

## Release of sperm clusters in spheres by the black coral *Cupressopathes pumila* (Anthozoa, Antipatharia)

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**Abstract** Fecund polyps from a bottlebrush-shaped colony of black coral *Cupressopathes pumila* (Brook 1889) from Ambon Island (Maluku Archipelago, Indonesia) were studied at the structural and ultrastructural levels. Five fragments, each 5 cm long and containing about 60 polyps, were cut from a single parental colony. The fragments underwent different treatments: two were fixed in 70% alcohol for species identification; the remaining three were reared in aerated aquaria and then processed for anatomic studies by light and transmission electron microscopy. Some polyps from one of these reared fragments displayed spheres of various sizes protruding from the mouth. Four hours after sampling, spheres settled on the bottom of the aquarium. Comparative analysis of the fecund polyps showed: (i) the differentiation of spermatocysts inside the transverse primary mesenteries that separate the lateral tentacles from one another; (ii) spermatocysts entering the gastric cavity after breakage of the mesentery wall and (iii) location of spermatocysts close to the basal part of the pharynx. Analysis of the largest spheres, both close to the external surface of the mouth and settled on the bottom of the small aerated aquaria, showed that they were irregularly bordered with residual mesentery tissue and contained clusters of spermatocysts. Gametes presented various phases of differentiation up to the final sperm, as it occurs in the spermatocysts developing inside the mesenteries of the fecund polyps. In consideration of the particular distribution of the colonies of *C. pumila*, which grow very far

apart, the release of buoyant spheres is a particular modality of spawning which can be viewed as a strategy for successful fertilisation over long distances.

**Keywords** Cnidaria · Coral reef · Spermatocysts · Ultrastructure

### Introduction

The number of studies on the reproduction of black corals or antipatharians is very limited and only available for handful of species (Parker et al. 1997; Miller 1996). This feature probably reflects the inaccessibility of many species, which are usually found in deep water (Grigg 1965). By contrast, in other groups of Hexacorallia, such as zoanthids (Yamazato et al. 1973; Lyke and Robson 1975; Cooke 1976; Karlson 1981; Fadlallah et al. 1984; Ryland and Babcock 1991) and scleractinians (Kojis and Quinn 1982; Harrison and Wallace 1990; Richmond and Hunter 1990; Fadlallah 1993; Pires et al. 1999; Goffredo et al. 2000; Neves and Pires 2002) reproduction has been more thoroughly investigated.

Some aspects of the reproductive biology of the Hawaiian black coral *Antipathes* cfr. *dichotoma*, recently attributed to *Antipathes griggsi* (Opresko 2009), is described by Grigg (1976). Additional data on antipatharian gametes can be found in Schmidt and Zissler (1979) and in Schmidt and Schäfer (1980). Histological techniques coupled with field observations allowed Parker et al. (1997) to give information on the fertility of the colonies of the endemic *Antipathella* (formerly *Antipathes*) *fiordensis* (Opresko 2001). Later, ultrastructural studies were carried out on *Cirrhopathes* cfr. *anguina* (family: Antipathidae), enabling spermatocysts and sperm morphology to be investigated, and they provided

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details of some organizational traits (Gaino et al. 2008). Subsequently, the fine organization of the oocyte of this species was analysed, with particular attention to the location of the gametes in the primary transverse mesenteries and the organizational changes during oocyte growth (Gaino and Scoccia 2008). Presumably, in *Cirripathes* cfr. *anguina*, external fertilisation occurs after the synchronous release of gametes, a strategy that enhances the probability of their meeting. Indeed, in some scleractinians it has been demonstrated that synchronization of spawning generates high gamete concentration, which maximises the probability of successful fertilisation (Babcock et al. 1986; Olivier and Babcock 1992; Kruzic et al. 2007).

The objective of the present study was to gather data on gamete morphology in *Cupressopathes pumila* (Brook 1889), a species belonging to the family Myriopathidae (Opresko 2001), through structural and ultrastructural investigation of the fecund polyps and their released buoyant spheres.

## Materials and methods

The parent colony of *Cupressopathes pumila* (Brook 1889) is located along the reef of Ambon Island (Maluku Archipelago, Indonesia 3°47'29.16" S; 128°05'39.16"). On 17th October 2008, fragments were cut from the colony with scissors and then brought to the surface, after having placed them in sealed containers. Specimens were collected by SCUBA DIVING at –30 m.

No apparent differences between fecund and non-fecund polyps were detected underwater. Therefore, sampling was carried out in various randomly selected regions of the colony. Five fragments, each of 5 cm in length and containing about 60 polyps, were investigated: two fragments were preserved in 70% alcohol for species identification; the remaining three were individually reared in small aerated aquaria. When observed under a stereomicroscope, some polyps showed spheres protruding from the mouth. Four hours after sampling, a single fragment released spheres of various sizes (from 50 to 300 µm in diameter) which, after initially floating, gradually settled on the bottom of the aquarium.

For light and transmission electron microscopy investigations, fragments were fixed for 12 h in 2.5% glutaraldehyde buffered with filtered sea-water (adjusted to a final pH of 7.5–7.8 with NaOH 0.1 N), repeatedly rinsed in the same buffer, and stored at 4°C before being transferred to our laboratory in Italy. The same procedure was applied to the buoyant spheres (~100) released from the single reared fragments.

For transmission electron microscopy, selected materials (10 polyps with enlarged columns, some of which showing

spheres protruding from the mouth or located next to its external surface, and the 30 largest spheres) were post-fixed in 1% osmium tetroxide in an artificial sea-water buffer for 1 h at 4°C, then repeatedly washed in the same buffer, dehydrated in an incremental alcohol series and propylene oxide, and finally embedded in an Epon–Araldite mixture.

Semithin sections, 0.5–1.0 µm thick, were cut on a Leica DC 300 F Ultracut (Leica Microsystem AG, Rijswijk, The Netherlands), stained with toluidine blue and observed under a Leica microscope (Leica LSM Holings GmbH, Wetzlar, Germany).

Ultrathin sections were cut with the same Ultracut device, collected on formvar-coated copper grids, stained with uranyl acetate and lead citrate, and examined with a Philips EM 208 electron microscope.

## Results

The colony of *Cupressopathes pumila* presented a main stalk supporting a branching apical region. This unusual morphology, defined as bottlebrush-shaped, is characterized by a central axis surrounded by numerous rows of pinnules (Tazioli et al. 2007).

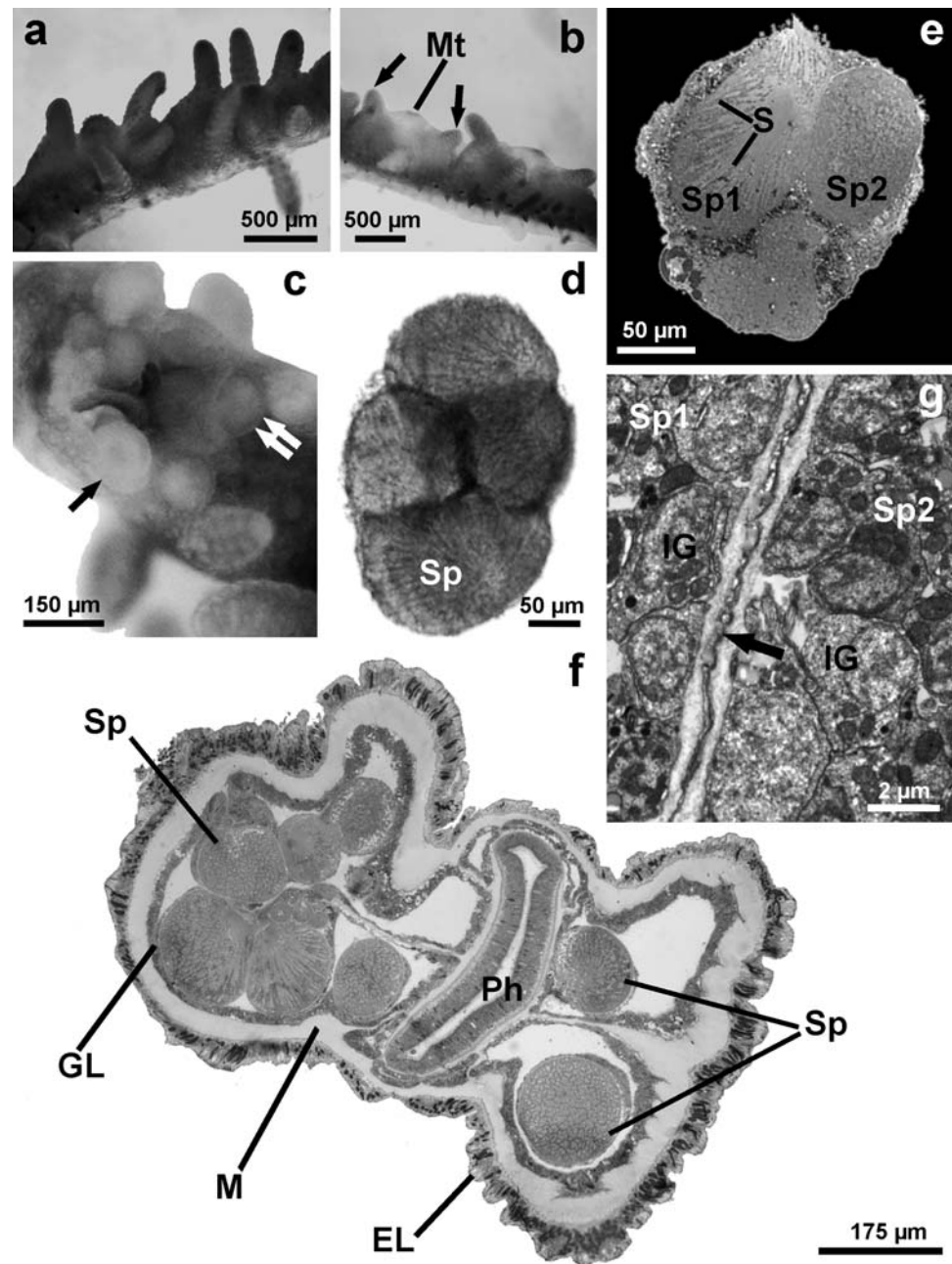
Examination of the reared *C. pumila* fragments (see “Materials and methods” section) revealed polyps with the typical morphology of antipatharians (Opresko 1972), as shown in Fig. 1a (six tentacles encircling the mouth, which is located on a slight prominence, the four lateral tentacles being shorter than the two sagittal ones). Interspersed among these polyps, however, there were others, which were notable for their far shorter tentacles, enlarged body (Fig. 1b) and the presence of numerous spheres. Some spheres protruded directly from the mouth, whereas others were located close to its external surface (Fig. 1c).

The largest spheres varied from quite round to fairly elongated in shape, the latter with a maximum diameter of 300 µm. All the spheres consisted of several discrete units, each with a maximum diameter of about 50 µm (Fig. 1d).

Analysis of the semi-thin sections of the spheres revealed that they consisted of multiple spermatocysts, spherical or oval in shape, the sperm of which were arranged in rows, as became evident on moving from the periphery towards the innermost region of the cyst (Fig. 1e). Numerous small spheres resulted from a single spermatocyst.

Semi-thin sections of modified fecund polyps revealed the presence of spermatocysts filling the entire width of the transverse primary mesenteries that separate the lateral tentacles from one another (Fig. 1f). On electron microscopy, each spermatocyst was delimited by a thin fibrillar coat and contiguous spermatocysts were separated by long, thin, inwardly penetrating cytoplasmic extensions of the mesenteric cells (Fig. 1g).

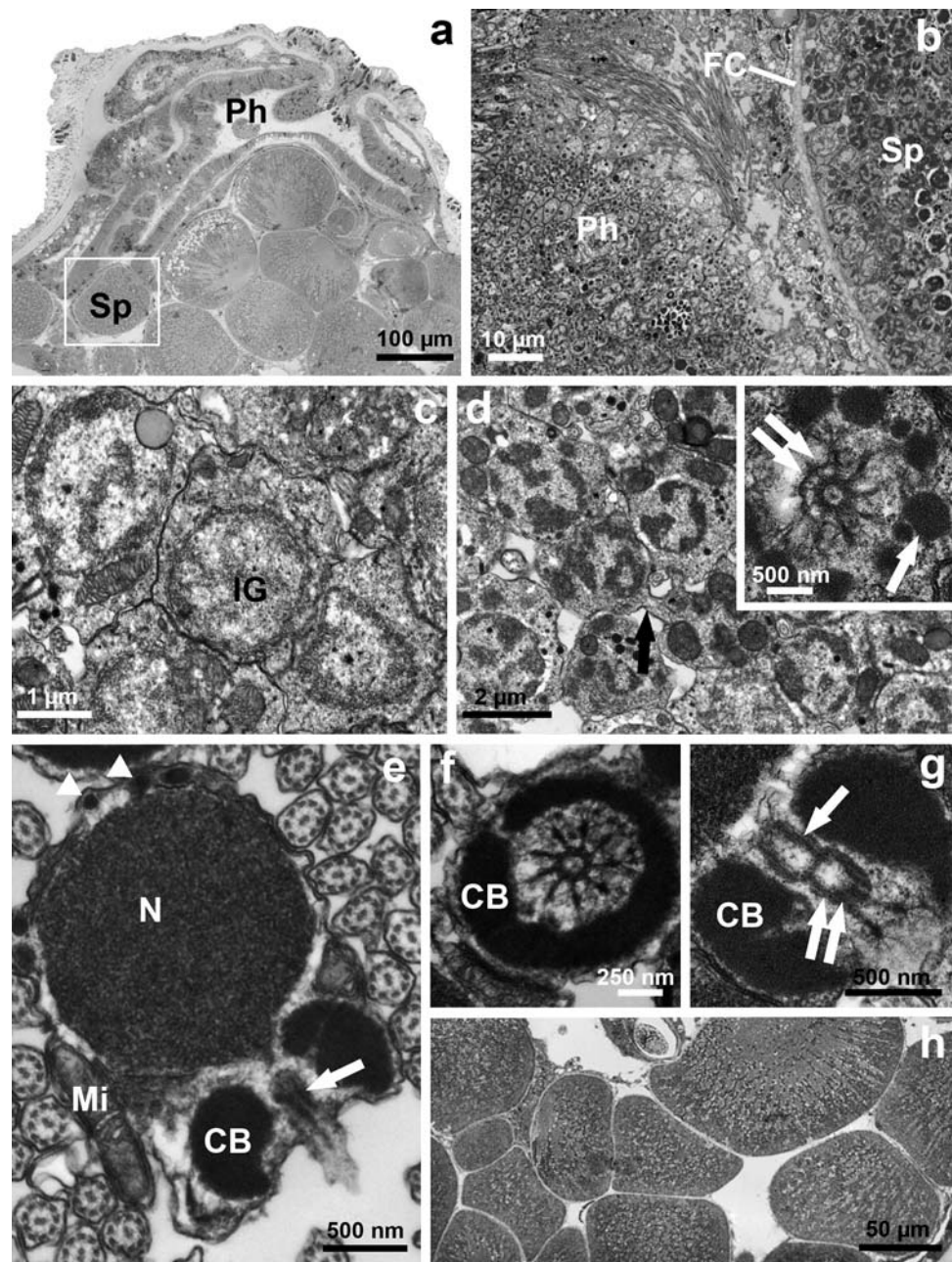
**Fig. 1** Typical (a) and modified polyps (b), released spheres (c–e), and sections of a fecund polyp (f–g) of *C. pumila*; a morphology of the polyps; b a fecund modified polyp with an enlarged body and much shorter lateral tentacles (arrows); c numerous small spheres both protruding from the enlarged mouth (arrow) and located close to its external surface (double arrow); d morphology of a released sphere constituted by a cluster of spermatocysts (Sp); e histological section showing the presence of sperm (S) filling each spermatocyst (Sp1, Sp2); f cross-section of a fecund polyp whose transverse primary mesenteries are filled with spermatocysts (Sp); g transmission electron microscopy of two adjacent spermatocysts (Sp1, Sp2) separated by the mesentery cell cytoplasmic extensions (arrow). Note immature germ cells (IG) located at the periphery. Mt mouth, Ph pharynx, EL epidermal layer, M mesoglea, GL gastrodermal layer



Longitudinal sections passing through the mouth of a fecund modified polyp, observed on light microscopy, revealed the presence of a spermatocyst in proximity to the terminal region of the pharynx (Fig. 2a). This feature was confirmed by ultrastructural images, in which the cyst, delimited by its fibrillar coat, was in close contact with the pharynx cells (Fig. 2b). At the periphery of this cyst, immature sperm closely adhering to one another were seen; these displayed small mitochondria and a nucleus with non-condensed chromatin (Fig. 2c). In this region, developing sperm were interconnected by cytoplasmic bridges

and were classifiable as secondary spermatocytes (Fig. 2d). Moving inwards, partially differentiated sperm became evident; these were characterized by pro-acrosomal vesicles (Fig. 2e) and by the gradual organisation of the pericentriolar system of the distal centriole, which consisted of nine arms arranged in a radial pattern connecting them to electron-dense granules (Fig. 2d inset). These latter constitute the precursor material of the cup-like body (Fig. 2e) to which the pericentriolar system is linked (Fig. 2f). The proximal centriole seemed to be fairly coaxial to the distal one (Fig. 2g).

**Fig. 2** Location of a spermatocyst in a fecund polyp (**a, h**) and some ultrastructural aspects of a spermatocyst (**b–g**); **a** section intersecting the pharynx showing a spermatocyst (Sp) closely adherent to the pharynx (Ph); **b** enlargement of the area in **a**, showing the spermatocyst (Sp), which is about to be released through the lumen of the pharynx (Ph); **c** immature germ cells (IG) along the peripheral border of a spermatocyst; **d** secondary spermatocytes still joined by an intercellular bridge (arrow). The inset shows the electron-dense granules (arrow), precursor material of the cup-like body, unique to antipatharians, which is linked to the peri-centriolar system (double arrow); **e** some organizational details of the sperm showing evidence of: a well-condensed nucleus (N), a section of the cup-like body (CB), the distal centriole (arrow), a part of the single mitochondrion (Mi), the acrosome-like vesicles (arrowheads); **f** peri-centriolar system whose radial spoke is linked to the electron-dense cup-like body (CB); **g** proximal centriole (arrow) fairly coaxial to the distal one (double arrow); **h** fecund polyp with spermatocysts in a loose mesentery tissue. FC fibrillar coat, CB cup-like body



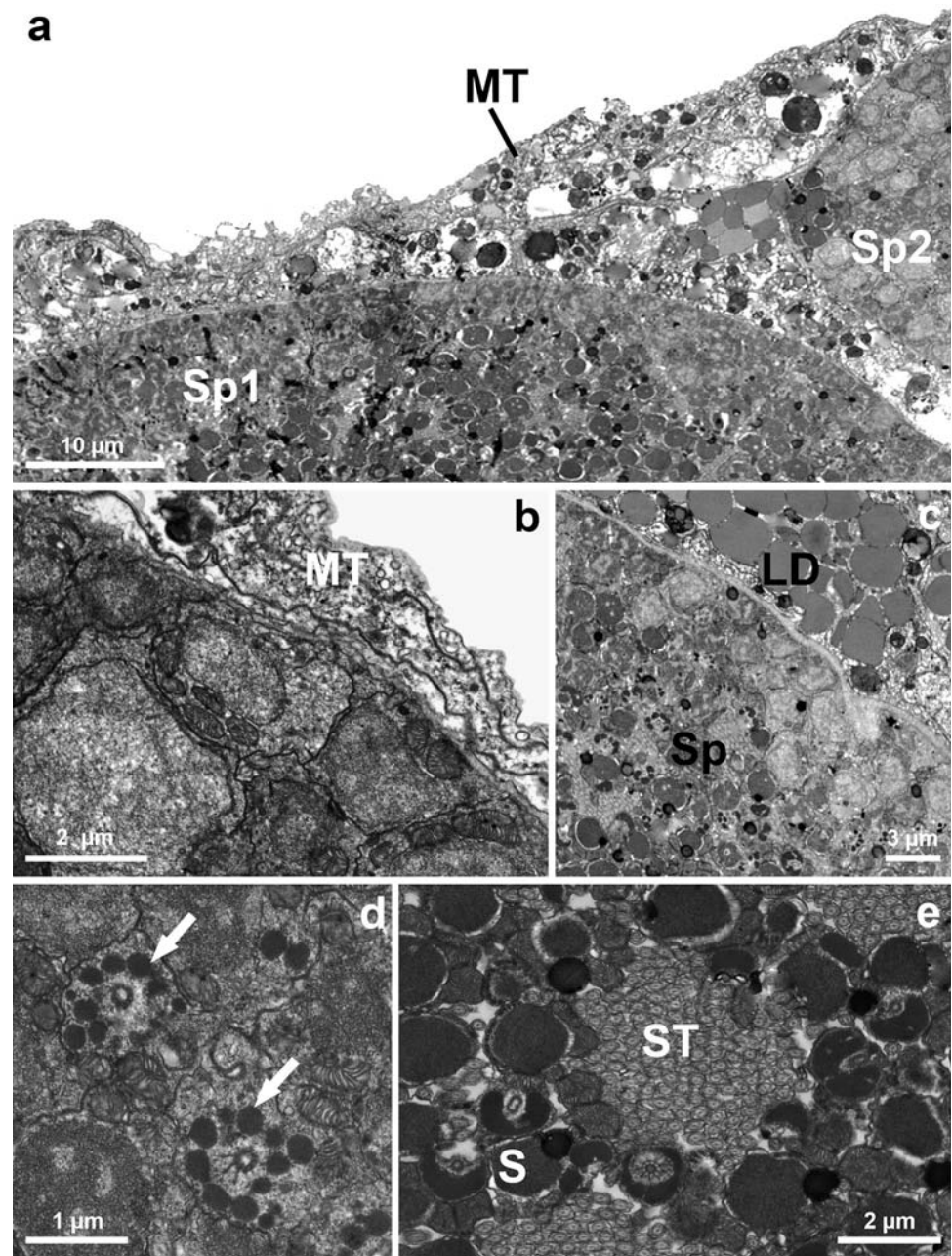
In some fertile polyps, the mesentery tissue presented a loose appearance and the spermatocysts were more separated from one another (Fig. 2h).

Spheres that settled in the aquarium were made up of spermatocysts and were bordered by a cellular coat of variable thickness, the components of which penetrated deeply inwards, thereby separating adjacent spermatocysts (Fig. 3a). In some areas, the coat was thick (Fig. 3a), in others thin (Fig. 3b), thus confirming that it originates from the irregular breakage of the mesentery walls. The coat included cells whose cytoplasm was full of lipid droplets

(Fig. 3c). Like the spermatocysts inside the mesenteries of fecund polyps, the periphery of the cysts contained immature gametes in various phases of differentiation; some of these gametes showed the precursors of the cup-like body in its initial form, which arises from discrete electron-dense granules (Fig. 3d) that subsequently merge together into the final wide electron-dense structure connected to the distal peri-centriolar system (Fig. 2f). The central region of the spermatocyst contains sperm and their clustered tails (Fig. 3e).

No eggs were observed in any of the sections.

**Fig. 3** Fine organisation of a sphere settled on the aquarium bottom; **a** outermost region showing the thick residue of the mesentery tissue (MT) penetrating inward to separate adjacent spermatocysts (Sp1, Sp2); **b** thin residue of the mesentery tissue (MT); **c** lipid droplets (LD) in the residual tissue, flanking a spermatocyst (Sp); **d** differentiating sperm in a peripheral region showing the synchronous organisation of the electron-dense material precursor of the cup-like body (arrows); **e** central region filled with sperm (S) and sperm tails (ST)



## Discussion

The morphological study of the gametes of the black coral *Cirrhopathes* cfr. *anguina* from the Indonesian Park of Bunaken has added new data to the reproductive biology of this species, allowing a hypothesis of external fertilisation after sperm and egg release to be put forward (Gaino et al. 2008; Gaino and Scoccia 2008).

As in *C.* cfr. *anguina*, the observations on the fertile polyps of *Cupressopathes pumila* were carried out on a single colony. In both species sperm gradually differentiate inside the spermatocysts located in the primary mesenteries

which separate the lateral tentacles from one another. In *C. pumila*, however, spermatocysts were also found in different phases: isolated from one another when still inside the mesentery in proximity to the innermost region of the pharynx; and protruding from the mouth. This feature, along with the spheres released from the reared fragments, corroborates the notion that, in this species, male spawning takes place through breakage of the mesentery wall; this is also supported by the morphology of the cell coat that delimits the spheres.

There are no apparent differences between the sperm of *C. pumila* and *C.* cfr. *anguina*; both are characterized by:

(i) almost coaxial proximal and distal centrioles; (ii) a similar peri-centriolar system; (iii) an electron-dense cup-like body to which the peri-centriolar system is linked and (iv) pro-acrosomal vesicles.

It is worth stressing that the presence of the electron-dense cup-like body is restricted to the antipatharian sperm (Schmidt and Zissler 1979).

Sperm cells in *C. pumila* are relatively simple and lack the distinct acrosome commonly reported in numerous anthozoans (Lyke and Robson 1975) and in antipatharians in particular (Schmidt and Zissler 1979; Gaino et al. 2008). The peri-centriolar system, which is associated with the distal centriole and radiates into the cytoplasm near the base of the flagellum, is a usual characteristic of many anthozoans (Szollosi 1964; Hinsch and Clark 1972; Corbelli et al. 2003), whereas the cup-like body, to which the spoke-like processes are linked, has so far been observed only in antipatharians (Schmidt and Zissler 1979; Gaino et al. 2008).

Animal aggregation in the environment plays a pivotal role in promoting further fertilisation, as demonstrated in hydroids (Yund 1990), in a brooding ascidian (Grosberg 1991), in sea urchins (Levitán 1991; Levitán et al. 1992) and in numerous sessile organisms that synchronise their reproductive activity to achieve an adequate concentration of sperm and eggs in the water column (see reference in Olivier and Babcock 1992). Indeed, sperm dilution in the field can result in low fertilisation rates (Olivier and Babcock 1992).

Some simultaneous hermaphroditic scleractinians release well-formed bundles containing both eggs and sperm, which are able to float to the surface to form “coral spawn slick” (Olivier and Willis 1987). By breaking up this slick in experimental conditions, Olivier and Babcock (1992) were able to evaluate the effects and fertilisation potential of sperm dilution. In these bundles, gametes are much more concentrated than they would be when shed throughout the water column. Generally speaking, in corals, mucous material binds the spawned gametes together into a slick, which reduces dispersion. In this regard, the spheres of *C. pumila* confirm the advantage of releasing aggregate sperm, a modality that recalls the well-known polychaete epitokes (Caspers 1984).

The release of buoyant compact spheres has been documented both in the reef flat and in experimental conditions in two hermaphroditic species of Australian scleractinians, namely *Favites abdita* and *Leptoria phrygia*, in which egg and sperm clusters are intermingled first in the same mesentery and then in the spheres (Kojis and Quinn 1982).

The release of spheres involves the rupture of mesogleal and gastrodermal layers. In normal egg and sperm spawning, the gametes usually pass into the gastric cavity and then out through the mouth (Dunn 1975). The main difference

between these different modalities of gamete release lies in the persistence of mesentery tissue, which forms an irregular coat filled up of lipid inclusions that could enhance the buoyancy and facilitate sphere transportation.

Around Ambon Island, *Cupressopathes pumila* shows a patchy distribution and develops in areas that are very far apart (pers. obs.), a feature that could hinder successful fertilisation. The floating spheres may therefore represent an adaptation strategy that increases the probability of long-distance dispersal.

It is quite surprising that gametes in various phases of differentiation coexist with mature elements inside the spermatocysts. We can speculate that the process of gamete differentiation might continue after release from the fecund polyps, thereby increasing the final number of sperm and their activity over time.

The release of spheres containing clustered spermatocysts might be a typical modality of gamete release in this species, in response to its particular distribution on the barrier reefs. This notion is also supported by our observations of fecund polyps of colonial fragments of *C. cfr. anguina*, which, when reared for 1 week in similar aquaria, did not release spermatocysts, either isolated or clustered in spheres. Therefore, we hypothesise that sphere release is not a stress response to laboratory conditions.

In conclusion, knowledge of coral sexual reproduction, in addition to its biological relevance, also provides insights into the feasibility of transplanting fertile colonies into areas where they have been depleted by excessive anthropogenic pressure (Romero 1997; Montgomery 2002; Petersen et al. 2006).

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