balanophyllia europaea* at Calafuria (Leghorn, Italy), in a phase of its reproductive cycle. This is the first report of hermaphroditism in *Balanophyllia*. Individuals of different sizes were collected in April 1997 and reared in laboratory for two months. Histological analysis showed the presence of immature and mature clusters of male gametes, vitellogenic oocytes and embryos at different stages of development. Early stages of embryogenesis were observed. Periblastulae were found free in the coelenteron. Developing embryos, already colonised by zooxanthellae, were localised in the interseptal spaces or in the mesenteries.

INTRODUCTION

Balanophyllia europaea (Risso, 1826) is a solitary, sessile, and zooxanthellate non-constructional coral, as it lives in symbiosis with dinoflagellates but does not form a bioherm, according to Schumacher & Zibrowius (1985). It is a member of the family Dendrophylliidae, colonising rocky substrates in the Mediterranean Sea, and its geographical distribution also includes the Atlantic coast of Spain (Zibrowius, 1980, 1983; Aleem & Aleem, 1992). At the site of our collection of *B. europaea* the highest population density was observed at a depth of 6.5 m. Symbiosis with zooxanthellae was probably a major factor in this distribution of *B. europaea* to shallower waters, whereas azooxanthellate corals of the same genus, that do not live in symbiosis with dinoflagellates according to Schumacher & Zibrowius (1985), can be found as low as 1100 m (Cairns, 1977).

Most of scleractinian corals whose sexuality is known are hermaphroditic, 68% according to Richmond & Hunter (1990). Of the fifty or so species of the genus *Balanophyllia* (Cairns, 1977), only the modes of reproduction of *B. pruvoti*, from the Gulf of Lions near Marseille (Lacaze-Duthiers, 1897) and of *B. elegans* from Monterey Bay of central California (Fadlallah & Pearse, 1982; Beauchamp, 1993) are known: both of them have been reported to be gonochoric brooders. Here we provide for the first time evidence of hermaphroditism in a *Balanophyllia* species, *B. europaea*, and describe the principal features of its sexual reproduction.

MATERIALS AND METHODS

In April 1997, thirty polyps of *B. europaea* (Fig. 1) of different dimensions were collected by SCUBA dives at a depth of 6.5 m from Calafuria (Leghorn, upper Tyrrhenian Sea, Italy, 43°28,4'N, 10°20'E). At this depth, the population density was maximum, 121 polyps·m^2. It decreased towards both lower and higher depths and no specimen was found at 1 m and 13 m of depth.
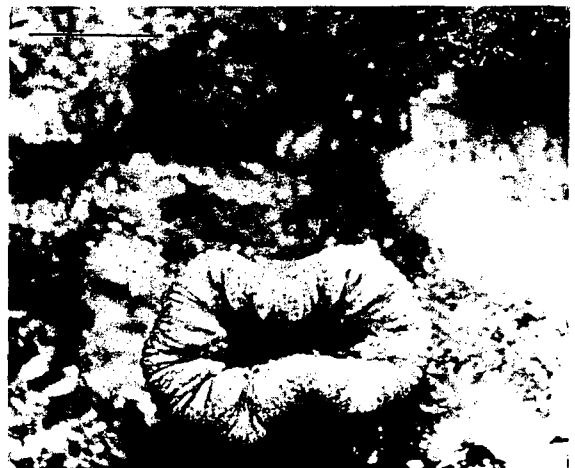

Fig. 1 - Adult specimen of *Balanophyllia europaea*. Bar, 10 mm.

The polyps were reared at the Department of Biology (University of Bologna) in an aquarium maintained at the same water temperature as that found in nature at the time of collection (14-15° C). The following measurements were taken on live polyps (cf. Table I): maximum oral disc diameter (axis parallel to stomodeum), minimum oral disc diameter (axis perpendicular to stomodeum) and maximum height. The volume of these animals was estimated, using the formula:

$$V = h \cdot R \cdot r \cdot \pi$$

where: V = volume; h = maximum height; R = maximum oral disc ray (that in *B. europaea* can be equated with maximum aboral disc ray); r = minimum oral disc ray (that in *B. europaea* can be equated with minimum aboral disc ray).

Two months after collection, a number of individuals of different sizes were selected for histological analysis. Polyps were fixed in Bouin's solution for 48 h, rinsed for 1 h in running tap water and decalcified in EDTA for 48 h. After rinsing for 2 h in running tap water, the whole polyps were dehydrated and embedded in paraffin. Serial cross sections were cut at 7 μm and stained with Mayer's hematoxylin and eosin. In order to identify the symbiontic zooxanthellae, some sections were stained either with Toluidine blue (Babcock & Ryland, 1990) or with Mallory's trichrome staining (Marshall & Wright, 1993). Also the PAS (Periodic Acid Shiff) reaction was carried out, and it was found the most effective method for revealing zooxanthellae. Histological preparations were examined and photographed by a Leitz Diaplan Photomicroscope.

RESULTS

All polyps analysed in the present work, whose sizes are reported in Table I, were in the same reproductive state. They were simultaneous hermaphrodites and brooders. Every examined specimen contained oocytes, spermatocysts, and embryos at different developmental stages (Fig. 2).

Gametes were found within mesenterial septa, oocytes and spermatocysts at different stages of development frequently occurring in the same septum (Fig. 3A, B).

Male gonads

Testes appeared as clusters of male gametes, completely surrounded by the mesoglear layer of the sep-

TABLE I - *Dimensions of polyps used for histological analysis.*

Individual code	Dimensions			
	Max. diameter[a] (mm)	Min. diameter[a] (mm)	Height (mm)	Volume (mm³)
I	10	7	18	440
II	17	9	13	1561
III	13	9	10	918
IV	15	10	15	1766
V	15	11	15	1943

[a] Measured at level of the oral disc.

Fig. 2 - Cross-section of the basal region of an adult specimen of *Balanophyllia europaea*. The following structures are indicated: o, vitellogenic oocytes; s, spermatocysts; e, embryos. Bar, 400 μm.

tum. Gametogenesis was synchronous within a cluster, but the same polyp contained clusters at different stages of differentiation. Up to seven clusters per septum were counted, but their number rarely exceeded three, and their maximum diameter ranged from 40 μm to 140 μm.

Immature clusters appeared as dense globular masses filled with spermatocytes or spermatids, containing densely stained nuclei and little cytoplasm. Mature clusters were more intensely stained with hematoxylin, because of tight packing of spermatozoa heads. Many of them had a bouquet-like arrangement of sperms, with all the sperm tails oriented in the same direction (Fig. 3A-C). The releasing of mature spermatozoa occurred through breakages of the mesoglear envelope (Fig. 3B).

Female gonads

True female gonads were not observed, but only scattered oocytes already engaged in vitellogenesis, whose maximum diameter ranged from 60 μm to 500 μm. These oocytes were located in the central portion of the mesenterial septa, where they appeared completely surrounded by a thin mesoglear layer. Their number never exceeded three per septum.

The oocytes were spherical, ovoid, or sometimes less regular in shape (Fig. 4C). The ooplasma was strongly eosin-positive and packed with yolk vacuoles. The nucleus appeared heterochromatic and centrally located in the smallest vitellogenic oocytes; it became pale, and
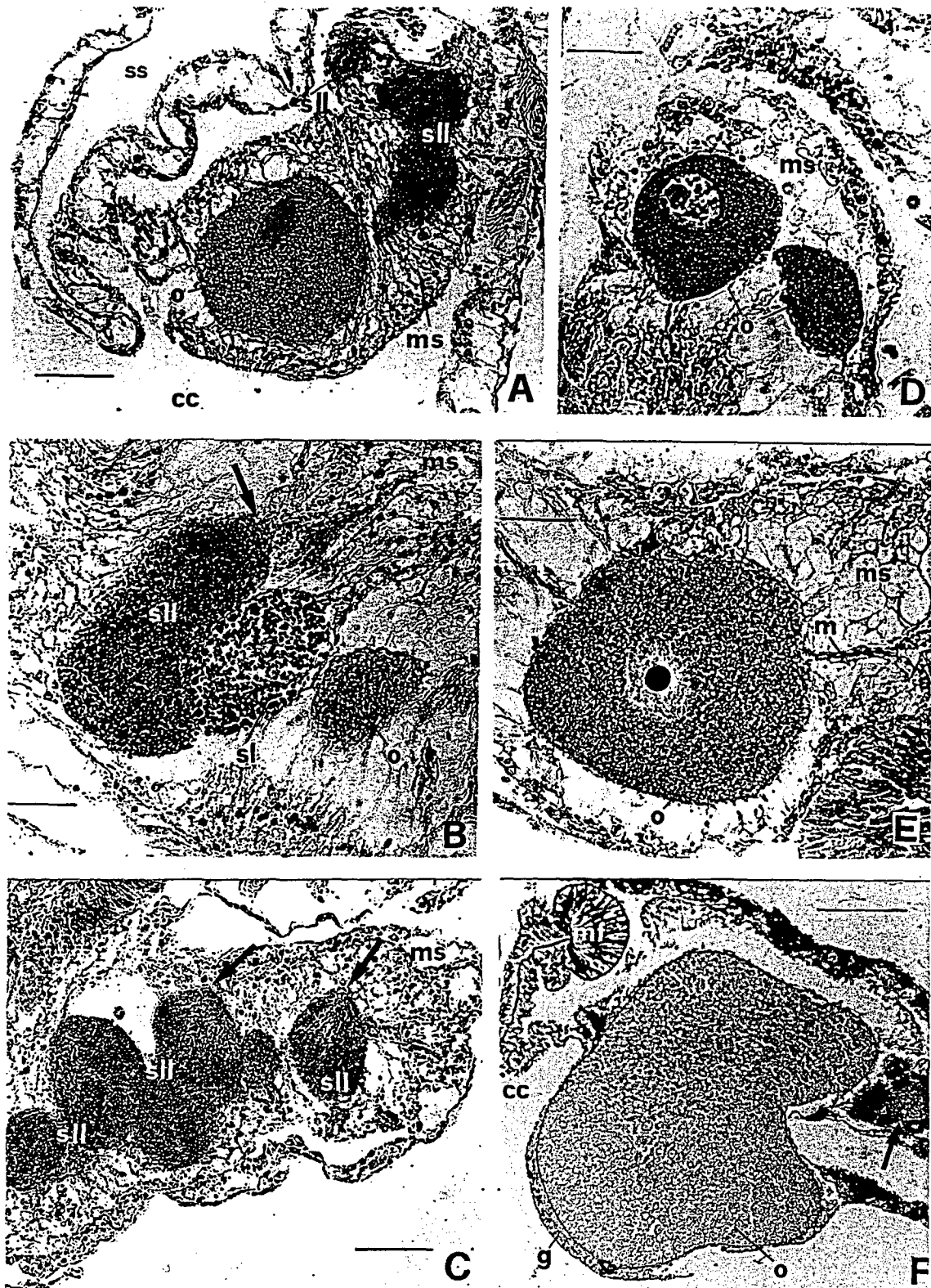
Fig. 3 - Male and female gametes in *Balanophyllia europaea*. All micrographs are from cross-sections through mesenterial septa. **A,** a vitellogenic oocyte (o), and three clusters of mature spermatozoa (sII). Bar, 50 µm. **B,** two spermatocysts at different developmental stages (sI, immature spermatocyst; sII, mature spermatocyst). The mature one has released some spermatozoa, through a breakage of the mesoglear envelope (arrow). In the same section, one can notice a vitellogenic oocyte (o). Bar, 30 µm. **C,** six clusters of spermatozoa (sII) are present, two of them (arrows) showing the characteristic bouquet-like arrangement of sperms (see 'Results'). Bar, 50 µm. **D,** detail of two small vitellogenic oocytes (o), one of these showing the heterochromatic nucleus, with a single prominent nucleolus. Bar, 30 µm. **E,** detail of a more developed vitellogenic oocyte (o) showing the typical pale nucleus, that is centrally located and contains a single prominent nucleolus. The oocyte is surrounded by a thin mesoglear envelope (m). Bar, 30 µm. **F,** a mature vitellogenic oocyte (o), bulging out of the internal edge of the mesenterial septum; it appears surrounded by the gastrodermal layer (g); a second oocyte (arrow) is also present. Bar, 100 µm. Other abbreviations: cc, coelenteric cavity; mf, mesenterial filament; ms, mesenterial septum; ss, skeletal septum.
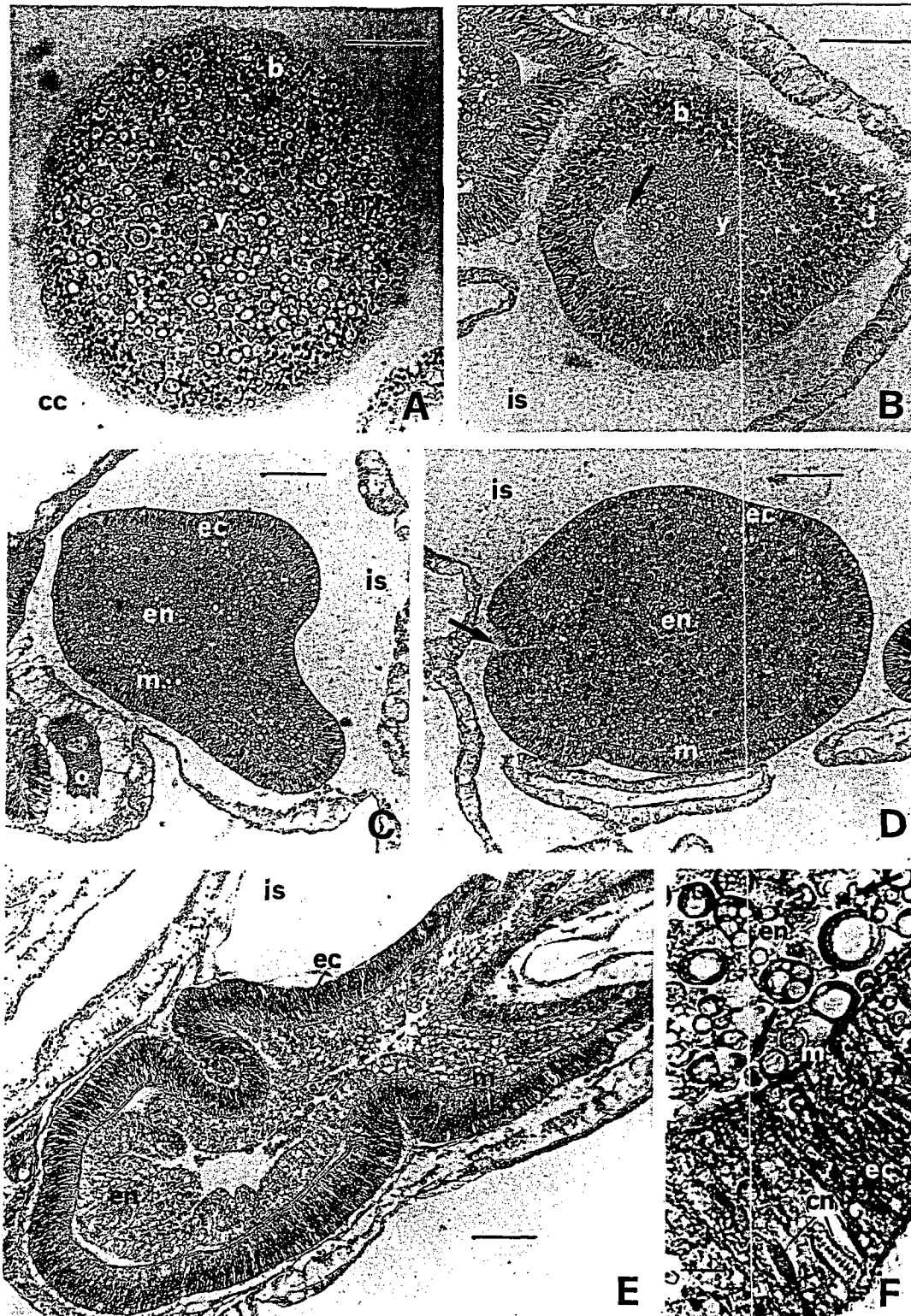
Fig. 4 - Embryonic development of *Balanophyllia europaea*. **A,** early periblastula, which is found free in the coelenteric cavity. Bar, 50 μm. **B,** late periblastula, with a small blastocoele (arrow), which is already located in the interseptal space (is). Bar, 100 μm. **C,** gastrula in the interseptal space (is); in the adjacent mesenterial septum a vitellogenic oocyte is also present (o). Bar, 100 μm. **D,** advanced gastrula, showing the stomodeal invagination at the oral pole (arrow). Bar, 100 μm. **E,** well-developed embryo, engaged in the primary mesenteries formation. Bar, 100 μm. **F,** detail of a gastrula, showing well-differentiated cnidocysts (cn) in the ectodermal layer (ec) and intensely PAS-positive symbiontic zooxanthellae (arrows) in the endoderm (en). Bar, 10 μm. Other abbreviations: b, blastoderm; cc, coelenteric cavity; ec, ectoderm; en, endoderm; is, interseptal space; m, mesoglea; y, undifferentiated yolk mass.

peripherally located in growing oocytes, and always contained a single prominent nucleolus. In mature oocytes the nuclear membrane gradually disappeared (Fig. 3A, D-F).

Fully grown oocytes were observed bulging out of the internal wall of the septum, where they appeared to be surrounded by the gastrodermal layer (Fig. 3F).

Embryos

Some early blastulae could be observed, always free in the coelenteron. They should be called periblastulae, since they were characterised by a cleaved superficial layer, which surrounded a large yolky central mass (Fig. 4A). The late blastulae, already located in the interseptal spaces, contained a small blastocoele (Fig. 4B). Zooxanthellae colonised embryos at these stages, and could be identified by their intensely PAS-positive starch inclusions (Fig. 4F).

In their basal portion, polyps were packed with embryos at different developmental stages (Fig. 2), whose maximum diameter ranged from 380 µm to 2500 µm. An average number of 125 (SD ± 11) embryos per animal was estimated, in polyps whose average volume, 1757 mm^3 (SD ± 191), corresponded with the maximum dimension of the polyps found at Calafuria, as estimated on a sample of 436 corals.

Most observed embryos had already reached the gastrula stage. The well-differentiated ectodermal layer already had many nematoblasts (Fig. 4F), and consisted of a ciliated columnar epithelium lined by a thin lamina of mesoglea; it surrounded a less differentiated endodermal mass, which contained zooxanthellae, mucus granules, and spherical vacuoles (Fig. 4C, F).

A stomodeal invagination was observed in some well-developed embryos (Fig. 4D); the early formation of the primary mesenteries occurred by outfolding of the endoderm and of the mesoglea into the coelenteric cavity (Fig. 4E). The embryos were usually incubated in the interseptal spaces (Figs 2, 4B-E); they rarely developed within the mesenteries.

DISCUSSION

The histological information described above indicates that *B. europaea* at Calafuria is a simultaneous hermaphrodite with asynchronous gametogenesis (i.e., mature and immature gametes of both sexes are present in the same polyp at the same time). Moreover, this coral broods its embryos. Gametogenesis and embryogenesis are temporally overlapping.

Hermaphroditism

According to Cairns (1977), the genus *Balanophyllia* consists of more than fifty species, but only the reproduction of *B. elegans* in Monterey Bay (Pacific Ocean, Central California) is known in detail (Fadlallah &

Pearse, 1982; Beauchamp, 1993): it is also a brooder coral, but, unlike *B. europaea* at Calafuria, it exhibits gonochorism.

Relative population densities are important for understanding the adaptive significance of the different types of sexuality of *B. elegans* in Monterey Bay and of *B. europaea* at Calafuria. The average population density of the former is 563 (SD ± 393) corals·m^2, at a depth of 6 to 13 m (Fadlallah, 1983a), while that of the latter is 9 (SD ± 17) corals·m^2, at a depth of 1 to 13 m. The high density of *B. elegans* is caused by the very low dispersal ability of the planulae, that settle less than 0.5 m from the parental polyp (Gerrodette, 1981; Fadlallah, 1983a). In such conditions, the population has a high breeding probability and gonochorism, that is energetically advantageous, can be maintained. The much lower density of *B. europaea* may be due to a higher dispersal ability of the planulae, that unlike those of *B. elegans* (azooxanthellate coral, Bruno & Witman, 1996), contain symbiontic zooxanthellae. These organisms should contribute to the energy requirements of larvae during dispersal, which would allow a delay in the time of settlement and metamorphosis. The low population density of *B. europaea* reduces breeding opportunities among individuals of the same population; in such conditions, simultaneous hermaphroditism becomes adaptive because, although energetically more expensive, it maximises the rate of fertilisation (Ghiselin, 1969).

Brooding

Brooding seems to prevail in the genus *Balanophyllia* (Lacaze-Duthiers, 1897; Abe, 1937; Lyons, 1973; Kinchington, 1981; Fadlallah & Pearse, 1982; Beauchamp, 1993) and generally, in the family Dendrophylliidae, to which *Balanophyllia* belongs (Fadlallah, 1983b). Fadlallah & Pearse (1982) suggested that in scleractinian corals the reproductive mode may be dictated by anatomical constraints and that skeleton morphology, in particular, may condition the evolutionary choice between free spawning or brooding modes. Corals of the family Dendrophylliidae are characterised by differential growth of skeletal septa (a developmental pattern known as the 'Pourtalès plan'), that produces very large skeletal chambers, apt to incubate a great number of embryos until advanced stages of development. This is a very specialised brooding mode, that maintains the coelenteric cavity free for food digestion, distribution and absorption.

The absolute fecundity of *B. europaea* at Calafuria proved higher than that of *B. elegans* in Monterey Bay. In fact, females of *B. elegans* whose volume ranges from 650 to 700 mm^3, produced an average of 40 (SD ± 15) embryos per polyp (Fadlallah, 1983a), while the hermaphroditic individuals of *B. europaea* observed here had an average of 125 (SD ± 11) embryos per polyp and an average volume of 1757 mm^3 (SD ± 191). However, dividing the absolute fecundity by the average dimension expressed in volume, comparable values

of relative fecundity (i.e., 0.068 embryos·mm^3 in *B. elegans*, against 0.071 embryos·mm^3 in *B. europaea*) are obtained. Greater size provides the polyp with larger and/or more numerous skeletal chambers, apt to brood a greater number of embryos. Moreover, the dimension of embryos in *B. elegans* is much greater than those of our sample of *B. europaea*. According to Fadlallah & Pearse (1982) the maximum diameter of embryos of *B. elegans* ranges from 1250 to 3000 μm, against a range of 380-2500 μm estimated for *B. europaea* embryos.

One should also bear in mind that the zooxanthellae living within the yolk endoderm could contribute to the energy requirements of *B. europaea* embryos, allowing the parental polyp to incubate a great number of them at sustainable energetic costs (Richmond, 1981; Ryland, 1997). On the other hand, both the transport and the stay in aquaria, at much higher population density than in the natural environment, are stressful conditions that could affect the reproductive activity of corals, probably enhancing their fecundity (Fadlallah, 1983b; Beauchamp, 1993).

Embryonic development

Our sample of *B. europaea* confirmed the hypothesis that brooding corals have centrolecitic eggs, undergoing superficial cleavage (Campbell, 1974; Fadlallah, 1983b). As far as we know, early stages of embryogenesis have never been observed in brooder corals (Fadlallah & Pearse, 1982; Stoddart & Black, 1985; Beauchamp, 1993). A possible explanation of this fact is that the development from fertilised eggs to gastrula is fast, and thus less likely to be observed (Stoddart & Black, 1985). According to Fadlallah & Pearse (1982), the presence of large amounts of yolk vacuoles in the mature oocytes of *Balanophyllia* may interfere with the histological observation of fertilisation and cleavage. The high fecundity of our sample may have increased the probability of observing some of the short-lasting stages of embryogenesis, such as early and late periblastula (Fig. 3A-B.).

From the localisation of the different developmental stages, possible movements of the mature egg and embryos in *B. europaea* may be proposed: the egg could fall from the mesenterial septum into the coelenteric cavity by breaking of the gastrodermic wall of the septum, as occurs in *Astroides calycularis* (Lacaze-Duthiers, 1873) and in *Astrangia danae* (Szamant-Froelich *et al.*, 1980); cross-fertilisation probably takes place in the coelenteric cavity; then by the time the cleavage has ended, the embryo moves to the interseptal space where development continues.

Lacaze-Duthiers (1873) in *Astroides calycularis* and Marshall & Stephenson (1933) in several coral species observed appropriate openings in the mesenterial septa for fertilisation to occur. No fertilisation could be observed in our sample. The lack of openings in the fertile septa suggests that in *B. europaea* cross-fertilisation may take place outside the mesenteries and that embryos lo-

cated within the mesenterial septa could have an alternative origin (asexual reproduction, parthenogenesis or self-fertilisation).

CONCLUSIONS

We have demonstrated that simultaneous hermaphroditism and brooding are the reproductive mode of *B. europaea* at Calafuria, at least in one phase of its reproductive cycle. Since this work is focused only on one phase of the reproductive cycle of this species, much work still needs to be done. For instance, the question about the origin of the embryos in the different locations (within and outside the mesenterial septa) remains to be solved. Brooding indicates internal fertilisation, but it is not known whether all brooded embryos originate from fertilised eggs, and nor whether self-fertilisation could operate with or instead of cross-fertilisation.

Histological observations do not exclude that self-fertilisation may occur within the hermaphrodite septa. Mature gametes of both sexes intimately close to each other have been observed, and clusters of spermatozoa often appeared surrounding and adhering to the membrane of mature oocytes. The absence of structures separating the testicular cysts from the oocytes has been already described in some echinoderms (*Asterina*: Cognetti, 1956; *Ophryotrocha*: Parenti, 1960) and in other coelenterates (*Ceriantheopsis americanus*: Hinsch & Moore, 1992), where it was interpreted as facilitating self-fertilisation. Ultrastructural investigations will be necessary to clarify whether proximity between mature gametes leads to fertilisation: this is an important question in the reproduction of sessile animals with limited dispersal ability (Strathman *et al.*, 1984; Edmands, 1996).

On the other hand, the embryos brooded within the mesenterial septa could also originate from asexual or parthenogenetic reproduction. In fact, asexual or parthenogenetic production of planulae has been already demonstrated in several scleractinian species (Stoddart, 1983; Ayre & Resing, 1986). This hypothesis needs confirmation through electrophoretical analysis of the genetical affinity between the parental polyp and embryonic tissues.

We are currently investigating the reproductive cycle of *B. europaea*, in order to define the differentiation of germ cells, and the precise time of fertilisation and planulation in its natural environment. Our aim is also to verify whether simultaneous hermaphroditism, here demonstrated in a limited sample of the population living at Calafuria, occurs throughout the year.

As sexual condition is an adaptive character among anthozoans (Bacci, 1975; Rossi, 1975; Glynn *et al.*, 1991; Fautin, 1992), we are planning further sampling in different points of the geographic range of *B. europaea*, in order to clarify whether simultaneous hermaphroditism is adopted in other populations of this species.

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