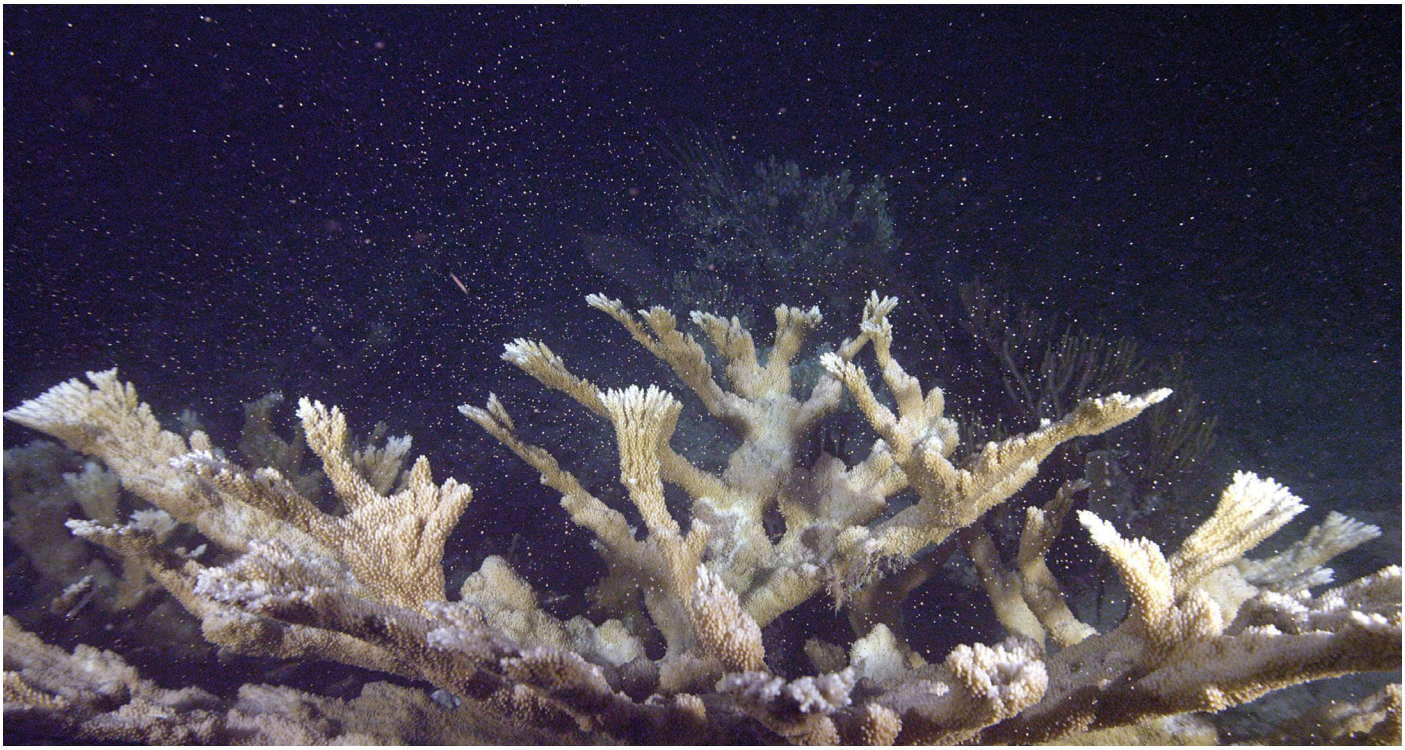


A rare glimpse of bundle broadcasting in healthy endangered elkhorn (*Acropora palmata*). Image courtesy of The Florida Fish and Wildlife Commission ©

5. Coral Rhythms: The Chronobiology of Gametogenesis, Embryogenesis, and Spawning

Chris Aslett

Welcome to the beginning of our delve into the generation of gametes and planulae in reef-forming corals where rigorous spermatogenesis typically commences a month or two prior to procreative fruition, while oogenesis may continue throughout the year (Fig 31.). Some corals release both kinds of meiocytes into the water whilst others retain eggs, broadcast and internalise spermatozoa, and brood endogenous larvae (planulae; Fig 29.).

Before we comprehend the underlying intra- and extra-cellular mechanisms that underpin these events, savour the welcome respite from the preceding thought-provoking editorials as we discover scleractinian natural history, while a glossary in Appendix I clarifies some unfamiliar terms.

Hermatypes are either iso-gonochoric with indistinguishable males and females or hermaphrodites where viviparous brood

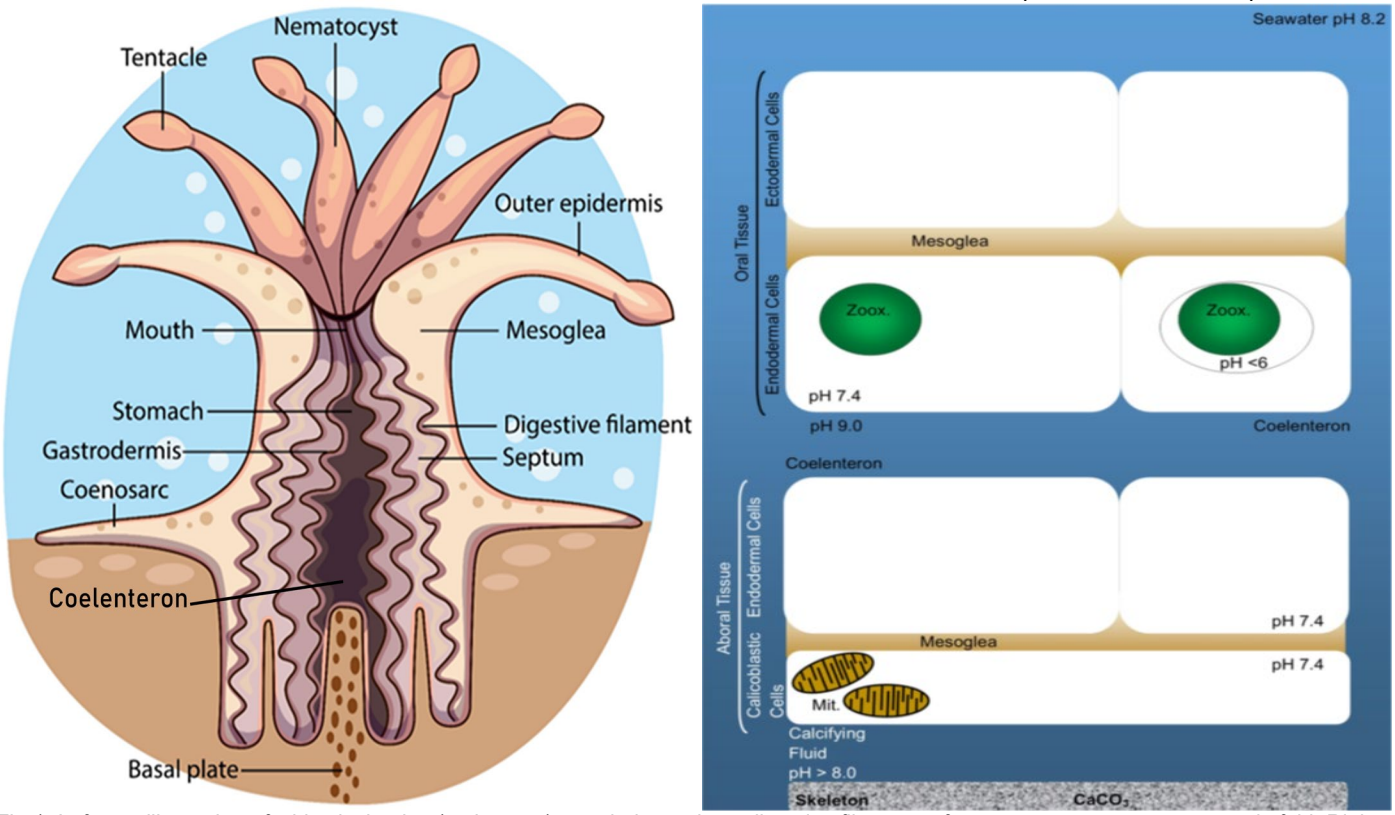


Fig 1. Left - an illustration of whimsical polyp (anthozoan) morphology where digestive filament refers to a mesentery or mesenteric fold. Right - diploblastic ecto- and endo-dermal architecture arising from two lineages of embryonic stem cell (Putnam et al. 2017), which are unified by a supportive gelatinous extracellular matrix called mesoglea. Featuring a zooxanthella (Zoox.) residing in a symbiocyte-constrained symbiosome and host mitochondrion-(Mit.)-rich calicoblastic cells. Consistent with the observations of Zoccola et al. 2015 and Putnam et al. 2017.

Keywords: ectodermis, egg, embryogenesis, endodermis, gametogenesis, mesoglea, oogenesis, ovum, Scleractinia, spermary, spermatogenesis.

Fig 2. Oocyte broadcasting from healthy but exceedingly SCTLD-susceptible maternal pillar coral (*Dendrogyra cylindrus*) which are approaching extinction in the wider Caribbean (Fig 6.). Image courtesy of The Florida Fish and Wildlife Commission ©.

Fig 3. Sperm and egg bundle setting and imminent spawning in *Acropora* consistent with the observations of Okubo & Motokawa 2008.

colonies retain eggs (oocytes) which are fertilised with internalised environmentally-broadcast sperm, where zygotes, blastulae, and then gastrulae are brooded until planulation releases zooplanktonic larvae (Shlesinger et al. 1998; Thompson et al. 2015). Brood colonies can raise asexual planulae in the absence of sperm (Smith et al. 2019), while ovary and testis analogues develop in the mesenteries of the polyp cavity (Rinkevich & Loya 1979), which may comprise as few as one or two gonads with one to three oocytes (Shlesinger et al. 1998). However, oogenesis reduces oocyte number to one in some species (Rinkevich & Loya 1979), and survivorship is enhanced by internal fertilisation and nurture.

Other Scleractinia broadcast eggs and sperm which enhances distribution (Shlesinger et al. 1998), whereas branching colonies frequently release gamete bundles (Thompson et al. 2015). Such packets take a couple of hours to reach the mouths of polyps (Brady et al. 2009), which leisurely float to the surface to discharge their cargo (Wallace et al. 1986). Each colony routinely broadcasts hundreds of millions of eggs (Oldach et al. 2017) which satiates predators and augments survivorship (Jokiel et al. 1985; Lin et al. 2021). *Acropora tenuis* liberate bundles enveloped in sulphated mucus (Okubo & Motokawa 2008) while fecundity and polyp-size appear directly proportional but oocyte diameter varies within genera (Shlesinger et al. 1998). Massive boulder colonies with sizeable polyps typically have mesentery-bound gonads and over one oocyte per ovary, which broadcast gametes or merely sperm (Rinkevich & Loya 1979; Thompson et al. 2015). Remarkably, most brooding species synchronise planulation (Marshall & Stephenson 1933; Harrigan 1972; Stimson 1978) with the lunar cycle (Harrigan 1972; Richmond & Jokiel 1984), which may be a compensative strategy to appease predation (Jokiel et al. 1985; Lin et al. 2021). Appendix II features the reproductive strategy and sexual mode of 277 species of Scleractinia where male colonies merely liberate sperm, while gonochoric females either broadcast ova like *Catalaphyllia jardinei* or brood akin to *Porites*

astreoides. Hermaphrodites like species of *Acropora* broadcast both kinds of gametes or colonies like *Favia fragum* brood and broadcast merely sperm (Baird et al. 2009).

Haploid meiocytes fuse into a diploid zygote which divides into a blastula that undergoes gastrulation from which a free-swimming planula emerges. These larvae remain waterborne throughout several developmental stages whereafter an environmental molecule induces their settling transformation. Some settlement is purely temporal (Morse et al. 1988), whilst several subsist as zooplankton for up to 244 days, but viability is significantly curtailed at 100 (Graham et al. 2008). Substratum adherence and adaptation occur within hours of planulation while the progeny of gamete broadcasters typically take three to four days. Cues from the holobionts of rhodophytan crustose coralline algae (Morse et al. 1988; Bonacolta et al. 2023) or other soluble signals induce settling morphogenesis, which guarantees suitable habitat. Established sessile coral spats commence rudimentary calcification within days (Smith 1992) and soon develop into first polyps (Rinkevich & Loya 1979; Thompson et al. 2015). Colonies develop by means of mitotic binary fission (vegetative reproduction; Thompson et al. 2015).

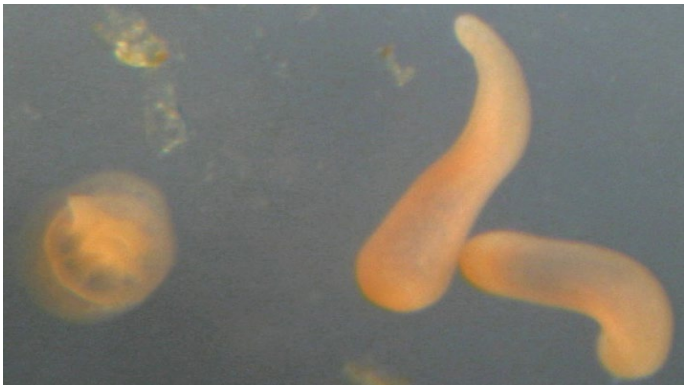


Fig 4. Left - a remarkable micrograph of a first polyp of cf. *Clavularia* resulting from the settlement of an elongate planula (right). This currently unclassified species is abundant in southern California, whilst its colonies spread using runners (stolons). Image courtesy of Jeff Goddard ©, Marine Science Institute, UCSB.

Several species of coral embryo acquire zooxanthellae and microbes vertically from the maternal colony or from pre-seeded broadcast oocytes (Sharp et al. 2012), whilst numerous kinds of planktonic larvae can requisition free-swimming prokaryotes and dinoflagellates (Morse et al. 1988; Boch & Morse 2012; Thompson et al. 2015). Likewise, substratum established azooxanthellate spats and first polyps acquire holobiont affiliates (Babcock 1985), whilst gamete mucus remains a potent source of microbial mutualists and commensals (Thompson et al. 2015).

Three-day-old spats of *Pocillopora damicornis* with developed mouths, tentacles, and mesenteries can reverse metamorphose, abandon their nascent skeletons, and resume a planktonic phase. Moreover, these planulae retain settling competencies or remain as tentacle and mouth-bearing zooplankton (Richmond 1985).

Phagocytosis assists the uptake of waterborne aposymbionts or zooxanthellae are captured and ingested through the mouth and internalised in the coelenteron (Mohamed et al. 2020). Host green fluorescent proteins (GFPs) attract free-swimming mastigotes (Aihara et al. 2019) which become coccoid upon symbiosome residency (Putnam et al. 2017). Symbiocytes and their symbiosome-inhabiting dinoflagellates are widely distributed throughout the endodermis, which is closely associated with mesoglea and the mesogleal canals that combine with the coelenteron's digestive mesenteric folds (Fig 1.). Zooxanthellae are replete in these canals which is redolent of adaptive bleaching whereby translocation to the mesenteries facilitates partial digestion before release (Rodriguez-Lanetty et al. 2005) or recruitment occurs via the canals after gastric phagocytosis. Nevertheless, these findings originate from a study of the "soft" polyps of *Zoanthus robustus* (Rodriguez-Lanetty et al. 2005).

Corals are diploid insofar as their nuclei comprise two copies of each chromosome which carry different forms of each gene from either parent called alleles. That said, gametes are haploid while each oocyte's mitochondria are passed down the maternal lineage because they are equipped with their own circular DNA genome like chloroplasts (Russell 1998b). Spermatozoa are much smaller than eggs because they must swim competently, whilst intracellular organelles likely arose from primordial endosymbiosis (Fig 7.; Janouškovec et al. 2010; Bonacolta et al. 2023). Genes encoding ribosomal proteins have been identified in mitochondria and chloroplasts (Maier et al. 2013), and thus ancestral cells may have accommodated up to four kinds of ribosomes. Phylogenetic sequence analyses of these laterally transferred rRNA-encoding genes may thus elucidate the origins of Eukaryota (Martin et al. 2015). The endosymbiotic paradigm was germinated in the 19th century when microscopy and the eminent deductions of the day proposed developmental reduction of a cyanobacterium led to the ascent of plastids (≅chloroplasts) inhabiting a heterotrophic host which descended from an amoeba that engulfed and cohabited with a micrococcoid mutualist responsible for the nucleus of eukaryotes (Mereschkowsky 1905, cited in Martin et al. 2015). The origins of mitochondria and flagella as well as the eukaryotic nucleus and cytoskeleton remain enigmatic with hypotheses too numerous to include (Martin et al. 2015). Nevertheless, Allen's co-location for redox regulation (CoRR) hypothesis explains why mitochondria and chloroplasts have retained genomes and the ribosomal proteins necessary to express them, inasmuch as they sustain their electron transport chains (Allen 1993; Allen 2003). Furthermore, the genes encoding their ribosomes have evolved convergently while their intra-compartmental co-expression is a prerequisite for their biogenesis (Maier et al. 2013).

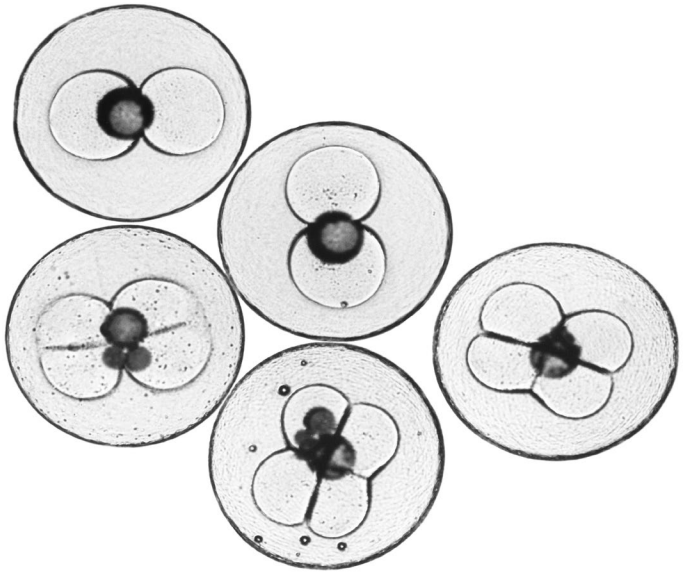


Fig 5. Sea bream eggs at initial or secondary cleavage.

When a spermatozoan penetrates an egg it prompts fusion of their nuclei to form a zygote which precedes the first cellular division (mitotic cleavage) whereafter further binary fission generates a multicellular mass, where pre-blastula morulae have over 16 cells (Fig 5.; Okubo & Motokawa 2008). Flattened prawn-chip late blastulae transform into spheroidal gastrulae that develop oral pores and metamorphose into late gastrulae planulae (Fig 8.; Barton et al. 2015). The larvae of *Acropora millepora* transmute after six days from elongate plankton to a pre-settling morphotype with nascent tentacle buds (Fig 4.; Fig 29.; Brady et al. 2011).

Brine shrimp (*Artemia salina*) take from 18 to 24 hours to hatch and feeding nauplii is neither complicated nor time-consuming, because several *Artemia* cysts are added to a small volume of warm continuously aerated seawater, while hatchlings contribute C, N, and P in ratios that support absorption, assimilation, and photosynthesis (Petersen et al. 2008; Osinga et al. 2011; Barton et al. 2015).

Brine shrimp nauplii, *Brachionus* species of rotifer (Monogononta: Brachionidae), and *Tetraselmis suecica* diatoms (Chlorodendrophyceae: Chlorodendraceae) were fed to first polyps of *Pocillopora damicornis* where the former enhanced survivorship (Fig 9.; Petersen et al. 2008). Upsurges of natural zooplanktonic abundance occur nocturnally but corals will feed around the clock (Osinga et al. 2012). Target feeding during flow interruption with a disposable Pasteur pipette is more efficacious and less polluting, and a 10-minute push button timer or a flow device feeding cycle guarantees timely wavemaker resumption. Hermatypic SPS corals demand oligotrophy and will persist in the absence of zooplanktonic feeds because overfeeding is the number one reason why captive reefs become polluted (eutrophic).

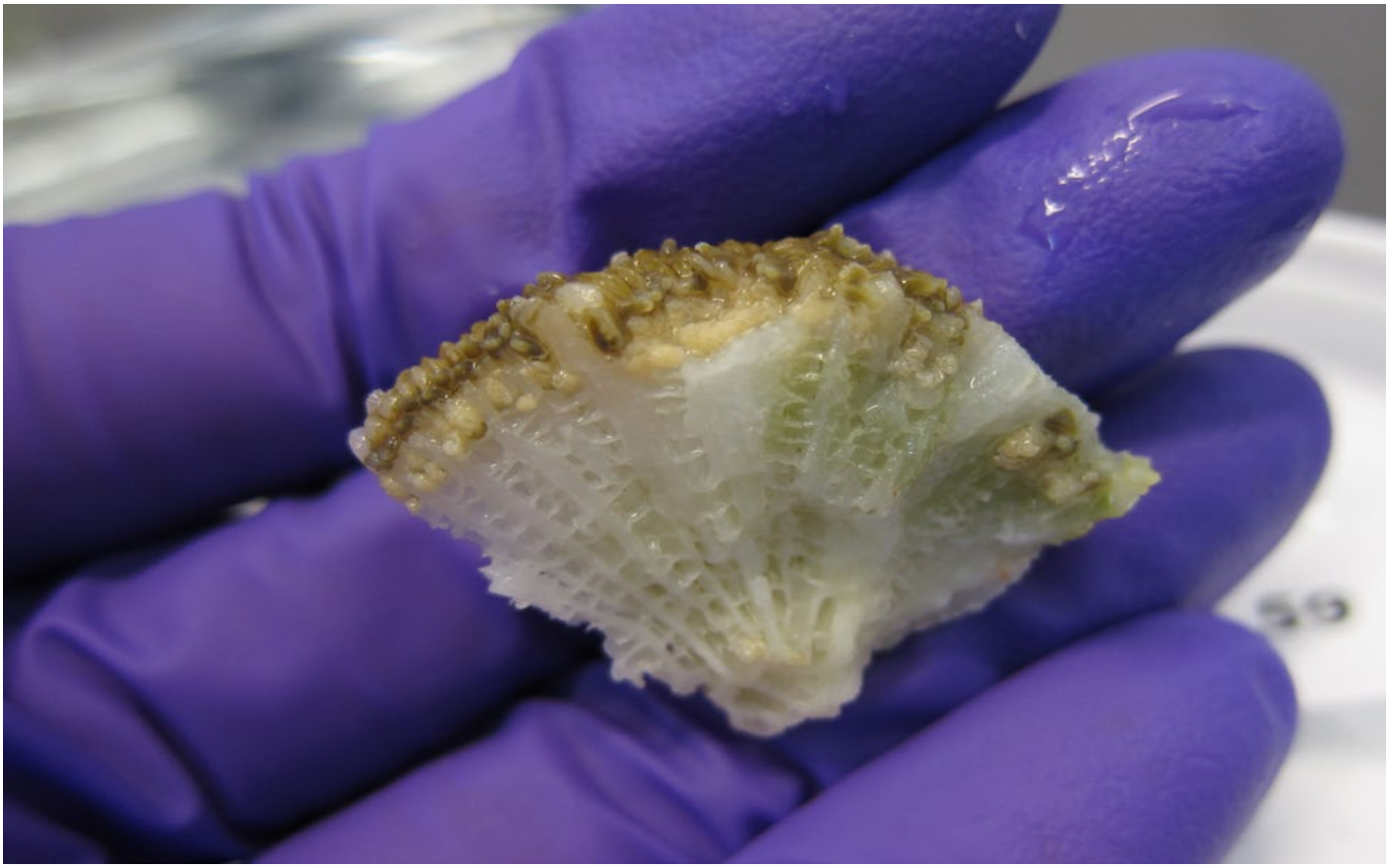


Fig 6. A section of female pillar coral (*Dendrogyra cylindrus*) featuring developing oocytes (eggs; Fig 2.). Image courtesy of The Florida Fish and Wildlife Commission ©.

Viviparous Caribbean *Favia fragum* (Faviina: Faviidae) are hermaphrodites that sexually reproduce each month (Fig 10.; Lang 1973; NCBI 2019) when spermatozoa are broadcast environmentally and internalised to fertilise oocytes, while embryos are brooded until free-swimming larvae (Shlesinger et al. 1998; Thompson et al. 2015).

These corals are usually constrained to upper or back reef slopes or shallow lagoonal flats whereas dumbbell-like colonies may be formed by the fusion of two or three neighbouring specimens (Szmant-Froelich et al. 1985). Longstanding colonial coalescence is extraordinarily inasmuch as allorecognition effectors are implicated in the detection and inhibition of chimeras (Miller et al. 2007) while intraspecific spats fuse which enhances performance but tissue rejection occurs when colonies mature (Raymundo & Maypa 2004). Furthermore, members of the suborder Faviina are significantly aggressive (Lang 1973; NCBI 2019), and the coral compatibility chart compiled by Agathos in 2015 on the Reef Central forum, suggests that species of *Favia* kill *Favia* (Agathos 2015; Aslett 2024). Even so, coral gametes often hybridise which is prohibited by precise and unique spawning windows (Vize et al. 2005; Levitan et al. 2011) while *Acropora prolifera* remains a stable cross of *A. cervicornis* and *A. palmata* (Pinzón et al. 2010; Reich et al. 2021).

The study of Szmant-Froelich and colleagues from 1985 elucidated the chronobiology and stage transformations associated with gameto- and embryo-genesis in *F. fragum*, and ascertained the impact of moonlight and whether these reproductive behaviours occurred on each month of the year (Szmant-Froelich et al. 1985). However despite commonalities, their findings are merely indicative of the processes that occur in *F. fragum*.

The germ cell aggregations of the polyp cavity that thicken

the mesenteries mid-way between the bands of longitudinal muscles and the mesenterial filaments do not constitute “true” gonads but are referred to as such in Anthozoa. These germlines derived from a reservoir of interstitial cells lack cytoplasmic masses (germplasms) consistent with the cellular progenitors of higher eukaryotes (Werner 1980). Gametes develop in the mesoglea associated with a single mesentery that distends and becomes indiscernible when meiocytes mature. Oocytes are predisposed to basal development with spermaries fostered overhead, where each one of the nine to 22 mesenteries of *F. fragum* can form gonads, whereas this coral becomes sexually mature much earlier than other Scleractinia when colonies are merely a handful of polyps (Szmant-Froelich et al. 1985).

Primary stage I interstitial cell-like oocytes with a 10- to 20-micron (µm) diameter and an enlarged nucleus and a nucleolus surrounded by minimal cytoplasm, were found either in the endodermal mesenteries but more often in the mesoglea where their nuclei grew until they reached 20 µm at stage II (Fig 21.). Vitellogenic secretions from vitelline cells commenced to assist yolk formation and egg development when their nuclei were 30 µm which continued until oocytes were 250 µm at stage III, during which the germinal vesicle destined to become the animal pole migrated to the periphery akin to all anthozoan eggs (Fig 21.). Heidenhain's stained stage II oocytes blue and stage III pink; however, oocytes appeared dark red after ovulation at stage IV when the peripheral nucleus developed a sizeable bite-like indentation. Only one or two eggs were associated with the base of each mesentery. Table 1. summarises these events and spermato- and embryo-genesis whilst figure 11. illustrates the development and distributions of the various kinds of oocytes throughout a lunar month (Szmant-Froelich et al. 1985).

The day of the inconspicuous new moon (●) is considered the first day of a lunar cycle where stage I and II oocytes were present on all lunar days but the former’s numbers increased between day 10 and 24. 20 to 30 and 75 percent of any daily population was made up of stage II and III respectively. Conversely, stage IV ova were merely present for a week after the full moon when they peaked which were totally absent by day 18 having developed into larvae (Szmant-Froelich et al. 1985).

Fig 7. Daylight broadcasting of spermatozoa from a paternal colony of flowerpot coral, *Goniopora* cf. *skokesi*.

Clusters of five to 10 enlarged (4 µm) interstitial cell-like stage I spermatocytes manifested in the endoderm proximal to mesoglea which migrated into and where enveloped by a mesentery at stage II, when peapod-like spermary sacs (≅testes) swelled from the recruitment of more from the endoderm (Fig 20.). Cellular division instigated further distention at stage III, when spermatocytes with conspicuous nuclei and cytoplasm shrank. Meiosis was implicated in the nucleic condensation and reduction in size commensurate with the cytoplasmic diminishment of stage IV, whereafter tails grew and became fully active as spermatocytes transformed into broadcast-ready spermatozoa with pink eosin-staining tails, when a lumen formed in each spermary sac (Figs 12., 13., & 20.; Szmant-Froelich et al. 1985).

Stage I and II spermatocytes were present throughout a

Fig 8. Brightfield micrographs of what are likely an early prawn-chip-like stage blastula of azooxanthellate *A. pruinosa* (left) and an abundantly zooxanthellate (speckled) late spheroidal gastrula of *Pocillopora damicornis* which acquires its initial “algal”-partners from the brood colony (Fig 16.). Micrographs courtesy of Gong et al. 2023 and the Creative Commons Attribution Licence (CC BY).

lunar cycle which peaked between days six to 26 and from six to 16 respectively, where the latter made up around 5 to 10 percent before proliferating to constitute 70 to 80 between days 18 to 28 when stage III spermaries reached a zenith then decreased

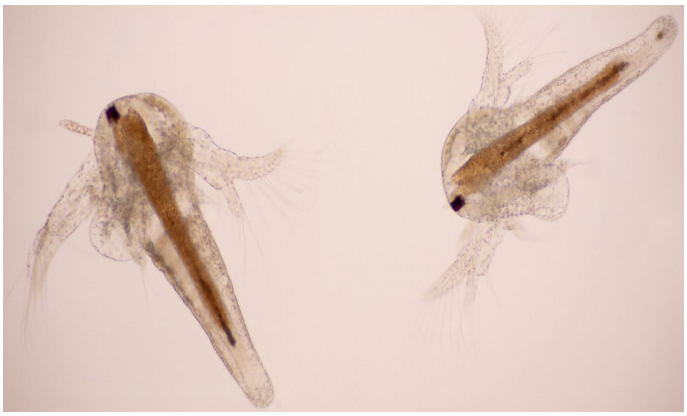


Fig 9. A micrograph of brine shrimp larvae (*Artemia* cf. *salina*) consistent with the observations of Calman from 1911.

Fig 10. Colonies of Caribbean golf ball coral, *Favia fragum* are typically less than 5 cm in diameter (Szmant-Froelich et al. 1985).

to day four while stage IV were merely present from days six to 18. Stage V spermatozoa were established by day 10 and remained until day 18 which synchronised with the maturation of ova, after which the signs of sperm broadcasting like vacuous spermary sacs became evident. Spermatogenesis is summarised in table 1., while figure 12. features the relative abundances of each stage during a lunar cycle (Szmant-Froelich et al. 1985).

Embryos began to appear at the bottom of the coelenteron as mature ova vanished from the lower mesenteries, which were the same size and stained like mesentery-bound oocytes. Although many blastulae comprise a hollow blastocoel, their bumpy texture was redolent of countless blastomeres (Reitzel et al. 2007). These first stage larvae were solid and stereoblastula-like which delaminated to form stereogastrulae. Their columnar ectoderm enveloped a syncytia-like endoderm formed from a multinucleated giant cell (coenocyte) that lacked cytokinesis-derived cross-walls. Their yolk diffused and mesoglea appeared as they matured into stage II when they commenced elongation, when oral pores developed from ectodermal invaginations, whilst coelenterons enlarged during endodermal reorganisation. “Algal” symbionts commenced to amass in the embryo-adjacent host endoderm where they began to enter planulae through a site adjacent to the oral pore. They remained ectodermal until they all migrated to the endoderm by the time stage III transitioned into IV. Nascent mesenteries were formed initially from threads of mesoglea that originated from the mouth and radiated throughout the syncytium-like endodermis which enveloped and consolidated around each strand. In due course, further mesenteric fold development otherwise referred to as gastrulation accompanied differentiation of the endoderm. All larvae with budding mesenteries and an evolved coelenteron were classified as stage III (Fig 1.). Three pairs of mature digestive folds were present before planulation while gastric cavities became established in free-swimming planulae, which typically measured 2 by 0.5 to 1 mm yet some colonies released tiny 1 by 0.25-mm larvae (Szmant-Froelich et al. 1985).

Figure 14. illustrates the synchrony of embryogenesis and the rise and fall of mature ova and spermaries throughout a lunar month in *F. fragum* (Szmant-Froelich et al. 1985), whilst figure 15. features the fraction of conspecific colonies with analogous gametes and gonads over an equivalent period from a different study (Hoadley et al. 2011). Fully mature stage IV planulae were shed over several days from as early as day six to day 15 which peaked between days eight and 11. All had vanished by day 17 at optimal spermary maturation which were mostly empty, while stage IV ova were diminished by day 20.

Several studies have observed lunar day-attuned synchronised planulation (Marshall & Stephenson 1933; Harrigan 1972; Stimson 1978; Richmond & Jokiel 1984), while waterborne gametic fusion windows remain synchronised and precise (Levitan et al. 2004; Baird et al. 2009). Specificity of this kind is likely crucial for those whose procreation is limited to a single or a handful of events per annum.

It took around four days for embryos to reach stage II which was much slower than previously reported for non-brooding species (Szmant-Froelich et al. 1985). White mature sausage-like planulae were observed nocturnally with a red flashlight moving within polyps when some had migrated to the tentacles (Fig 4.). The experimenters failed to identify the exact conduit by which planulae were released which occurred covertly after two hours of darkness. Consistent with Lewis from 1974, planulae initially ascended to near-surface waters where they were found swimming throughout the following day, yet they commenced to investigate substratum in the evening where most had settled by daybreak (Lewis 1974, cited in Szmant-Froelich et al. 1985).

The oocytes of *F. fragum* take several months to mature and thus sizeable eggs are present throughout a lunar month when merely one or two fully develop per mesentery. Each polyp retains numerous mesenteric pairs while early stage I spermaries are present throughout a lunar cycle. However, these wildly differentiate between days 16 and 17 to account for the inordinate number of stage II, which suggests that spermatogenesis occurs within a circalunar 29.5-day cycle (Szmant-Froelich et al. 1985).

The researchers postulated that the peripheral nucleus and its peculiar indentation which manifests during vitellogenesis, expedites fertilisation (Szmant-Froelich et al. 1985), whereas gonads were conventionally aligned between the mesenterial muscles and filaments consistent with the observations of Hyman from 1942 (cited in Szmant-Froelich et al. 1985). Protandry has been observed in other Faviidae (Rinkevich &

Loya 1979; Kojis & Quinn 1981) where immature colonies first procreate as males which appears lacking in *F. fragum*, yet this species becomes sexually mature much sooner than its sister taxa when only five to ten polyps at circa two years old. This faviid sexually reproduces each month throughout the year while colonies do not appear to self-fertilise, whereas the lunar cycle exerts a more profound impact on the synchrony of gametogenesis compared to the release of larvae. Self-fertilisation is likely impeded by the mouth proximate location of spermaries within each mesentery compared with their basal ova, where mature unfertilised eggs appear to remain (Szmant-Froelich et al. 1985; Heyward & Babcock1986).

Table 1. The Gametocyte and Embryonic Stage Transformations of *Favia Fragum*

Stage	Oocytes	Spermaries	Embryos
0	Mesenteries devoid	Mesenteries devoid	Coelenteron devoid
I	Sizeable interstitial cells with enlarged nuclei in mesenteries' mesoglea	Few small interstitial cells near mesoglea	Bilayered gastrulae the same size of an egg with equivalent staining
II	Nominal accumulation of cytoplasm surrounding nuclei	Aggregations of discrete spermatocytes with enlarged nuclei	Non-staining early planulae with mesoglea, oral pores, and coelenterons
III	Yolk forming stage with numerous-sized oocytes	Increased numbers of tinier spermatocytes with smaller nuclei	Mesoglea initiates mesenteric folds via endodermal invaginations
IV	Full-sized oocytes with nucleic indentations that stain dark red with *H-H	Spermatocytes with minimal cytoplasm and numerous spermatids	Mature planulae
V	-	Broadcast-ready active spermatozoa with tails	-

*Heidenhain's azocarmine-aniline blue stain

Table 1. The stage metamorphoses of *F. fragum*'s gametes and embryos adapted from Szmant-Froelich et al. 1985 (Figs 11. to 14.).

The post-fertilisation morphologies of the embryos of *Acropora digitifera*, *A. hyacinthus*, *A. solitaryensis*, *A. tenuis*, and *A. intermedia* were elucidated in the seminal study of Okubo and Motokawa from 2008 where vital stain was exploited to determine cell germlines. Yolk density conventionally influences the type of division (Wolpert 1992), insofar as cytoplasmic-bound platelets prohibit the formation of cell-dividing cytokinetic membranes (Gilbert 2003, cited in Okubo & Motokawa 2008). Species of *Acropora* undergo complete holoblastic cleavage in the face of significant yolk (Okubo & Motokawa 2008); however, cytoplasmic granules of vitellus migrate to the underside of cells where they are excreted into the blastula void (blastocoel), around eight hours after insemination (Okubo & Motokawa 2008). Previous studies had highlighted that the blastopore which typically develops into an oral aperture and gut was sealed before the development of the mouth and pharynx (stomodaeum; Hayashibara et al. 1997; Hayward et al. 2002; Ball et al. 2004), whilst gastrulation commenced at the blastopore-adjacent animal pole. Stinging cnidocyte-bound spirocysts were implicated in substratum recruitment inasmuch as they proliferated in the posterior aboral region prior to settlement (Okubo & Motokawa 2008).

Fragments of *Acropora tenuis* and *A. digitifera* were collected at depths ranging from 3 to 6 metres just before their forecast spawns in June 2003 and May 2005 from the reefs off Akajima Island in Okinawa, while part colonies of *A. hyacinthus* and *A. solitaryensis* were sampled at equivalent depths and gametocyte phases from the waters of Wakayaman in July and August 2006. "Frags" of *A. intermedia* were gathered from Okinawa's Churaumi public aquarium in June 2007. Specimens were observed each night in aquaria or the local anchorage until gamete bundles were seen approaching their polyp mouths when they were placed in 20-litre same-species plastic vessels kept in the laboratory at ~26 ± 0.5°C. Broadcast and dispersed bundles were mixed and washed to ensure adequate fertilisation and to prohibit ammonia spoilage, which were sampled every hour for the first 24 and then from four to six hours thereafter. ~50 ova and embryos were placed in a petri dish and observed using a stereo brightfield microscope (Okubo & Motokawa 2008).

Several samples of ~100 embryos and oocytes were fixed,

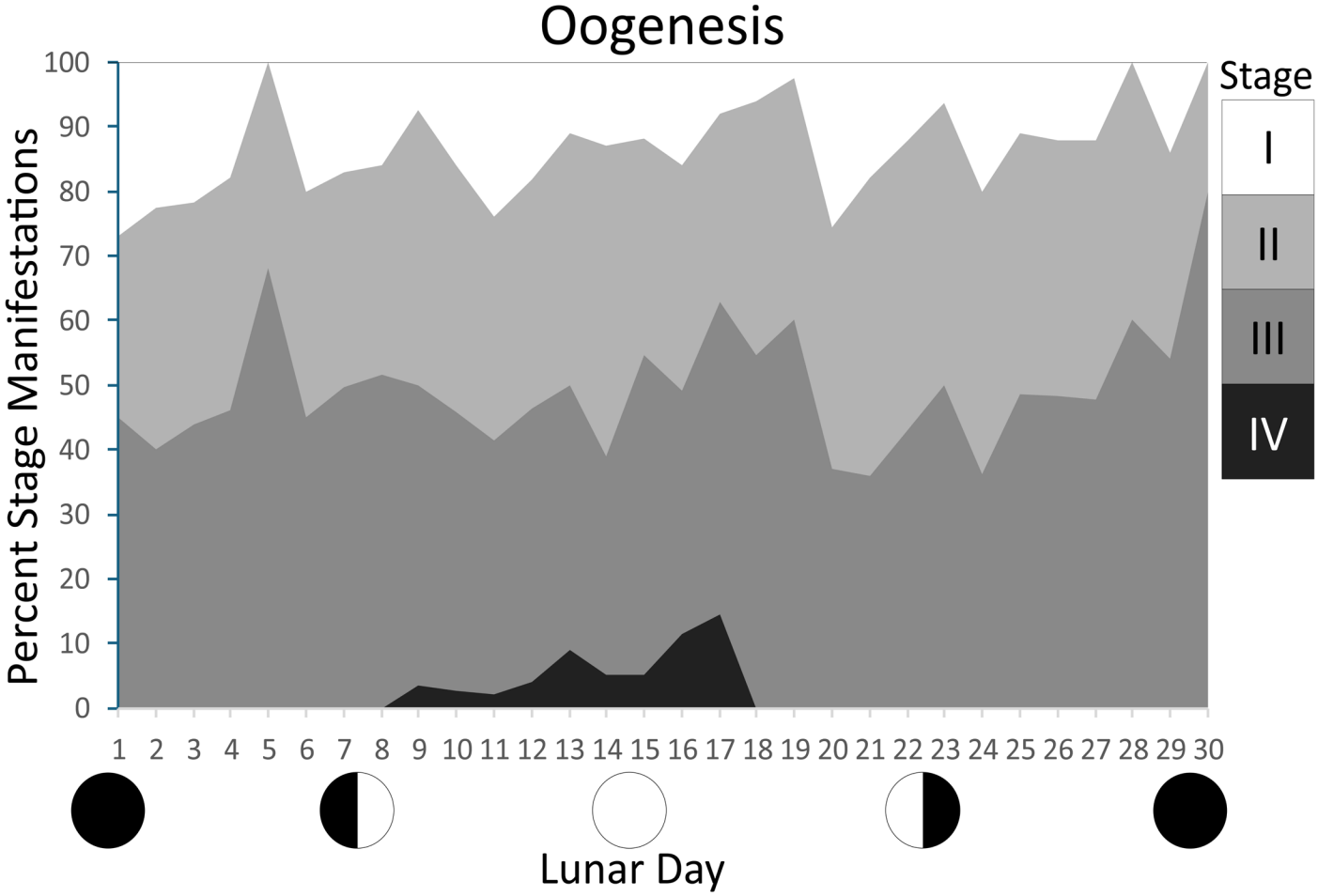


Fig 11. Area plots of the percent stage manifestations of oogenesis in *F. fragum* over a lunar month adapted from Szmant-Froelich et al. 1985. See: Table 1.

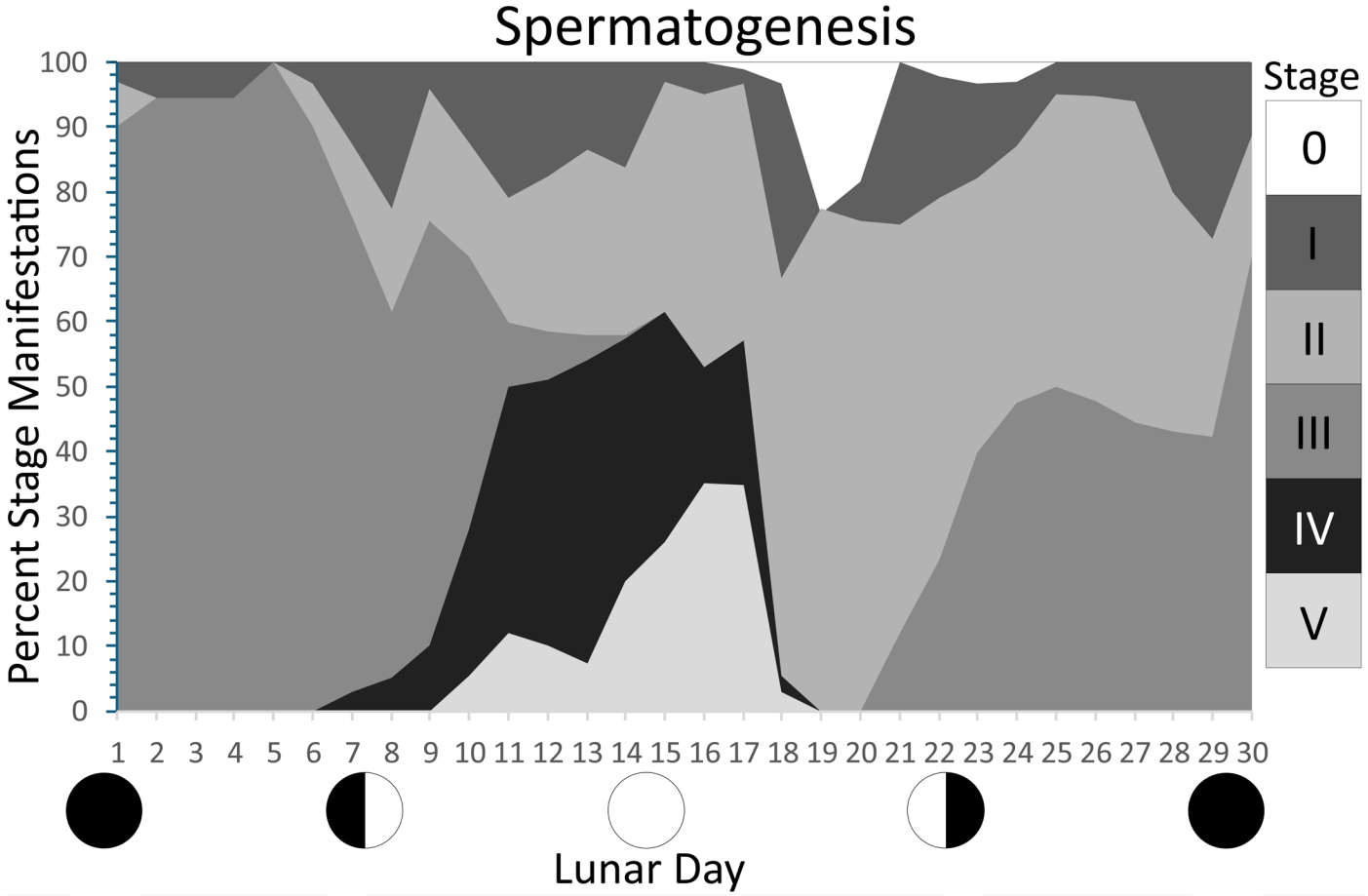


Fig 12. Area plots of the percent stage manifestations of spermatogenesis in *F. fragum* over a lunar month adapted from Szmant-Froelich et al. 1985. See: Table 1.

frozen, and sectioned with a cryostat or preserved and embedded in glycol methacrylate and shaved with a microtome

and mounted on glass slides. Their nuclei were stained with haematoxylin, Kernechtrot, or DAPI, whereas acidophilic structures, sulphated mucus, or microtome sectioned samples were highlighted with eosin, pH 1.0 alcian blue, or methylene blue respectively. The periodicities and trajectories of embryonic development were analogous across all species hence micrographs from merely histologically mounted *Acropora tenuis* appeared in the literature (Okubo & Motokawa 2008).

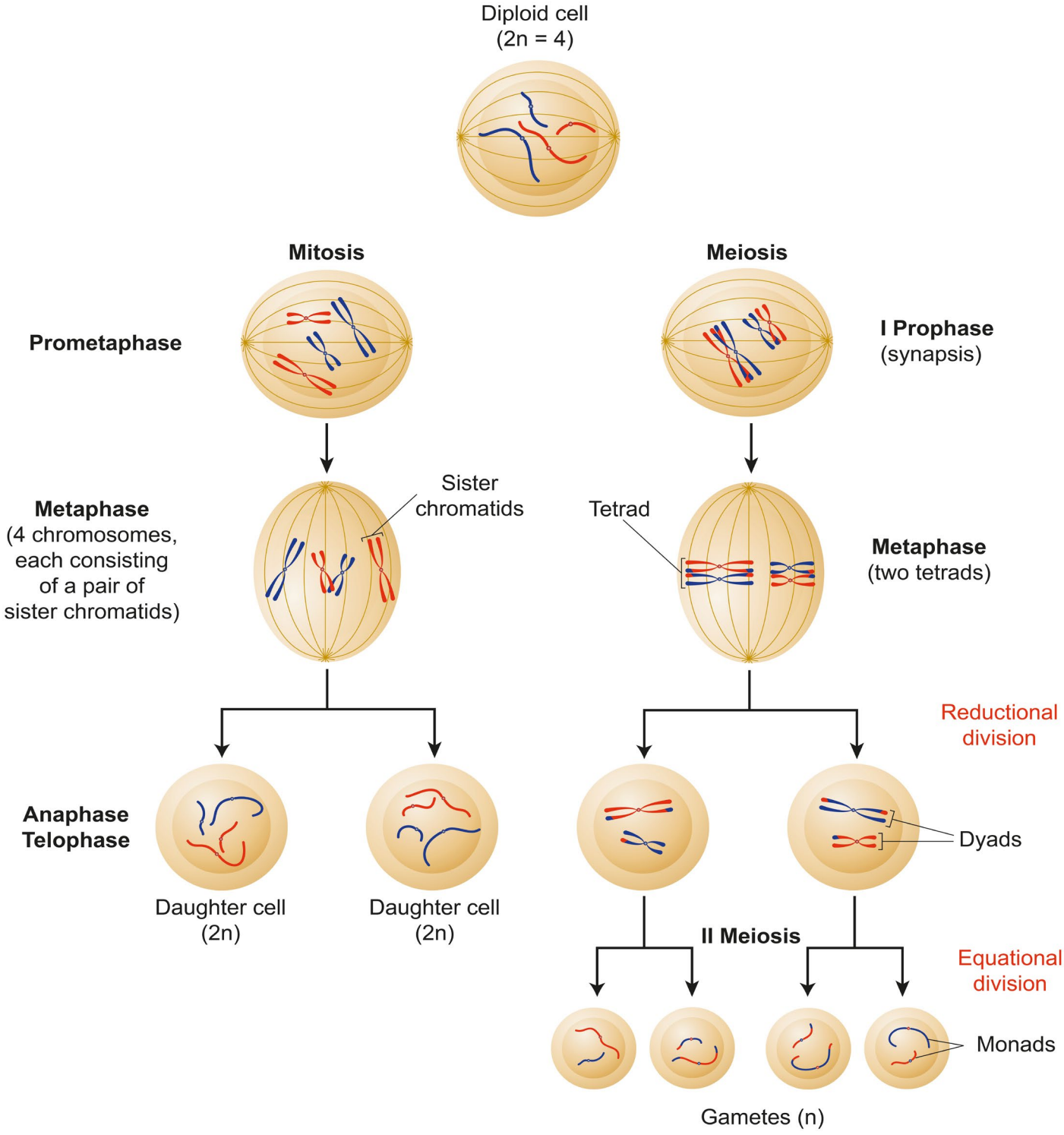


Fig 13. Diploid asexual cellular division: mitosis versus meiosis where meiosis II generates haploid gametes (meiocytes).

Cell lineage experiments became necessary as the study progressed insofar as the histology failed to discern each phase of gastrulation, the oral/aboral axis, and the developmental timekeeping of the blastopore and stomodaeum. The embryos of *A. intermedia* were vital stained using the methodologies established by Vogt in 1929 and Rugh in 1952 (cited in Okubo & Motokawa 2008). Each morphotype was held in place using dry, neutral, and red-stained agar which was overlayed with small pieces from a fine needle, after which the embryo was purged of agar and surplus stain after 30 seconds by washing in synthetic seawater (Okubo & Motokawa 2008).

Vital stain analyses unearthed first cleavage of the most mitotically active yolk-diminished cytoplasmic region called the animal pole (Fig 16. a), early concaved prawn-chip and mid-bowl-like stages (Fig 16. f & i), late-stage bowl-like blastopore-forming invagination of the concavity (Fig 16. k), and spheroidal epidermal realisation (Fig 16. l; Okubo & Motokawa 2008).

Gastrulation occurs in species of *Acropora* via delamination because the stained cells within the concavity of the late bowl-like stage surfaced (Fig 16. k to l; Okubo & Motokawa 2008).

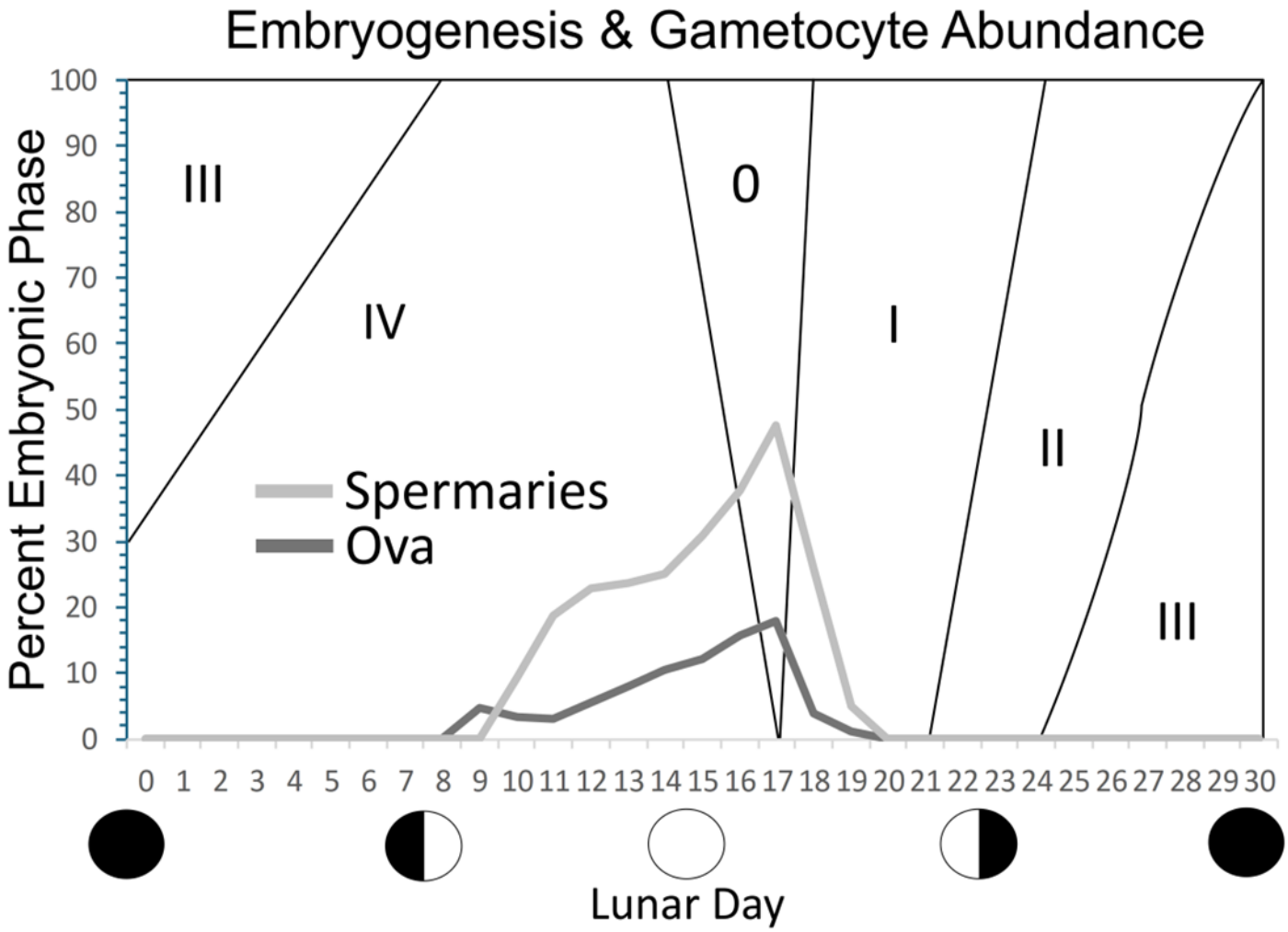


Fig 14. Percent embryonic stage in *F. fragum* over a lunar month overlayered with the percent abundances of mature spermaries and ova to exemplify the gametocyte maturation and the first window of embryo emergence from day 17 to 20 after the new moon [I], whereas liberation of free-swimming stage IV larvae (planulation) occurs gradually with peaks between days eight and 11. Adapted from Szmant-Froelich et al. 1985. See: Table 1.

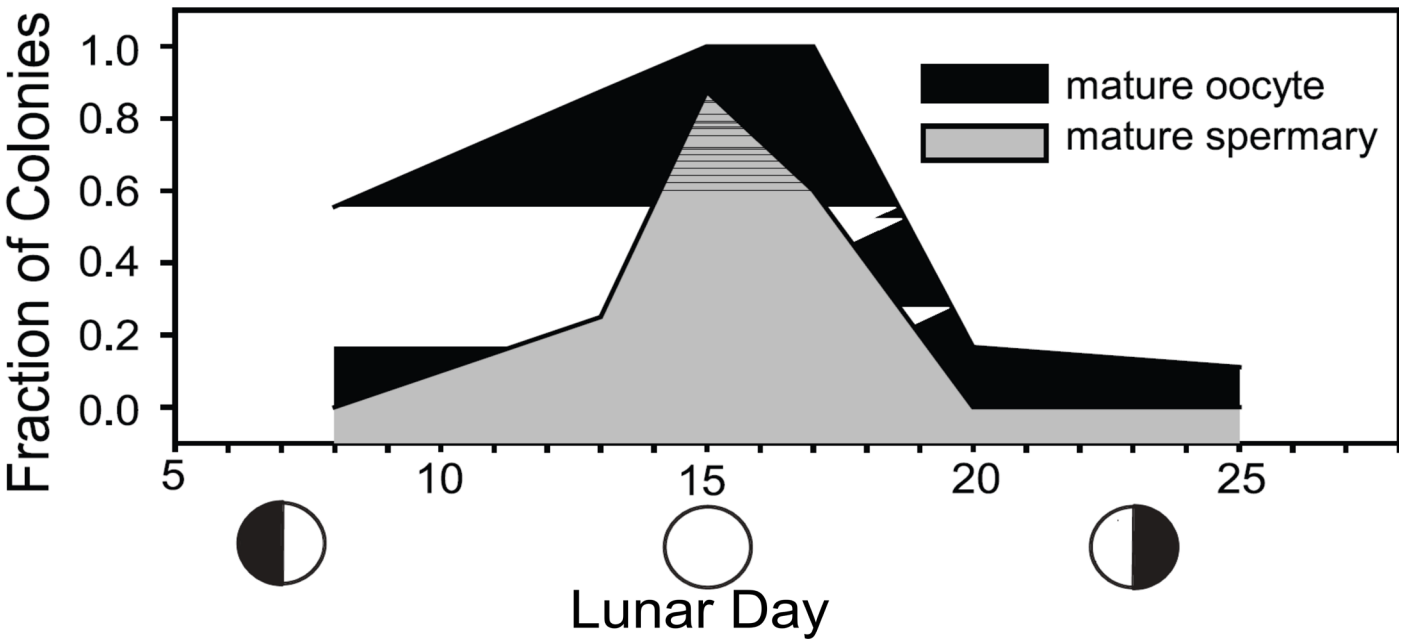


Fig 15. The fraction of colonies that contained mature oocytes (eggs; black) and spermaries (grey) over lunar month in *F. fragum* courtesy of Hoadley et al. 2011 and the Creative Commons Attribution Licence. See: 1. Pioneering Studies.

An alcian blue- and Kernechrot-staining buoyant sulphated mucus-enveloped sperm and egg bundle was liberated through the mouth of each polyp which comprised several ova surrounding a spermatozoan core (Fig 23.; Appendix III A & B; Okubo & Motokawa 2008).

Time zero of embryogenesis commenced from release, where a tiny nodulus polar body attached via a peduncle to each ova was observed at 30 minutes which had vanished when eggs became rounded and engorged with yolk after an hour (isolecithal) as a peripheral pro- or -nucleus became evident (Okubo & Motokawa

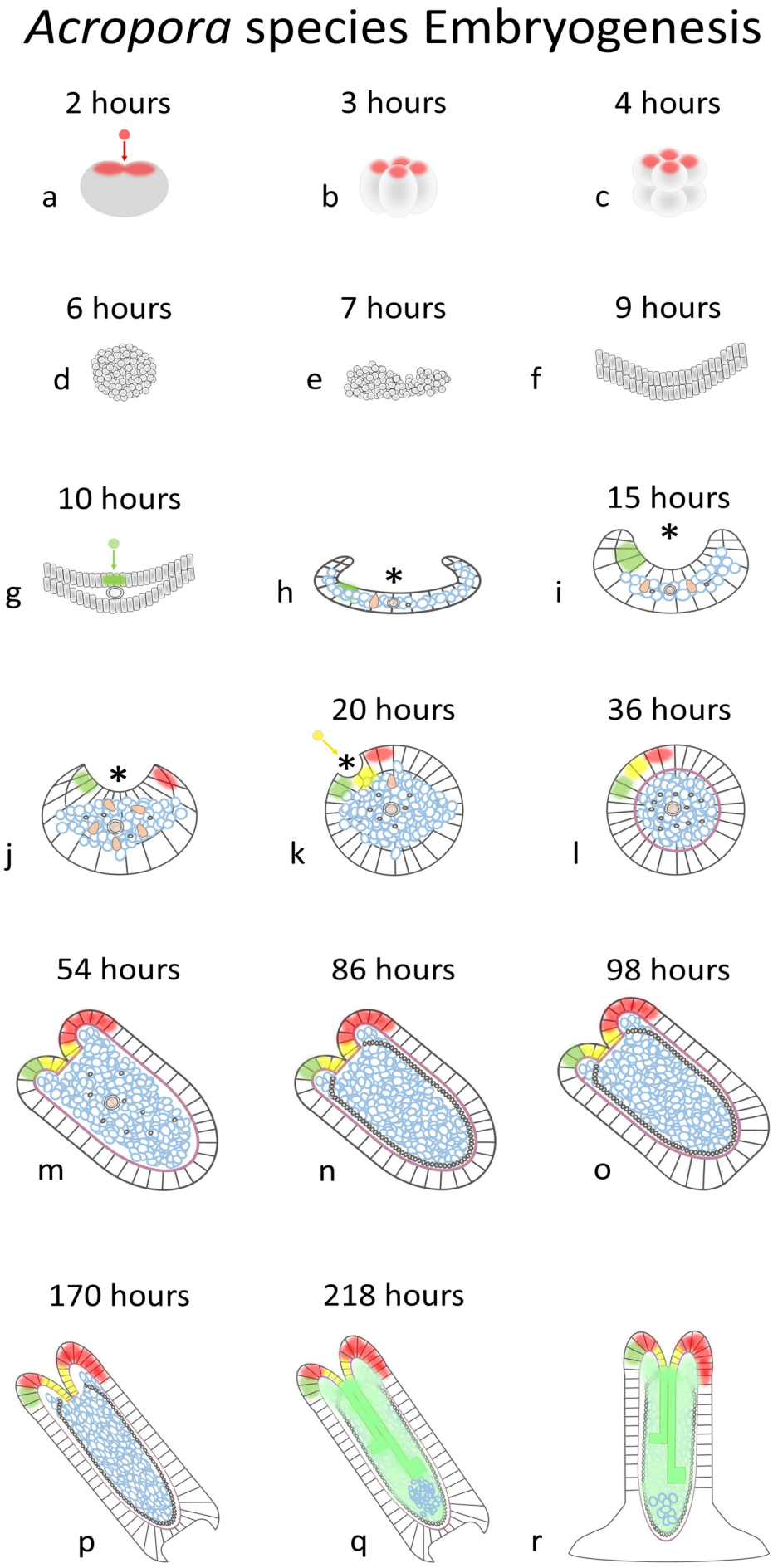


Fig 16. Embryogenesis of *Acropora*: [a] initial cleavage; [b] the product of secondary cleavage; [c] blastomeres resulting from third stage cleavage; [d] morula; [e to g] lateral view of concaved prawn-chip late-stage blastulae; [h to j] bowl-like stage; [k to l] spheroidal stage; [m to o] teardrop stage; [p to q] elongate planula stage; [r] settlement and spat formation. h to r illustrate sections of embryos as viewed through a light microscope. The vital red-stained animal pole occurs on one side of the blastopore lip, the cells of which migrate during embryogenesis. **Green**-staining prawn-chip concavity and successive translocation. **Yellow** blastopore staining and development. [○] endodermal cells; [◎] yolk; **green-shading** stomodaeum and mesenterial filaments; **purple line** mesoglea; [✱] blastopore; [◎] blastocoel into which the intracellular yolk granules were excreted from g to k. [h to k] **green**-staining cells of the prawn-chip concavity rise to the surface to reside on one side of the blastopore lip; [m] mouth forms at the animal pole. Images drawn from the accurate anatomical representations in Okubo and Motokawa 2008 and Okubo and collaborators from 2013. Consult: text, figure 27., and Appendix III for clarification.

2008).

Holoblastic fission initiated at the nucleus-comprising animal pole which created a zygote with a heart-shaped cleft at two hours (Fig 16. a). Some divisions were asymmetric, yet the plane twisted at secondary cleavage consistent with the "pseudospiral" holoblastic mitosis of other studies (Fig 16. b; Szmant-Froelich et al. 1980; Hayashibara et al. 1997), when blastomeres became kidney-shaped before splitting into four at three hours (Okubo & Motokawa 2008). Third cleavage was unremarkable which commenced at the equator and split the four blastomeres into eight after four hours (Fig 16. c). All eight blastomeres split into 16 along their meridional axis at fourth stage cleavage which despite misalignment became eight by two juxtaposed oblongs. Morphogenic synchronicity drifted where a 50/50 blend of third and fourth stage cleavage was evident at four hours. Nuclei had migrated from the inner most edge of each cell of the blastula to a central position by the morula phase at six hours (Fig 16. d). Despite dense isolecithal yolkiness, all early to mid-stage blastulae (Fig 16. d to g) were stereo and solid yet comprised a small blastocoel from the prawn-chip stage into which the yolk was excreted to expedite holoblastic fission (Fig 16. g to m; Okubo & Motokawa 2008).

All embryos with blastomeres organised into two layers with central nuclei adopted a concaved prawn-chip morphology from seven hours. Their central nuclei and evenly distributed yolk granules contra-migrated towards the apical and basolateral membranes over the next hour, yet they were transformed into

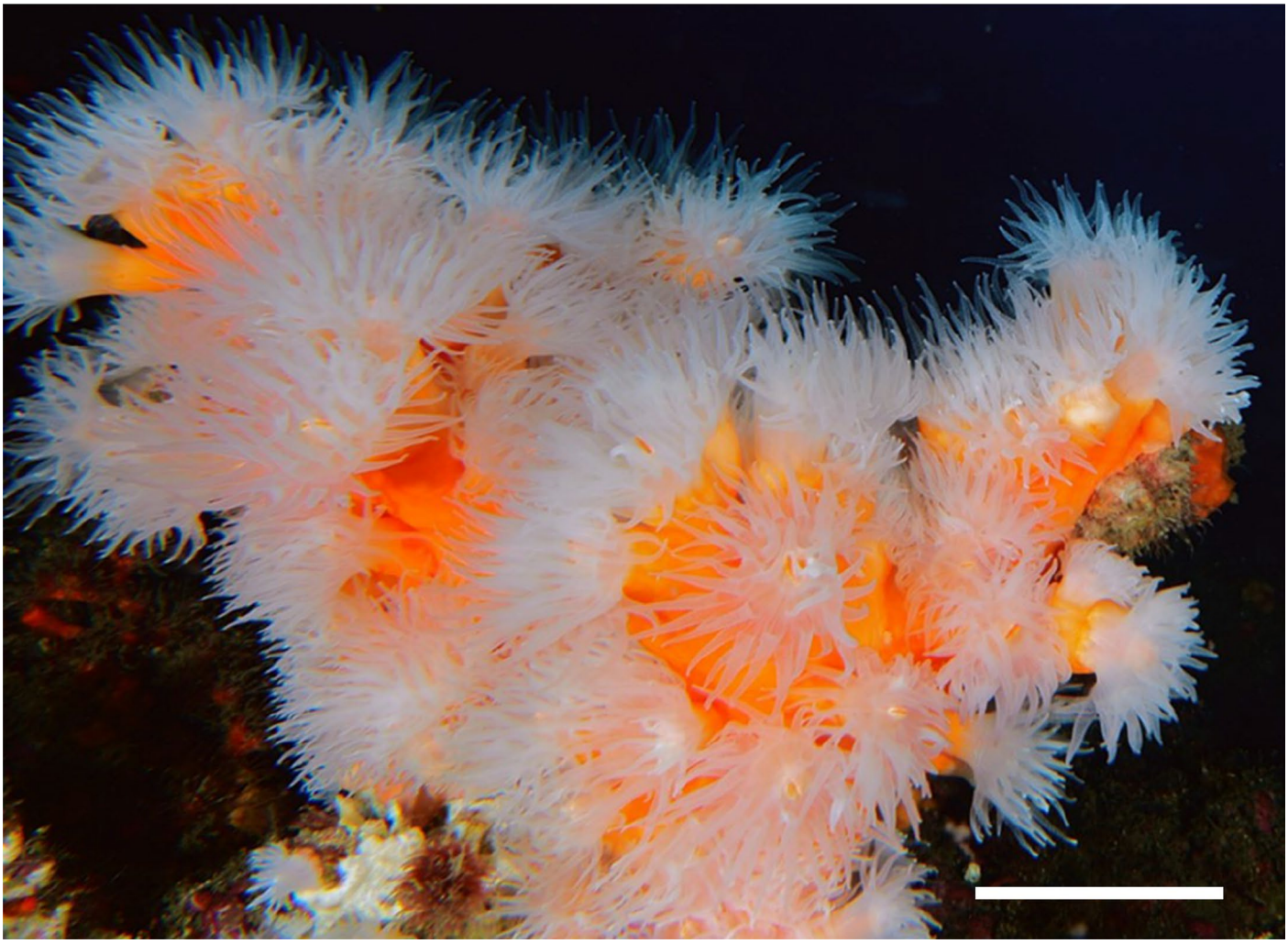


Fig 17. A photograph of the temperate meso-/a-photic-dwelling azooxanthellate scleractinian, *Dendrophyllia ramea* with a 5-centimetre bar. Courtesy of Orejas et al. 2023 and the Creative Commons Attribution Licence 4.0 (CC-BY).

Table 2. Gametogenic Stage Transformations of *Dendrophyllia ramea*

Stage	Oocytes	Spermatozoa
I	<42 µm pre-vitellogenic with "alkaline-loving" (basophilic) cytoplasm	Early loosely packed spermatocytes
II	42 to 160 µm early vitellogenic with few cytoplasmic yolk granules and central nuclei when granular enveloping cortices are underdeveloped or lacking	Spermatocytes with few spermatids maturing towards each spermary's core where few spermatozoa had tails
III	160 to 350 µm late vitellogenic abundant in yolk granules and encapsulated in granular cortices with displaced nuclei	Mature spermatozoa densely packed in spermary lumens with spermatids on their periphery
IV	>350 µm fully mature ova with animal pole proximal nuclei	Spermary sac lumen devoid or comprising remnants

Table 2. The gametogenic stage transformations of gonochoric *Dendrophyllia ramea* (Dendrophylliidae) which contrast with those of *Favia fragum* described by Szmant-Froelich and colleagues from 1985. Adapted from Orejas et al. 2023.

smooth columnar cells with a central blastocoel void from 10 to 12 (Fig 16. g; Okubo & Motokawa 2008).

The nucleus of each blastomere became further displaced to the apical membrane while yolk granules were excreted into the void, where spheroidal gastrulae ascended from blastulae from 18 to 20 hours (Fig 16. h to k; Okubo & Motokawa 2008).

The animal pole was discovered to one side of the blastopore lip in the vital stained histological sections, to where the cells that stained within the concavity of the bowl-like phase journeyed as the embryo thickened and rounded (Okubo & Motokawa 2008).

Spherical planulae became swathed in cilia and acquired tumbling motility at ~36 hours when the blastopore remained externally inconspicuous and closed, which soon invaginated and then sealed during establishment of the ectodermal epithelium surrounding a spheroidal layer of mesoglea (Fig 16. l). At this time, each planula's core was filled with granules of yolk and various kinds of differentiated free-floating cells (Okubo & Motokawa 2008).

Each planula elongated from 42 to 54 hours when a blastopore-adjacent invagination of the animal pole initiated development of the mouth and pharynx (stomodaeum; Fig 16. m to p). Aggregations of ectodermal cells accompanying a secondary off-centre pore, and a discrete concavity formed in several larvae the purpose of which remains enigmatic (Fig 16. m). Stomodaeum development progressed, while the dispersed cells of the blastocoel began to model an endodermal layer just inside the mesoglea at 86 hours (Fig 16. n), whereas spirocysts proliferated in the thickening substratum-destined aboral region that grew an indentation after 96 (Fig 16. o to p). Conspicuous eosin-staining spirocysts continued to amass, whilst the aboral indentation became jigsaw cutout-like at 170 hours (Fig 16. p; unillustrated). Other surface regions had comparatively few spirocysts while methylene blue-staining mucus-secreting cells began to develop. Mesenterial filaments arose from continuous inward buccal folds at 218 hours (Fig 16. q). Basal regions touched and extended into substratum at which juncture two mesenteries were present which later became four to eight symmetrically coordinated pairs (Okubo & Motokawa 2008). Substratum established spats commenced rudimentary skeletal accretion and continued to recruit microbes (Fig 16. r) and transformed into tentacle-bearing first polyps.

Species of *Acropora* undergo holoblastic cleavage which like snails, sea urchins, and mammals occurs despite their isolecithal ova (Okubo & Motokawa 2008). A similar influx of intracellular fats occurs in the blastocoels of *Montipora digitata* (Hirose & Hidaka 2006), which remained hitherto unobserved in the embryonic development of other animals (Okubo & Motokawa 2008).

As the name suggests, gastrulation typically results in the development of a rudimentary gut (archenteron; Technau & Scholz 2003) which transpires in species of *Acropora* during the bowl-like stage when a surface blastopore is evident (Fig 16. h to k). Nevertheless, the stomodaeum is formed from an ectodermal inward fold at a location near to, albeit not through, the blastopore. The green-staining cells in the concavities of bowl-like gastrulae, became the blastopore lip-proximal ectoderms of spheroidal planulae (Fig 16. g to l). The germlines of the ecto- and endo-dermis may thus ingress and delaminate (Okubo & Motokawa 2008), while the expression of *snail* remains implicated in cellular introversion in *Acropora* (Hayward et al. 2004). Bowl-like morphotypes were established by invagination (Hayashibara et al. 1997; Ball et al. 2004). Hirose and Hidaka suggested *Montipora digitata*'s gastrulation occurred via infolding and epiboly in 2006, whilst the current study's vital staining suggests that the formation of the stomodaeum initiates via a cellular ingression that is unrelated to ecto- or endo-dermal development (Okubo & Motokawa 2008). All the same, gastrulation is a juncture when germ layers are established in *N. vectensis* (Kraus & Technau 2006), which infers the bowl-like stage of *Acropora* corresponds to gastrulation (Okubo & Motokawa 2008).

The mouth of the acroporid genus, *Montipora* develops from an open blastopore, while secondary mouths are formed in some Faviidae which exemplifies extraordinary diversification (Okubo & Motokawa 2008).

Scleractinia are divided into two clades: Complexa like *Pseudosiderastrea tayamai*, *Galaxea fascicularis*, *Montipora hispida*, *Pavona decussata*, and species of *Acropora* or Robusta stony corals akin to *Oulastrea crispata, Platygyra contorta, Favites abdita, Echinophyllia aspera, Goniastrea favulus, Dipsastraea speciosa* (synonym: *Favia speciosa*), and *Phymastrea valenciennesi* (synonym: *Montastrea valenciennesi*), where the mouths of this latter class develop from a continuously open blastopore (Okubo et al. 2013). Appendix III.

Notwithstanding the prevailing paradigm of a cellular invagination-derived endoderm combined with a surface-descended ectoderm, the differentiation of the diploblastic progenitors of species of *Acropora* remained unelucidated from the current study. Expression of *A. millepora*'s *snail* appears a harbinger of gastrulation when embryos become concaved (Fig 16. e to g; Hayward et al. 2004), which proposes the green-staining blastomeres in the concavity become endodermal, whilst the external convex cells establish ectoderm (Okubo & Motokawa 2008). Nevertheless, later research discovered that these green-staining cells were overgrown by ectodermis (Okubo et al. 2013).

Hayashibara and collaborators had recognised that peak spirocyst abundance coincided with settlement in *Acropora nasuta* (Hayashibara et al. 2000). The spirocyst analogues of hydrozoan hydra and anthozoan anemones act as adhesive bodies that assist substratum recruitment (Will 1909, cited in Okubo & Motokawa 2008; Mariscal et al. 1977; Yamashita et al. 2003), which implies an equivalent role in Scleractinia. Moreover, the observed surface area-augmenting aboral indentation may strengthen spat holdfasts or accommodate a range of orientations because wild substratum is often granular (Okubo & Motokawa 2008).

Gonochorism may be the most ancient scleractinian reproductive *modus operandi* (Goffredo et al. 2002; Harrison 1990a; Harrison 1990) which makes broadcasting the original strategy even at significant depth (Waller 2005; Harrison 2011).

Temperate azooxanthellate *Dendrophyllia ramea* (Dendrophylliidae) are colonial LPS Scleractinia that withstand a range of bathymetric settings to dwell in zooplanktonic-abundant twilight from 40 to 240 metres (Fig 17.; Orejas et al. 2023). Robustly phenotypically plastic (Orejas et al. 2017; Orejas et al. 2019a; Orejas et al. 2019b), a study aimed to unravel the chronobiology of gametocyte maturation, gametogenesis, and

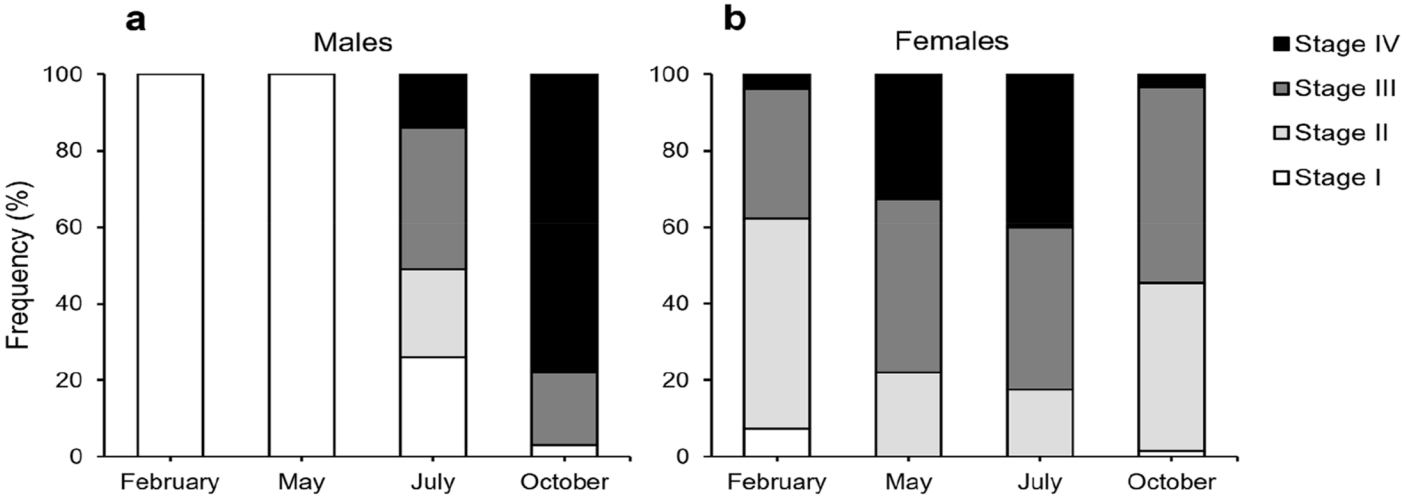


Fig 18. The percent abundances of each spermatozoan and oocyte stage from February to October within the Mediterranean gonochoric reef-forming broadcaster, *Dendrophyllia ramea*. The presence of mature oocytes and stage I spermatids suggests late summer spawning from August to October. Consult: Fig 17. and Table 2. Courtesy of Orejas et al. 2023 and the Creative Commons Attribution Licence 4.0 (CC-BY).

spawning in this temperate deepwater light cue-deprived reef-forming coral (Orejas et al. 2023). The Mediterranean collection site off Granada's Punta de La Mona is a marine sanctuary characterised by summer anticyclone-derived nutrient-rich upwellings and gyres created by Atlantic incursions through the Strait of Gibraltar. Five polyps were sampled from each of the target colonies from a *D. ramea* densely-populated reef in February 2018, May 2017, July 2018, and October 2017 to represent northern hemispheric winter, spring, summer, and autumn. Polyp dimensions were measured to ascertain if size influenced fecundity which was deemed proportional to mesenteric oocytes (Orejas et al. 2023), while histological mounts were prepared using protocols like those outlined by the author (Aslett 2024a; Aslett 2024b).

Potential relative fecundity (PRF) and effective relative fecundity (ERF) were defined as the number of mesenteric oocytes irrespective of maturity versus the quantity of ripened stage IV ova, which were averaged then multiplied by the mean sum of mesenteries per polyp (Orejas et al. 2023).

Average sea surface temperatures (SSTs) and environmental chlorophyll *a* (Chl *a*) were downloaded from oceanographic datasets, whereas polyp diameters and heights ranged from 6 to 14 mm and 6 to 37 mm respectively. Each polyp comprised 20 ± 4 pairs of mesenteries whilst maternal and paternal colonies remained phenotypically alike. 45 and 42 percent of the 38 colonies were males or females which conferred a gender ratio of 1 to 1, while a further 13 percent were devoid of gametocytes. Gonads were nestled in each mesenteric fold enveloped by filaments, where nil brood planulae verified dedicated environmental fertilisation (Orejas et al. 2023).

Merely stage I spermaries were observed in male colonies in winter- and spring-analogous February and May. 26, 23, 37, and 14 percent of summer's spermatozoa were stages I, II, III, and IV respectively, whereas 3, 19, and 78 percent of autumn's were stages I, III, and IV (Fig 18.; Fig 20.; Orejas et al. 2023).

Stage IV ova were present throughout the year, while 2 and 7 percent of oocytes were yolkless stage I in autumn and winter, which were lacking in spring when stages II, III, and IV constituted 22, 45, and 33 percent. 18, 42, and 40 percent were stages II, III, and IV in summer when stage I were absent.

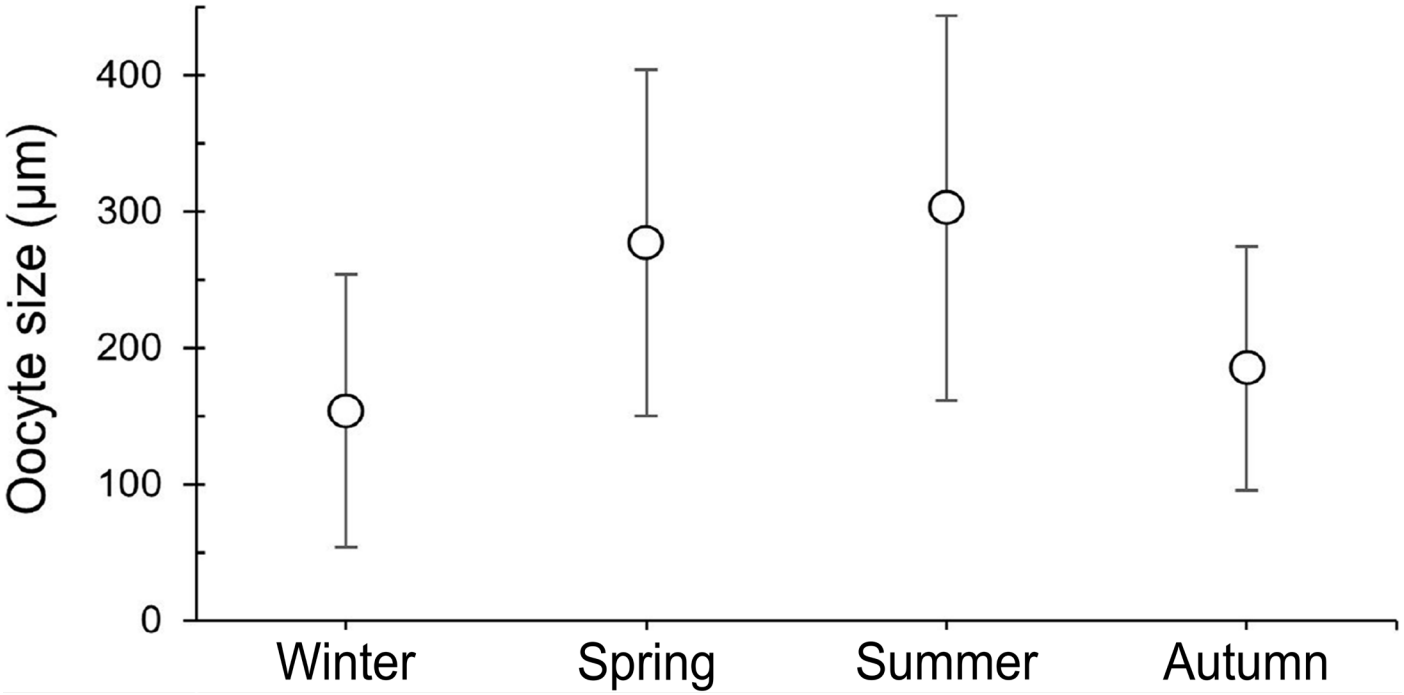


Fig 19. *Dendrophyllia ramea*'s mean diameter of 154, 277, 302, and 184 oocytes from winter, spring, summer, and autumn, respectively. Adapted from and courtesy of Orejas et al. 2023 and the Creative Commons Attribution Licence 4.0 (CC-BY).

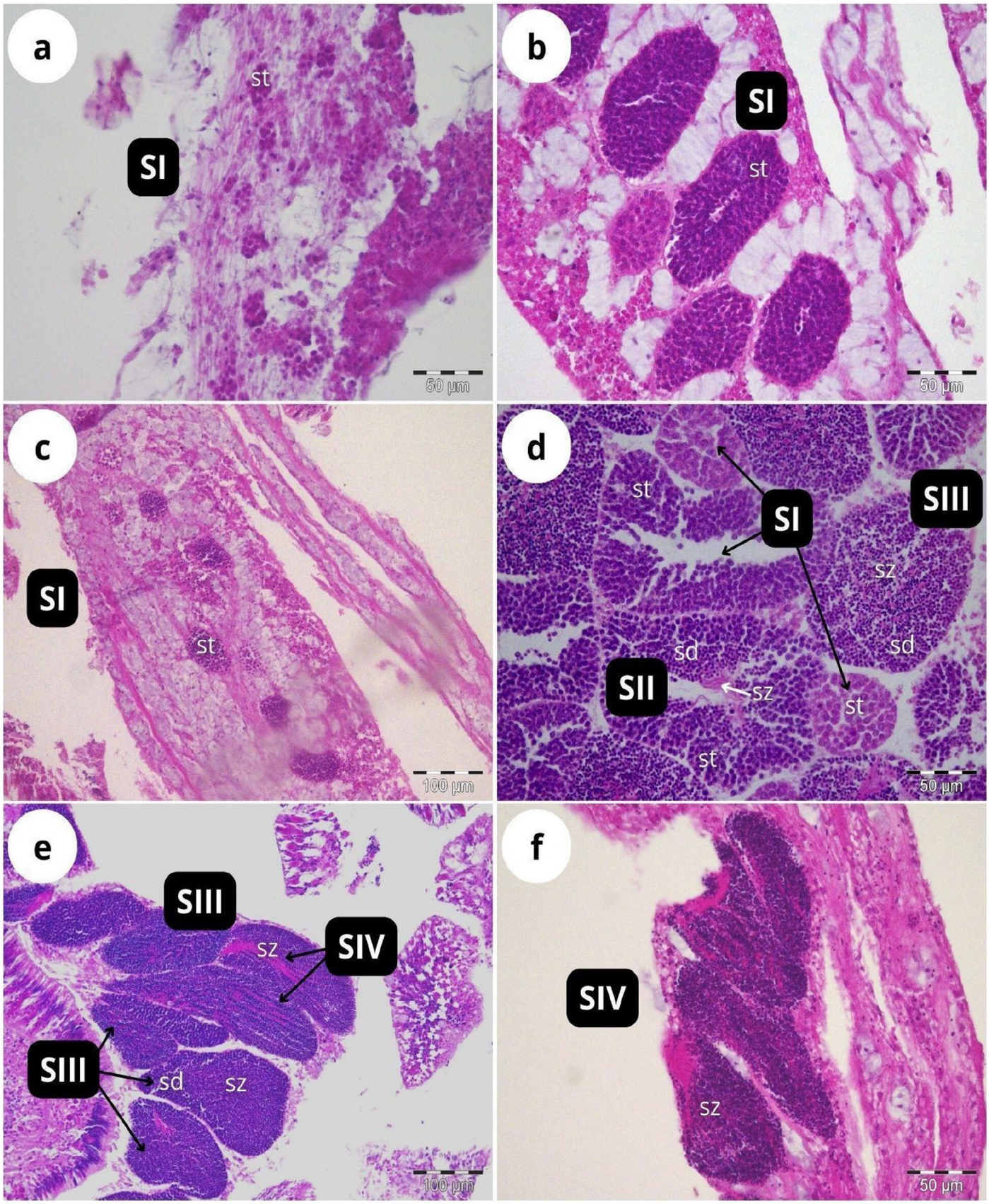


Fig 20. Micrographs of the mesentery-bound gonads from a male colony of *Dendrophyllia ramea*: [a] stage I spermatocyst (st; spermary) sampled in the winter of 2018; [b] stage I peapod-like spermary (st) from spring 2017; [c] stage I "st"s from summer 2018; [d] "st"s with stages I, II, and III spermatids (sd) and spermatozoa (sz) from polyps collected in summer 2018. The former likely resemble the interstitial-like cells described by Szmant-Froelich and collaborators in 1980 and 1985; [e] virtually mature spermary with stage III spermatids (sd) and IV "sz" from corals sampled in summer 2018, and [f] partially empty and ripened spermary with merely broadcast-ready IV "sz" with pink eosin-retaining tails sampled from the autumnal polyps of 2017. Courtesy of Orejas et al. 2023 and the Creative Commons Attribution Licence 4.0 (CC-BY).

Stage IV ova had been broadcast by autumn where merely 3 percent remained, where stages II and III made up 44 and 51 percent (Figs 18., 21., & 22.; Orejas et al. 2023).

Figure 19. illustrates *Dendrophyllia ramea*'s seasonal mean egg diameter which appeared proportional to maturity with an absolute minimum of 14.41 and maximum of 642.71 µm occurring in winter and summer. Averages of 154.0 µm ± 99.9, 277.0 µm ± 127.0, and 302.4 µm ± 141.1 were observed in

winter, spring, and summer, while a significant mean reduction to 184.8 µm ± 89.5 was discovered in autumn (Fig 19.; Orejas et al. 2023).

The stage transformations of oocytes were differentially distributed from February to July, despite comparable diameters in spring and summer when stage I oocytes were lacking and were nominal in autumn. A residual stock of stage I and II oocytes punctuated with periods of rapid development epitomises iteroparity where organisms procreate seasonally once a year (Orejas et al. 2023). However, a similar trend was observed in *Favia fragum* which broadcasts spermatozoa and broods every month (Fig 11.; Szmant-Froelich et al. 1985). Ovum development appears significantly more complex and protracted compared to spermatogenesis (Figs 20. to 23.).

There were no statistically significant differences in the quantities of stage I to IV oocytes found in polyps throughout the year (potential relative fecundity; PRF) despite marked changes in the effective relative fecundity (ERF) which enumerated

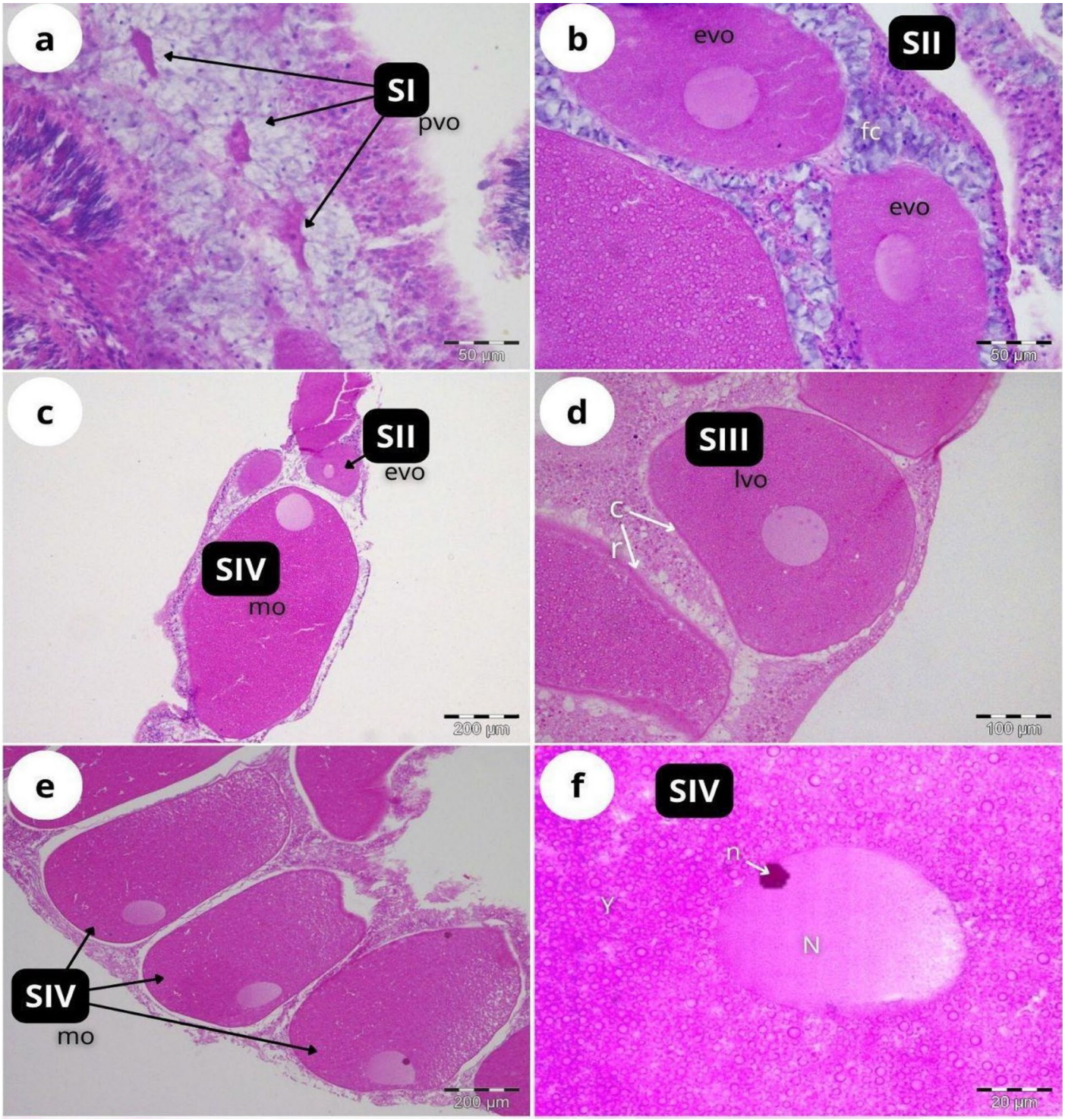


Fig 21. Micrographs of the mesentery-bound gonads from a female colony of *Dendrophyllia ramea*: [a] previtellogenic (pvo) yolkless stage I oocytes from the winter polyps of 2018; [b] top and right - stage II early vitellogenic oocytes (evo) enveloped in follicular cells (fc) with central nuclei and left - the edge of a much larger stage IV chorion-defined mature ovum (mo) filled with yolk granules found in a winter polyp in 2018; [c] a stage II early vitellogenic oocyte (evo) and a mature stage IV ovum (mo) observed in polyps from spring 2017; [d] a stage III late vitellogenic oocyte (lvo) with a developed chorion (c → r) seen in polyps from summer 2018; [e] stage IV mature oocytes (mo) with peripheral nuclei in the summer polyps of 2018, and [f] a magnified section of a mature stage IV ovum with a nucleolus (n), a nucleus (N), and yolk granules (y) discovered in the summer polyp mesenteries of 2018. See figure 22. Courtesy of Orejas et al. 2023 and the Creative Commons Attribution Licence 4.0 (CC-BY).

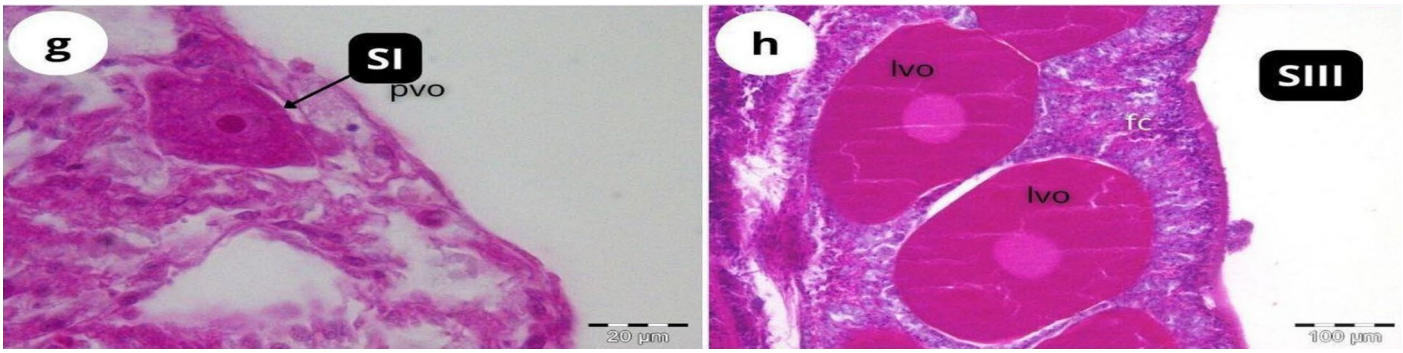


Fig 22. Micrographs of the mesentery-bound gonads from a female colony of *Dendrophyllia ramea* sampled in autumn 2017: [g] previtellogenic (pvo) stage I oocyte with a central nucleus, and [h] late-vitellogenic oocytes (lvo) with central nuclei surrounded by follicular cells (fc). See figure 21. Courtesy of Orejas et al. 2023 and the Creative Commons Attribution Licence 4.0 (CC-BY).

merely broadcast-ready stage IV ova. The highest average of 187.6 ± 81.9 mature ova per polyp (mop) were seen in spring while the least (10.4 ± 5.2 mop) remained in autumn. An average of 20.8 ± 25.4 mop occurred in winter whereas 181.6 ± 90.3 were found in summer. Remarkably, ERF and polyp dimensions appeared unrelated (Orejas et al. 2023), insofar as corallite size and fecundity appear directly proportional in numerous species while oocyte diameter varies within genera (Shlesinger et al. 1998). A maximum of 536 mop were observed in *D. ramea* while the largest oocyte had a 617 µm diameter (Orejas et al. 2023).

The autumnal decrease in mop coincided with a reduction in environmental chlorophyll *a* (Chl *a*) and soaring temperatures (Orejas et al. 2023). A decrease in local chlorophyll most likely reflects a lack of nutrients and subsiding phytoplanktonic blooms which accompany anticyclonic elevated barometric pressure, a lack of advection, and nil upwellings. That said, Chl *a* increased from October to April reaching a maximum by May, while sea surface temperatures (SSTs) steadily increased from March reaching their maximum in August. Winter storms expedite nutrient- and CO_2-enriched upwellings which draw dormant "algal" cysts from the seafloor, which likely germinate in spring (Marshall & Hallegraeff 1999; Padmakumar et al. 2011; Viana et al. 2019). ERF peaked from May to July which coincided with a dip in Chl *a* and rising temperatures. Even so, Mediterranean *D. ramea* likely spawn August/September, whilst escalating phytoplanktonic blooms in autumn would support zooplankton which sustain developing planulae/first polyps. Waterborne nourishment that lasted to spring would provide a welcome satiative glut that bolstered coral reproductive reserves, while nutrition remains a potent cue for gametogenesis (Orejas et al. 2023).

80 percent of the previously studied Dendrophyllidae were gonochoric where most brooded, while merely the genera *Heteropsammia* and *Turbinaria* were hitherto recognised broadcasters. Gonochorism appears rife in temperate corals while the yearlong prevalence of two oogenetic phases combined with a July peak of stage IV ova suggests protracted ovum development and a single annual spawn from August to October. However, 200- to 300-µm late vitellogenic oocytes (lvo) may be indicative of a zooplanktonic or demersal planulation consistent with the observations of Strathmann from 1978 (cited in Orejas et al. 2023).

Remarkably, primary oo- and spermato-gonial progenitors were not detected in *Dendrophyllia ramea*; however, the study focussed on mesentery-bound gonads while such stage 0 germlines likely migrate from the gastrodermis and mesoglea (Szmant-Froelich et al. 1985; Orejas et al. 2023).

Nutritional dearth is implicated in the delayed maturation of ova (Burgess & Babcock 2005) while the opportunities for zygotic fusion remain typically precise and brief (Vize et al. 2005; Levitan et al. 2011). Nevertheless, monthlong synchronised broadcasting has been documented in *Oculina varicosa* (Brooke & Young 2003). Orejas and allies' study suggests that oogenesis takes longer than 12 months in *D. ramea*, whilst low frequencies of previtellogenic oocytes obscure its onset (Orejas et al. 2023). A study discovering the development of the oo- and spermato-gonia of *D. ramea* and their subsequent migration may be warranted. Spermatogenesis likely begins in winter with an autumnal broadcasting trajectory (Orejas et al. 2023).

Some Scleractinia spawn annually or less than five times per annum (Barton et al. 2015) while species of *Acropora* do not sexually reproduce every year and thus exploit cryptic strategies (Baird et al. 2002). All the same, environmental stress depletes resources which impacts procreative competency (Gilmour et al. 2016). Oocyte colouration switches from white to pinkish-red, tan, or green approximately 21 days before spawning, whereafter the heads of spermatozoa condense, and their flagella become active (Harrison et al. 1984).

Osman and colleagues revealed that several kinds of *Acropora* broadcast in synchrony around the full moon in the Red Sea, whereas seven-to-nine-day earlier spawns in other regional territories were caused by lower SSTs and progressive increments in weekly warming up to six weeks beforehand (Osman et al. 2024).

Anomalous or rapid transitions of SSTs have initiated premature or delayed spawning (Keith et al. 2016; Lin & Nozawa 2023), yet asynchrony diminishes the gene pool and gamete concentrations which may hinder zygotic fusion (Shlesinger & Loya 2019), whilst spermatozoa older than two hours lose fecundity, and very young eggs resist fertilisation (Levitan et al. 2004). Furthermore, precise conspecific dissemination windows (Fukami et al. 2003) minimise the variable outcomes of interspecific hybridisation (Willis et al. 1997).

Several hundred-kilometre increments in latitude shift conventional acroporan spring spawns to summer (Shlesinger & Loya 1985; Bouwmeester et al. 2015), whereas extraordinary predator-abundant daytime procreations of *Pocillopora verrucosa* occur in May/June in the central Red Sea (Bouwmeester et al. 2011), but in June/July in the north (Shlesinger & Loya 1985). Most species of the Red Sea's *Acropora* spawn in spring around April/May or May/June while *A. humilis* broadcast months later (Fig 25.). Their oocytes mature from white to pink/red a few days beforehand, whilst their eggs are totally undetectable 14 days afterwards (Osman et al. 2024).

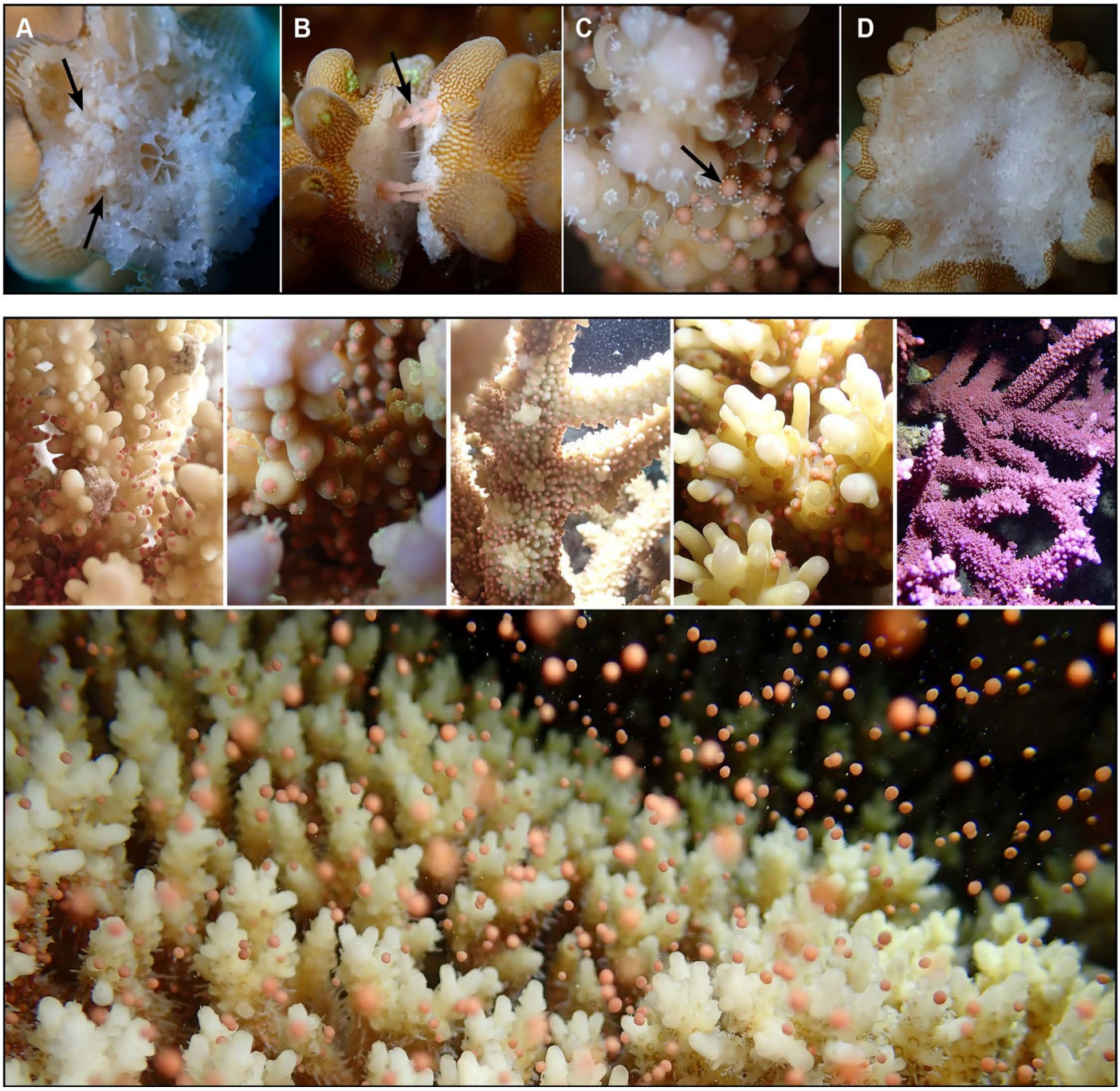


Fig 23. Wild reef in situ gametogenesis and spawning of some species of *Acropora* in the Red Sea. Top panels - black arrows indicate gametes in various stages of development: [A] white immature oocytes; [B] pink gamete maturation; [C] set broadcast-ready bundles behind polyp mouths; [D] a lack of gonads or gametes consistent with earlier spawning. Bottom panels - the liberation of bundles through the polyp mouths of various species of *Acropora*. Eslam Osman © and Alexander Stead © courtesy of Osman et al. 2024 and the Creative Commons Attribution License (CC BY).

The oocytes of female estuarine burrowing starlet sea anemones (*Nematostella vectensis*) develop in specialised thickened mesenteric strands called macronemes, where each gonadal cyst comprises up to seven ova at various developmental stages from which a single mature ovum emerges. The eggs of polyp-like organisms of the class Hydrozoa like species of *Hydra* acquire their yolk from the fusion of developing oocytes (Aizenschtadt 1980, cited in Retizel et al. 2007; Miller et al. 2000), yet experimenters were unable to identify the same mechanism in *N. vectensis* (Retizel et al. 2007). Before the aggregate of eggs are enveloped in mesentery-secreted gelatinous matrices which emanate from the mouths of female spawning anemones, they are coalesced with multicellular spheroidal nematosomes that comprise flagellated-cells and stinging cnidocysts (Fig 26. A to C).

Although *N. vectensis* lack a type of embryonic stem cell exploited by numerous anemones called a neoblast which propagate adults from a single cell, their blastomeres retain extraordinary and comparable regenerative proficiencies (Wilcox 2001, cited in Reitzel et al. 2007).

Cytokinesis is the final phase of mitosis which pinches and spits maternal cells into two daughters or embryonic blastomeres, which typically follows nucleic division and formation of their nascent membranes (karyokinesis). However, secondary and third cleavage was interspersed with groups of two or three conventional uninucleate blastomeres alongside a single elongated binucleate cell. These odd numbers and shapes may have been formed by blastomeric fusion but were most likely from delayed cytokinesis which did not affect later development (Fig 26. D; Reitzel et al. 2007). Nevertheless, atypical

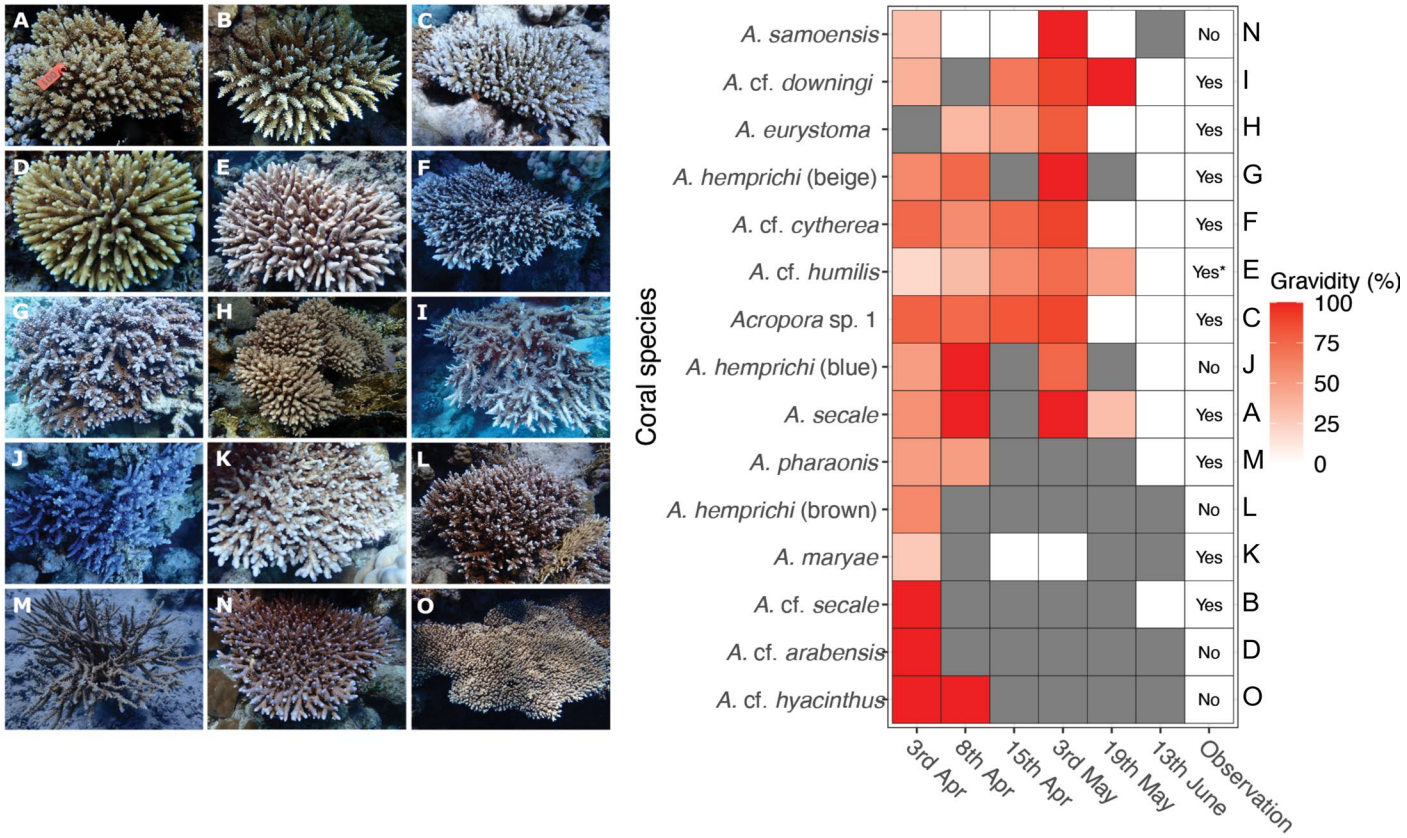


Fig 24. Heatmaps of the percent polyp gravidity of 13 species of *Acropora* surveyed off the northeastern Red Sea's Shushah Island on six spawning windows around the full moons of April and May 2023, where "No" in the observation column indicates nil broadcasting while grey squares reflect a lack of scrutiny. Analyses and images courtesy of Osman et al. 2024 and the Creative Commons Attribution License (CC BY).

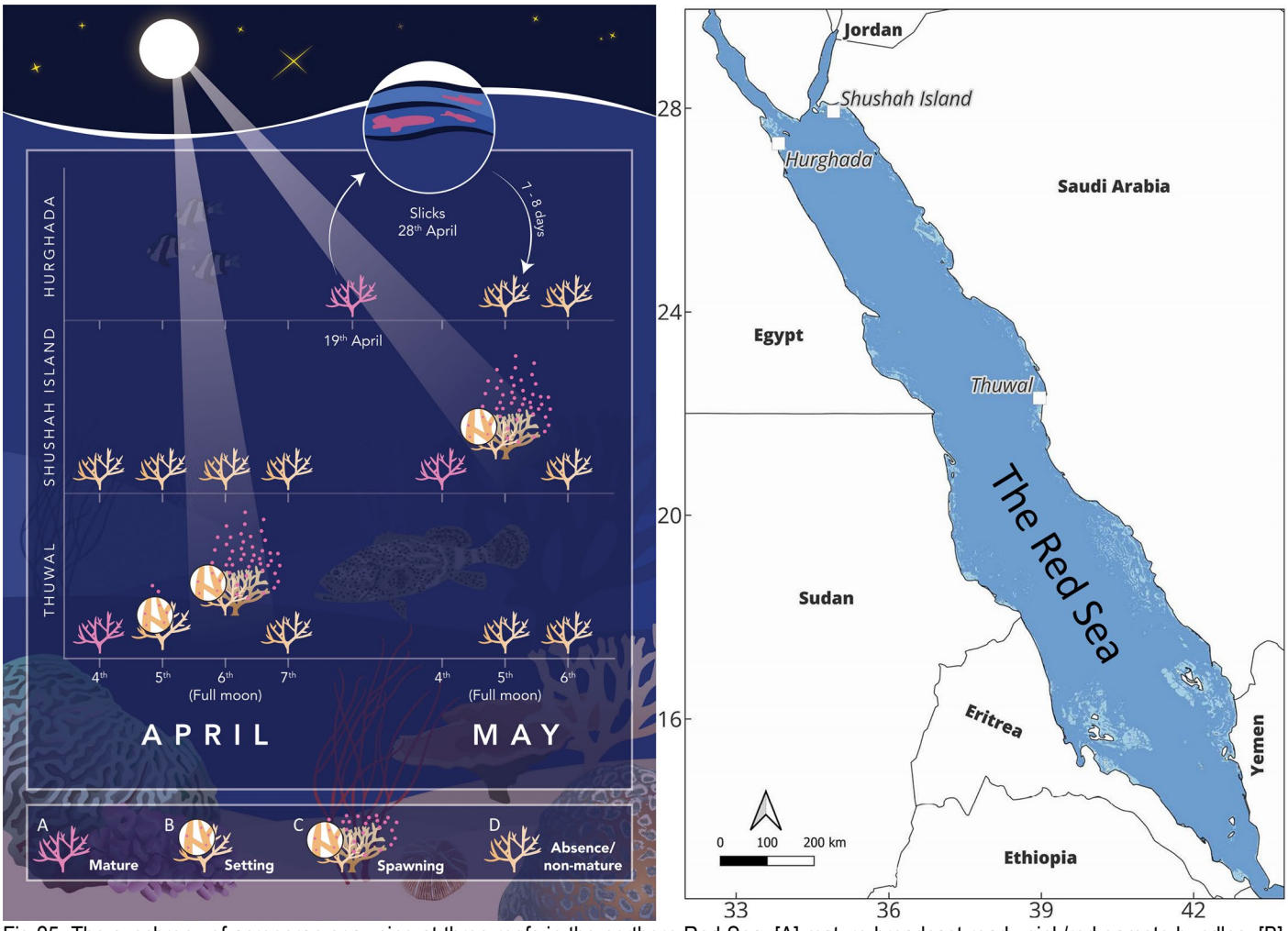


Fig 25. The synchrony of acroporan spawning at three reefs in the northern Red Sea: [A] mature broadcast-ready pink/red gamete bundles; [B] bundles set in polyp mouths; [C] broadcasting; [D] polyps devoid of oocytes/gametes or merely white immature oocytes. Adapted from and courtesy of Osman et al. 2024 and the Creative Commons Attribution License (CC BY).

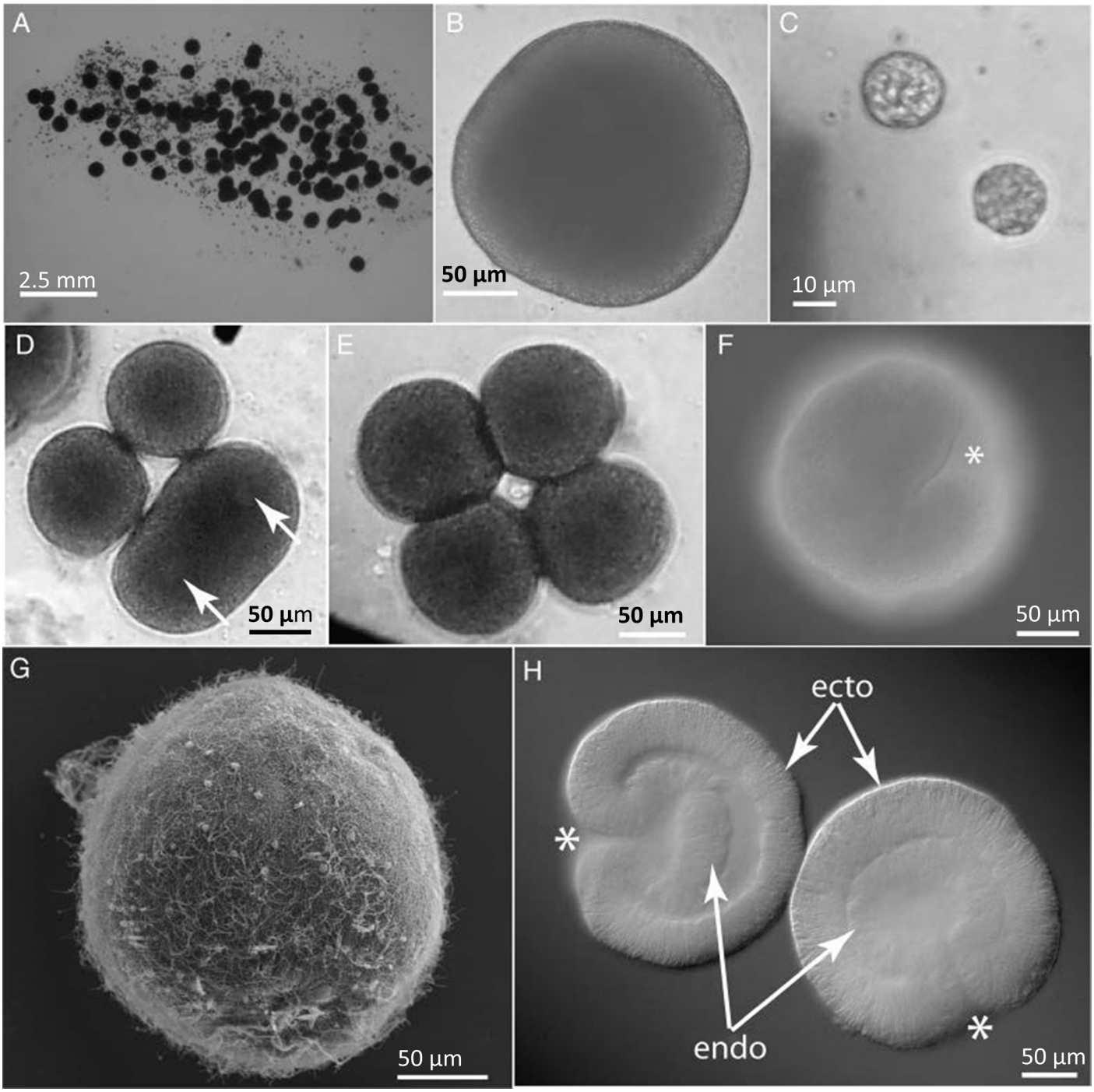


Fig 26. Brightfield and high magnification scanning electron micrographs (SEMs) of embryogenesis in the starlet sea anemone, *Nematostella vectensis:* [A] egg mass; [B] ovum; [C] Nematosomes (Appendix I); [D] asynchronous second cleavage with arrows pointing to the two nuclei of an elongated blastomere; [E] the same embryo after delayed cytokinesis; [F] a brightfield micrograph of gastrulation with a central cleft and blastopore; [G] SEM of a gastrula with a lower central blastopore and associated cilia; [H] a brightfield micrograph of a younger gastrula on the left with a disorganised endodermis, while the ecto- and endo-dermis are defined and separated by mesoglea in the oldest (Tucker et al. 2011). Asterisks indicate blastopores whilst micrographs are courtesy of Reitzel et al. 2007 and the Creative Commons Attribution Licence.

"pseudospiral" secondary fission has been observed in Anthozoa including *Acropora* (Hayashibara et al. 1997; Szmant-Froelich et al. 1980; Okubo & Motokawa 2008), albeit distinct from what is described here, it may be driven by an underlying oncogenic predisposition or bias.

Late blastulae were hollow and swathed in cilia where gastrulation commenced after an invagination of the animal pole, while the ecto- and endo-dermis were established by late gastrulation (Fig 26.; Reitzel et al. 2007).

Free-swimming but torpid planulae emerged from gelatinous matrices after two days that retained their swimming competency for up to 10. An aboral ciliated tuft was evident on spherical blastulae which was lost in later mouth-bearing elongate parsnip- or teardrop-like larvae (Fig 28.; Reitzel et al. 2007).

Cilia surrounded the mouth and anterior of these planulae which later developed tentacle buds before settling. A mouth, four tentacles, two to four mesenteric folds, and a rudimentary stomodaeum manifested in substratum-established first polyps whose heteropoles were 400 to 500 µm (Fig 29.; Appendix I; Reitzel et al. 2007).

These newly settled juveniles soon elongated and developed eight to 16 tentacles, four or more mesenteries, and gastrodermal lamellae extending to their pharynx (Reitzel et al. 2007). Figure 30. features a remarkable image of an atypical late juvenile illustrating defined pairs of mesenteries like the

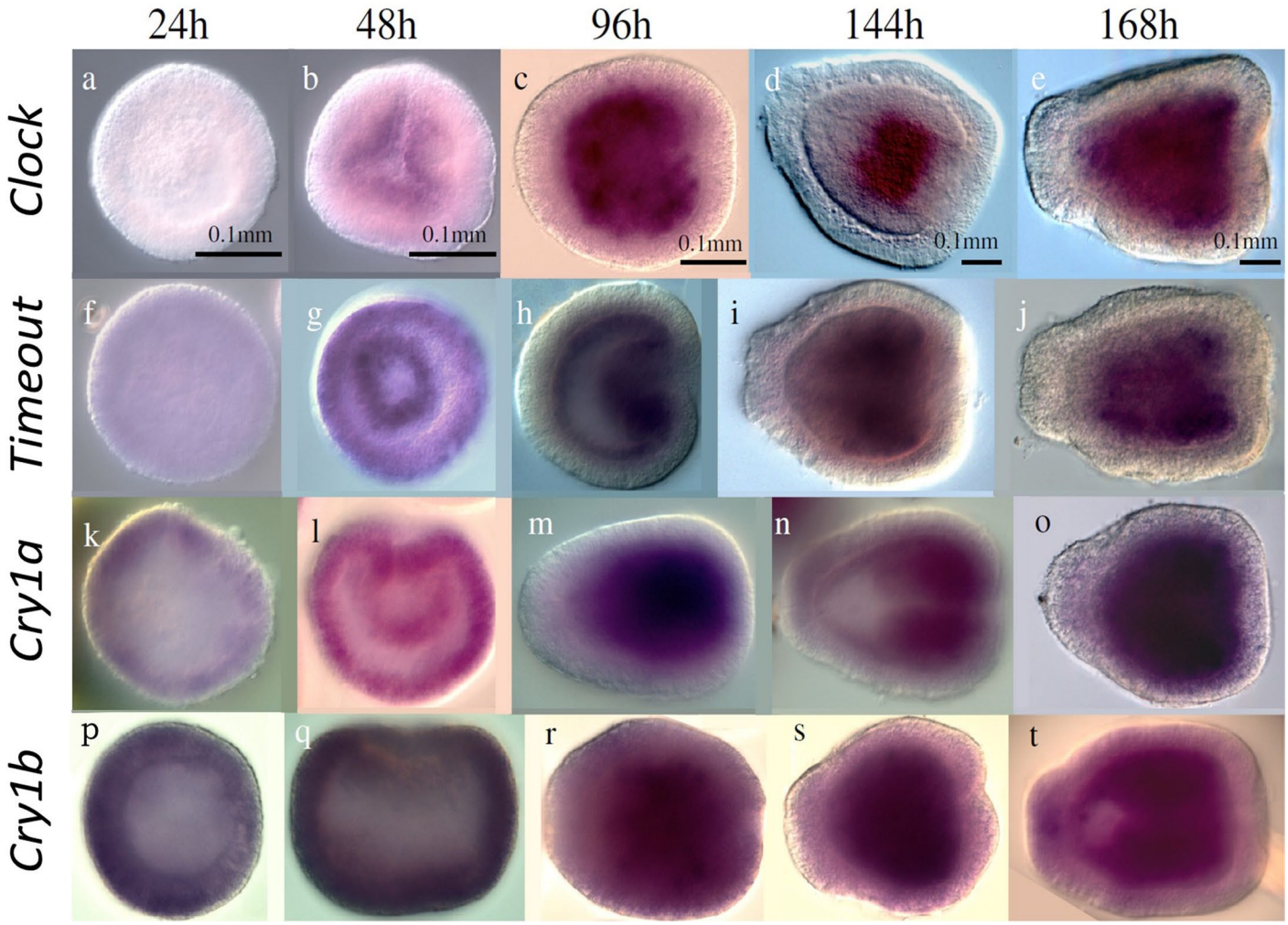


Fig 27. Wholemount micrographs of the temporal expression dynamics of the canonical circadian orthologues: *Cry1b*, *Cry1a*, *Timeout*, and *Clock* in the blastomeres of developing embryos of *Nematostella vectensis*. Featuring in situ hybridisation exploiting digoxigenin-labelled complimentary (c)DNA probes specific for the transcript of each gene, whereafter real time visualisation was expedited by an enzymatic colorimetric assay of digoxigenin-specific monoclonal antiserum conjugated to alkaline phosphatase (Peres et al. 2014). Early *Nematostella* and *Acropora* morphotypes are remarkably similar despite the extensive pre-settlement tissue remodelling of the latter, which is not required in *N. vectensis*: [a] early hollow blastula which looks like the solid stereoblastula (d) of figure 16.; [b] prawn-chip late blastula analogous to "f" and "g" of figure 16.; [g] bowl-like gastrula akin to "h" and "l" from figure 16.; [h] late bowl-like to spheroidal gastrula similar to "j" and "k" of figure 16.; [c and r] spheroidal gastrulae comparable to "l" of figure 16.; [m] equivalent of the teardrop-like early planula (m) of figure 16.; [i and n] match the mid-teardrop-like planula (n) of figure 16.; [d] late teardrop-like planula with a flattened aboral region like "o" in figure 16., and [e and j] akin to early elongate "p" and late pre-settling planula "q" of figure 16. Analyses and micrographs courtesy of Peres et al. 2014 and the Creative Commons Attribution Licence.

cartoon anthozoan of figure 1.

Acropora cervicornis, *A. formosa*, *A. grandis*, species of *Diploria*, *Montastraea annularis*, and *Siderastrea siderea* are hermaphroditic bundle-formers with extended gametogenic cycles that broadcast once a year in midsummer. Modified Heidenhain's aniline-blue was used to stain the gametocytes of Florida's *A. cervicornis* where interstitial cell-like stage I appeared red, purple, or grey, where oocytes and spermatocytes were first recognised migrating towards the blue-staining mesenteric mesoglea in October and the following January respectively.

Deep cranberry to fuchsia-staining quasi-spherical, -ovoid, or oblong 20 to 70 µm oocytes with dense granular cytoplasm and uneven peripheries had circular comparable-coloured nuclei comprising vivid cranberry staining nucleoli (Vargas-Angel et al. 2006) like plate "f" of figure 21.

Stage II oocytes were 40 to 245 µm which stained mauve/rose or beige/grey with marginally expanded, delicately granular, and nominally yolky cytoplasm (Vargas-Angel et al. 2006).

Comparatively enlarged stage III ranged from 200 to 600 µm with beige-, red-, or mauve-staining voluminous and granular yolky ooplasm. Bright cranberry staining-nucleoli were evident within smooth, grey, rose, or pink nuclei, while a darker-staining lipid-enriched polar region of each mid-stage III oocyte sampled in May to June 2001 or June to July 2002 had vanished in late-stage III oocytes by mid-July. Nuclei commenced to migrate towards egg peripheries while vitellogenesis was the only ovum-nourishing mechanism insofar as nil oocytic fusion, reabsorption, or nurse cells were evident, which are oocyte-adjoining specialised oogonial-derived phagocytes that provide the ovum with development-assisting molecules via a cytoplasmic bridge. 30 to 40 percent of these oocytes had vitellogenic membrane invaginations, whereas 21, 53, and 24 percent developed tiny scallop- and notch-like voids in their peripheral yolk or significantly lengthy and meandering pathway-like incursions which were retained throughout stage IV (Vargas-Angel et al. 2006).

The diameter of isolecithal stage IV oocytes ranged from 325 to 700 µm with peripheral round to dome-shaped nuclei touching their multilayered yolk-confining vitelline membranes. Less discernible nucleoli manifested on the circumference of

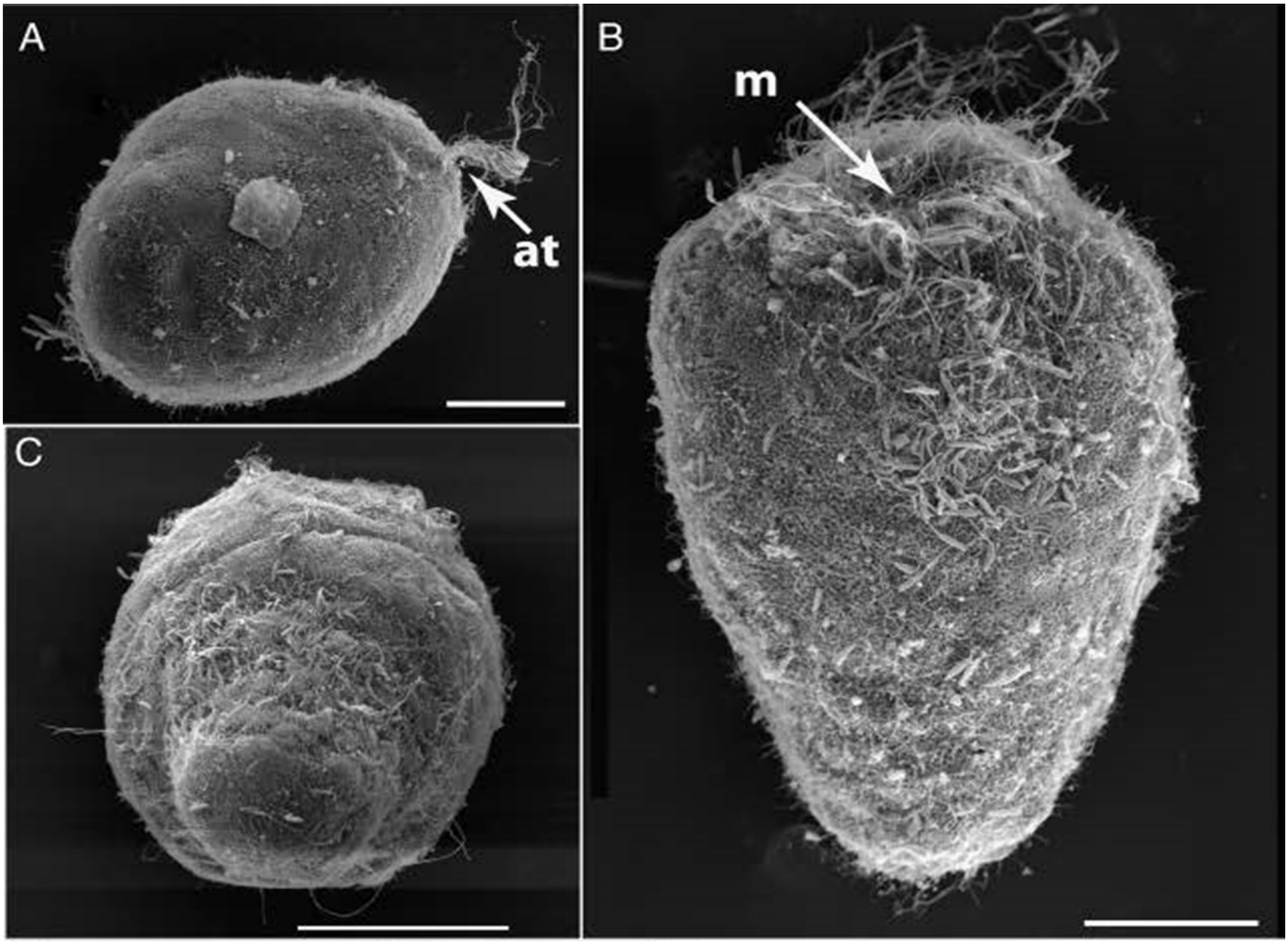


Fig 28. High magnification scanning electron micrographs (SEMs) of the stage transformations of planulae to early juveniles of starlet sea anemones, *Nematostella vectensis* with 550 µm bars: [A] early ellipsoidal planula with a conspicuous apical ciliated tuft (at); [B] late-stage teardrop- or parsnip-like planula where the "at" is absent yet extensive ciliation is evident around the mouth (m), and [C] tuftless aboral region of the parsnip-like planula from plate B with a demarcating ridge that transforms into the narrowing of the pre-settling planula of figure 29. Courtesy of Reitzel et al. 2007 and the Creative Commons Attribution Licence.

profoundly peripheral lavender to mauve sickle-shaped nuclei with conspicuous indentations which had moved from the mesoglea into the mid-mesenteries the day before spawning. Bundles are therefore packaged within 24 hours of broadcasting, while hair-like microvilli swathe the exteriors of ova.

Like the observations of Babcock from 1985, zooxanthellae remained absent in all phases including zooplanktonic planulae (Vargas-Angel et al. 2006), which suggests *Acropora* acquire their "algal"-partners as substratum established first polyps.

The stage I spermary sacs of *A. cervicornis* appeared as small aggregates of irregular-shaped 2.5 to 3.8 µm mesoglea-associated grey- or red-staining interstitial-like cells, whereas some manifested as mesoglea-enveloped putative spermatogonial progenitors with indiscernible features (Fig 20. a to d). Stage II spermaries with a 13 to 59.8 µm diameter comprised organised pockets of wedge-shaped spermatids with discrete nuclei; however, stage III magenta-, cranberry-, or burgundy-staining spermatocysts with mean diameters of 41.5 µm ± 13.9 were observed in June, which had doubled to 83.3 µm ± 21.0 by late-July, when each developed a defined lumen (Fig 20.). Stage III to IV was accompanied by a logarithmic increase in cell number and an equally meaningful reduction in meiosis-derived cellular diameter. 87.1 µm ± 22.1 wide polyp-constrained mesenteric male gonads comprised polar-aligned sprays of beige-, yellow-, or gold-tailed spermatozoa from Floridian *A. cervicornis* sampled from 23 to the 29 July 2002 and 5 of August 2001 (Vargas-Angel et al. 2006).

Spermatozoan cores enveloped in ova and mucus had moved into the gastric cavities of Florida's *A. cervicornis* sampled around 90 minutes before broadcasting on the night of 3 August 2004, when around 90 percent of available space was monopolised by bundles. All the same, around 5 percent of mesenteric gametes remained. Packet setting behind polyp mouths occurs from 90 to 120 minutes before nocturnal liberation days after the full moon or on the next quarter (Fig 3.). Vacuous distended/distorted mesoglea and mesenteries pervaded the gastrodermises of post-spawning fragments from 1 August 2002. Small unspawned and partially degraded ova were observed in each coelenteron along with remnant spermatozoa within relic spermaries, whilst unbroadcast parcels were not detected (Vargas-Angel et al. 2006).

67 to 77 percent of cross-anatomy polyps developed gametes excluding those of the growing tips (Fig 3.; Vargas-Angel et al. 2006), which likely reflects a prudent allocation of resources. Each of the eight polyp mesenteries of hermaphroditic *A. cervicornis* developed either a single male or female gonad comprising numerous ova or spermary sacs, which remarkably formed in alternating folds with a ratio of 1 to 1 (Vargas-Angel et al. 2006). Mesenteric symmetry appears exceedingly conserved amongst Anthozoa where parallel

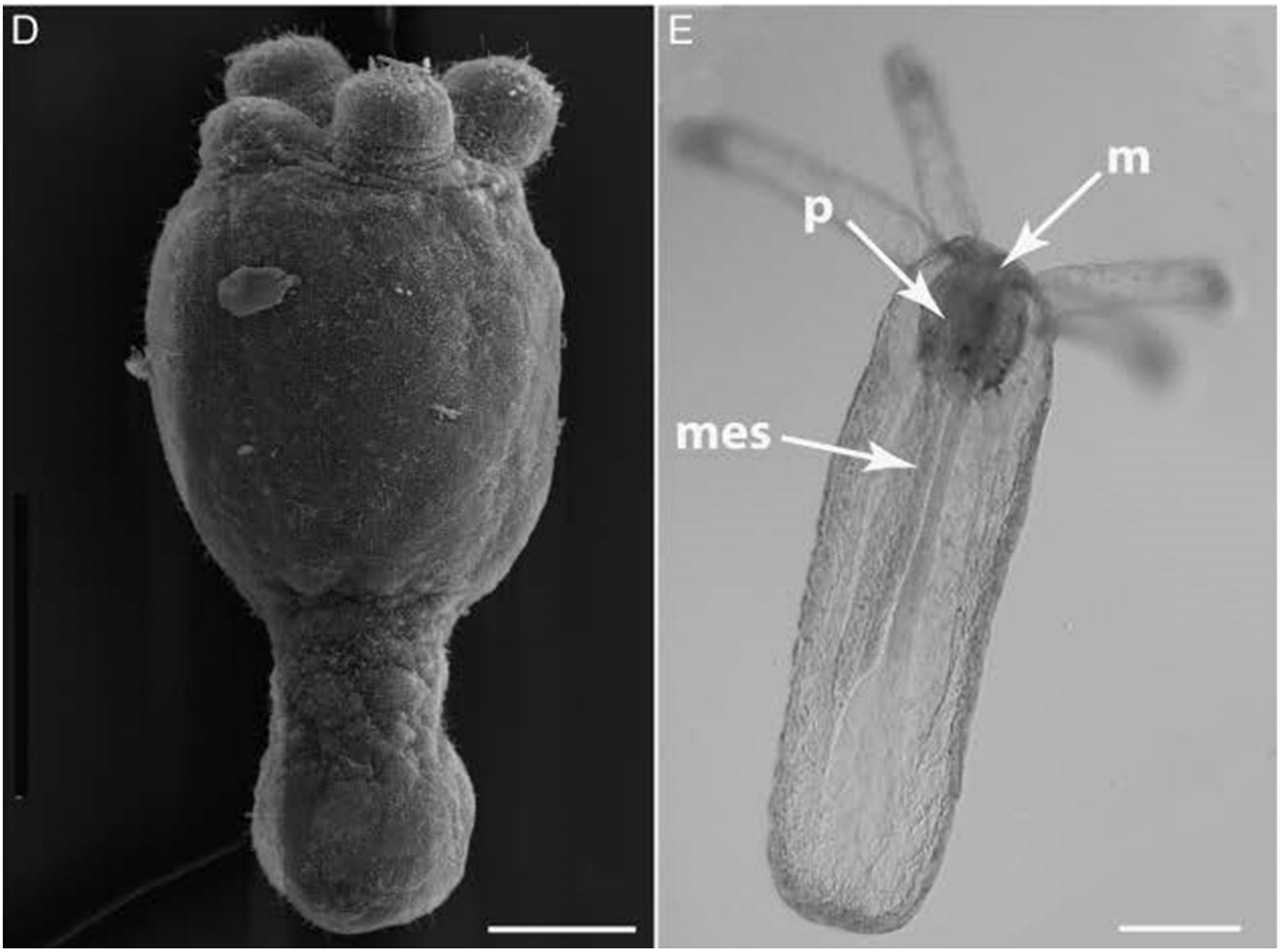


Fig 29. Scanning electron and brightfield micrographs of a late planula and early juvenile of the starlet sea anemone, *Nematostella vectensis* with 550 µm bars: [D] a SEM of an unsettled planula with four tentacle buds; [E] brightfield micrograph of a four tentacled first polyp with a mouth (m), nominal mesenteries (mes), and a pharynx (p; stomodaeum). See figure 28. Courtesy of Reitzel et al. 2007 and the Creative Commons Attribution Licence.

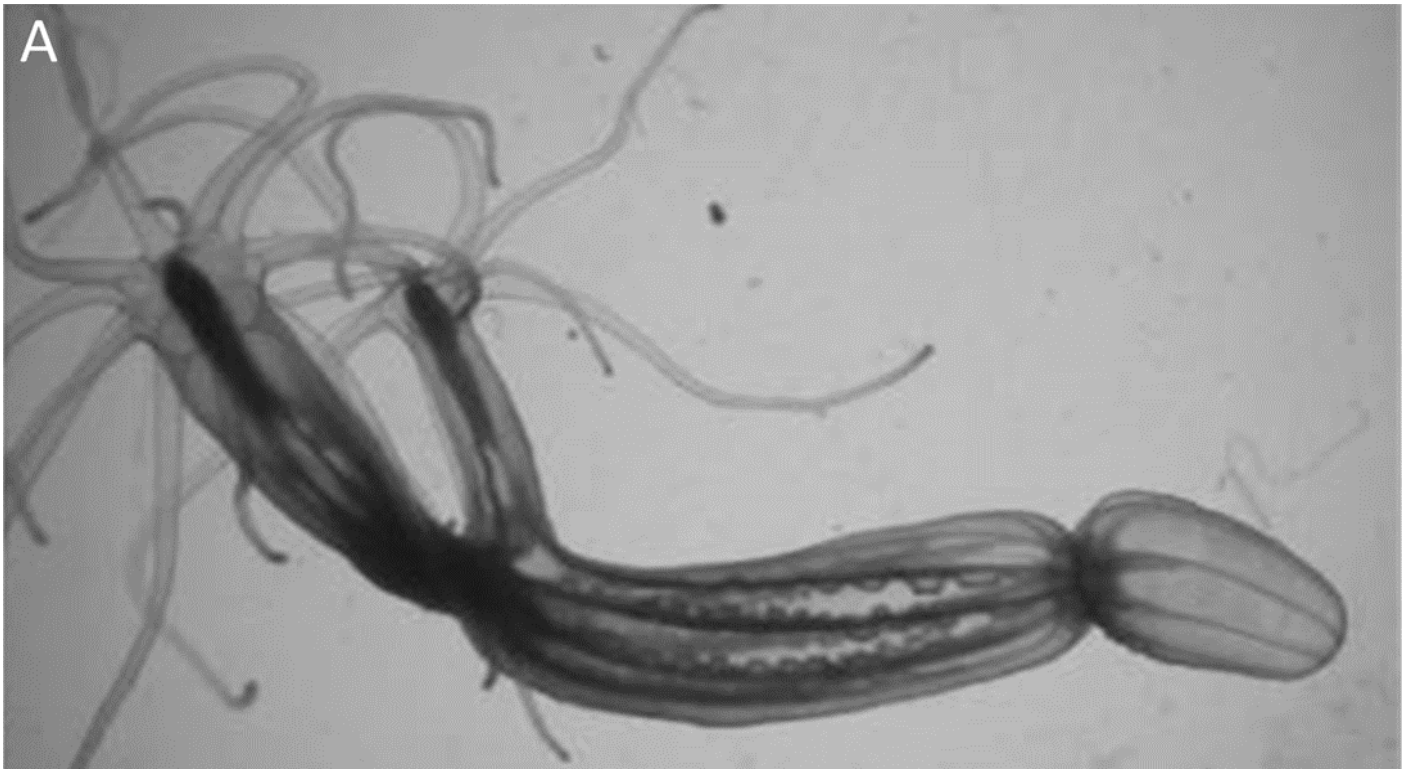
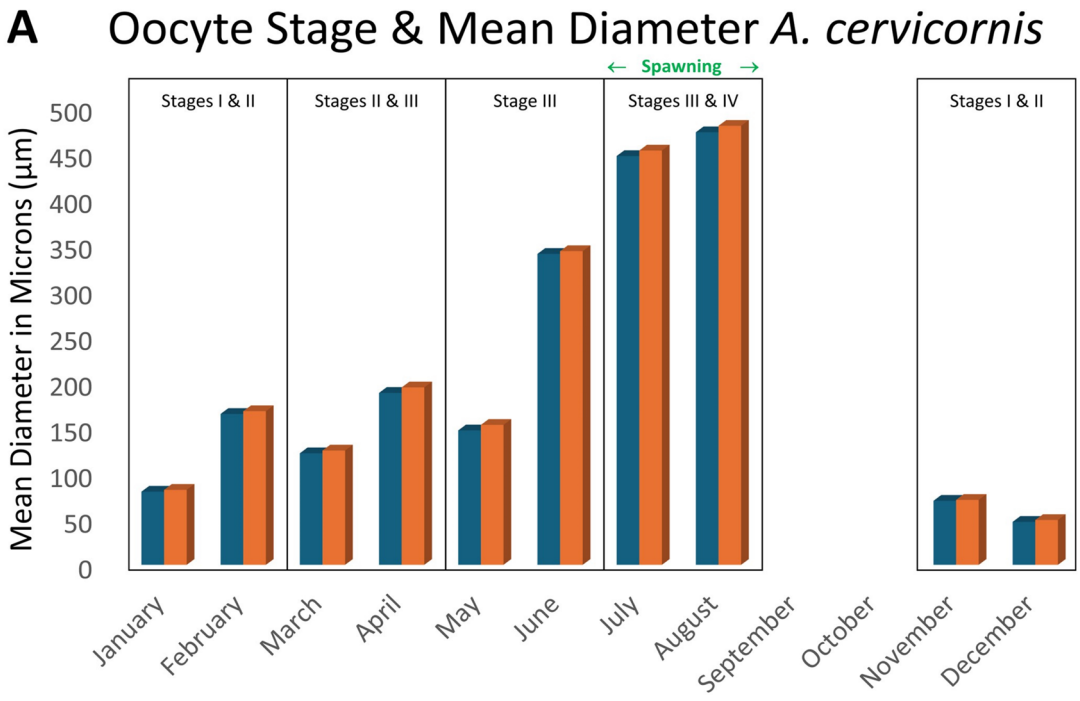


Fig 30. A juvenile eight-tentacled twin oral disced *N. vectensis* exhibiting atypical postinjury regeneration with defined mesenteric folds while adult anemones with multiple crowns are not uncommon in the wild. See figures 26. to 29. Courtesy of Reitzel et al. 2007 and the Creative Commons Attribution Licence.



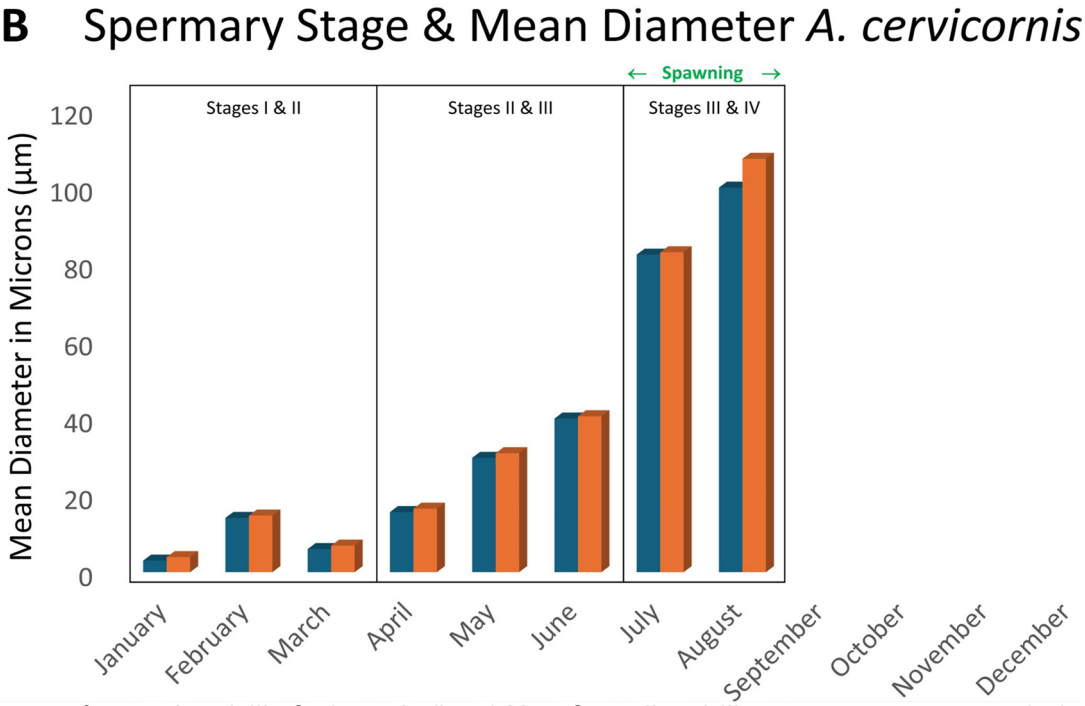


Fig 31. Mean oocyte and spermary diameters, gametogenic stage transformations, and spawning of Florida's *A. cervicornis* over a year. Adapted from Vargas-Angel et al. 2006.

configurations of gonads were observed in *Pocillopora damicornis* (Fig 30.; Harrison 1985; Harrison & Wallace 1990, cited in Vargas-Angel et al. 2006). Merely a solitary string of vertical stage III or IV oocytes with a maximum length of 3,200 µm manifested in each female mesentery where two had nominally four to six ova reaching an optimum of eight, whilst the other two held merely one to four. Such disparities are a likely consequence of protracted and asynchronous cycles of oogenesis (Fig 23. B).

The spermary sacs of each male mesentery routinely comprised from 1 to 21 and 7 to 79 oval or elongate stage III spermaries, while the strings of gonads fostering stage IV spermatozoa reached over 2,600 µm (Vargas-Angel et al. 2006).

Oogenesis began with stage I oocytes from October to December while nearly 90 precent were stage II from February to March with sporadic occurrences of stage I and III. Cycles synchronised from May to July when eggs had reached macroscopic stage III. Conversely, stage IV ova merely developed from seven to two days prior to broadcasting but were the only stage observed in samples suggesting near 100 percent conversion. The trajectory of egg development was epitomised by a gradual increase in size until diameters swelled logarithmically from April to July which plateaued just prior to spawning. Mean monthly diameters were positively correlated to sea surface temperatures (SSTs) and solar irradiance (insolation; Vargas-Angel et al. 2006).

Macroscopic examinations of snapped branches revealed gradual changes in oocyte colouration from ivory/pale-yellow to a pink/peach which occurred in stage III oocytes as early as 17 days prior to spawning (Vargas-Angel et al. 2006).

A thickening of paternal mid-mesenteries harbingered January's onset of stage I spermatogenesis which continued through March with sporadic mesenteric swelling occurring in April and May. Stage II and III spermary sacs were routinely observed in April/May and June respectively, whereafter cross-anatomy maturation of spermatozoa synchronised in all colonies from all sites with a concomitant meiosis-derived size reduction occurring from stage III to IV. Monthly increases in spermary size also accompanied increments in SSTs but not insolation. Broadcast-ready stage IV spermatozoa were present seven days prior to the emergence of stage IV ova a fortnight before spawning (Vargas-Angel et al. 2006).

Invasive field examinations revealed that stage I and II spermary sacs changed from ivory to tan at stage III, which was earlier than the colour transformations occurring in female ova (Fig 31.; Vargas-Angel et al. 2006).

Apart from Appendices II and III, this article concludes our exploration of anthozoan gameto- and embryo-genesis, whereas next we discover the interactions of exogenous cues with coral rhythms that expedite the mechanisms responsible for the synchrony of spawning.

Appendix I Glossary

Allele refers to different forms of a gene.

Amplicon is an amplified sequence of DNA (Merriam Webster 2018).

Animal Pole is a surface zone of an egg which marks the most mitotically active yolk-diminished region.

The class **Anthozoa** comprises the polyp morphotypes corals, anemones, sea fans, and sea pens, the non-mineralised ancestors of which first appeared five hundred and fifty million years ago (MYA). Nevertheless, their rudimentary beginnings may have arisen in the Ordovician around 500 MYA (Burchett & Dando 1996).

Aposymbiosis - when symbiotic organisms live separately.

Archenteron is the rudiments of a developing gut.

Autotrophic organisms satisfy their nutritional requirements from simple inorganic chemicals and usually but not exclusively light.

Azooxanthellate is an organism without symbiotic "algal"-partners.

Bathymetric refers to the environmental dynamics of deep and diverse ecosystems which vary in temperature, salinity, dissolved gasses, current, and pressure.

The infrakingdom **Bilateria** is a clade of bilaterally symmetrical animals with anteriors, posteriors, dorsums, flanks, and ventrums like dogs, humas, flukes, and mice.

Blastomere is a discrete nucleated cell formed from the mitotic division of a fertilised egg's cytoplasm.

Blastopore is an opening that develops from an ectodermal invagination during the gastrulation phase of a developing embryo, which is usually destined to become the mouth.

Bootstrap replicates are equal-sized multiple sequence aligned fictional substitute nucleic acids with confidences proportional to percentage identity.

Canonical, substantiated; acknowledged.

Chorion is an embryo-enveloping membrane.

Clade describes a class of organisms comprising all the descendants from a common ancestor.

Codons are triplet bases in mRNA that encode for one kind of amino acid.

Contig is a DNA molecule made up of smaller overlapping sequences.

The cells of a **Diploid** organism have a chromosome from each parent (2_n), whereas the copy number of **Haploid** organisms is 1_n.

The suffix "**cyte**" means cell.

Diurnal simply means daily or daytime, yet contextually, it refers to a **Diel** synonymous cycle of typical daylight followed by nighttime-analogous darkness.

Endocrine refers to hormone-secreting ductless suprarenal, thymus, thyroid, parathyroid, pituitary, pancreas, ovary, and testis glands.

Endogenous factors originate from within.

Endonuclease, see **Nuclease**.

Epiboly refers to the thinning and spreading of multiple layers of cells during gastrulation.

Exon is a gene-integral coding sequence separated by an **Intron** (Dale 1998).

Expression, see **mRNA**.

Germ refers to a cellular lineage or layer derived from one kind of embryonic **Stem Cell** (**Progenitor**). **Anthozoa** are **Diploblastic** because their ecto- and endo-derms develop from two discrete progenitors.

Gonochoric organisms are female or male.

Hermatypic and **Ahermatypic Corals** - the terms hermatypic and ahermatypic have been misused. Irregularities such as sea fans with rigid skeletons are constructive, but they may or may not contain symbionts and do not contribute to reef substratum. Ahermatypes may have large or small polyps and do not contain zooxanthellae. Scleractinian corals are "true" reef builders but may be azooxanthellate or contain symbionts. Scleractinia and hermatype are not interchangeable. Hermatypic corals contain zooxanthellae and are constructive. Ahermatypes are azooxanthellate and non-constructive. This clear definition also applies to non-Scleractinia (Schuhmacher & Zibrowius 1985).

Heteropole refers to an imaginary core axis that spans the anterior oral and posterior aboral ends of an organism.

Heterotrophs cannot utilise inorganic carbon for growth so they must acquire organic plant or animal derived nourishment. Their sources include glucose, yet several microscopic taxa retain the capacity to transform inorganic compounds which are frequently used as substrates for chemical reactions.

Heterozygous refers to different forms of a gene usually originating from each parent on opposing chromosomes in a diploid (2_n) organism where each one of an individual's 1_n gametes carry one kind of **allele**.

Holoblastic Cleavage utterly divides the blastomeres of a fertilised egg.

Homozygous refers to the same form of a gene usually originating from each parent on opposing chromosomes in a diploid (2_n) organism where each one of an individual's 1_n gametes carry the same kind of allele.

Intron is a gene-integral interrupting (intervening) sequence which is removed by splicing (Dale 1998).

The yolk of **Isolecithal** ova is dense, granulated, and extensively distributed.

Macronemes are thickened mesenteries that develop gonads in the starlet sea anemone, *Nematostella vectensis*.

Meiocyte is a cell generated by meiosis which is contextually synonymous with gamete within which diploid chromosome copy number is halved (**haploid**). See figure 13.

Incomplete **Meroblastic Cleavage** leaves an indentation/cleft because compartmentalising nascent membranes cannot usually form in isolecithal ova with enriched and dispersed fat (yolk).

Mixotrophs utilise both autotrophic and heterotrophic metabolisms.

Monoclonal Antiserum comprises one kind of antibody.

mRNA stands for messenger ribonucleic acid which is transcribed in the nucleus from an organism's active genes before translocation to the cytoplasm, where a ribosome translates its sequence and concatenates **Amino Acids** supplied by transfer ribonucleic acids (**tRNAs**) into a **Polypeptide** that later folds into a functional protein. See figure 3. of Pioneering Studies.

Nematosomes are motile multicellular bodies comprising nematocysts (≅spirocysts) and flagellated cells of the starlet sea anemone, *Nematostella vectensis* (Fig 26. C).

Nuclease enzymes cleave the phosphodiester bonds between the deoxy- or -ribonucleotides of the sugar phosphate backbone of DNA or RNA but usually only from 5 or 3' (prime) ends (Russell 1998). The cells of all "living" organisms retain complex DNA proofreading-, damage recognition-, and repair system-competencies. **Endonuclease** excises a section of ssDNA on either side of damage or aberrations from within a double helix (dsDNA) after which DNA polymerase fills in the gap and ligase seals the sugar-phosphate backbone (Russell 1998a).

Nucleic Acid is typically molecular ribonucleic acid (RNA) or deoxyribonucleic acid (DNA) which maybe complementary (cDNA), double or single stranded (dsDNA or ssDNA).

Nucleolus is a dark staining intranuclear body comprising RNA, stored ribosomes, and their auxiliary machinery, which is present during anaphase but degrades during mitosis, yet they are reconstituted following the reorganisation of nuclear membranes (Wallace et al. 1996). See figures 13. and 21. f.

Oligonucleotide is a short, typically synthetic nucleic acid.

Oligotrophic refers to aquatic environments with few pollutants such as ultralow dissolved inorganic nitrogen (N) and phosphorus (P) akin to pristine reef ecosystems.

Ontogeny/Ontogenesis describes the development of an organism from the moment of fertilisation to a mature adult.

Ontology is used contextually to describe the intra- and extra-cellular metabolic pathways associated with an organisms day-to-day housekeeping, homeostatic, and reproductive processes.

Oolemma is an egg's cellular membrane.

Ooplasm is the cytoplasm of an egg.

Open Reading Frames (ORFs) are the transcriptional parts of genes that lack start and stop sequences but encode for triplet mRNA bases (**Codons**) which correspond to each kind of **Amino Acid**.

Orthologue refers to a sequenced and characterised gene integral to an elucidated pathway in numerous organisms.

Paralogues are two or more copies derived from a single ancestral gene residing at two or more distal loci in the same genome.

Phenotype, see **Phenotypic**.

Phenotypic Plasticity foregoes the accepted developmental and evolutionary paradigms and expedites swift morphological responses to environmental change.

Phenotypic traits are an organism's observable characteristics which include how it interacts with its environment that originate from its **Epigenotype** and **Genotype**.

Photic Zones are sea surface regions extending to approximately 120 metres that receive sufficient light to drive photosynthesis.

Phylogenetic Tree "is a graphic representation of the interrelations and evolutionary history of a group of organisms, indicating the relative order of successive divisions of the line of descent, coincident with speciation events" (Wallace et al. 1996).

Phylogeny facilitates organism classification by comparing the sequences of identical or very similar genes (**Homologues**).

Planulation refers to the release of free-swimming larvae from brood colonies.

Plasmid is a self-replicating typically circular and mostly prokaryotic extrachromosomal molecule of ss or dsDNA. See **Nucleic Acid**.

Polyclonal Antiserum comprises many kinds of antibodies, which are typically specific for a range of epitopes on a single antigen.

Spawning - countless marine organisms broadcast their spermatozoa and eggs into the water that later fuse and ultimately transform into planktonic larvae. Corals are gonochoric or hermaphroditic where brood colonies internalise sperm released by others which fertilises oocytes (eggs) where blastulae and then gastrulae are nurtured until free-swimming planulae are released. Other corals liberate sperm and egg bundles that float leisurely to the surface where they degrade and release their cargo (Wallace et al. 1986), or colonies broadcast eggs and sperm directly whose nuclei fuse into a zygote from which zooplanktonic planulae develop. Several brooding species can raise vegetative larvae after the failure of cross-fertilisation (Aslett 2024).

Spermary or **Spermatocyst** is a male reproductive organ (gonad) that produces spermatozoa.

Spermatocyte is a spermatogonium-derived cell that undergoes meiosis to generate four haploid tailless spermatids. See figure 13.

Spirocysts, cnidocysts, or nematocysts are the capsular stinging apparatuses of cnidocytes that develop from cnido-, nemato-, or spiro-blasts.

Stomodaeum, foregut.

Thyroid-stimulating hormone (TSH) beta is manufactured by the pituitary gland in response to low serum concentrations of thyroxine and thus regulates thyroid gland activity.

Transcription, see **mRNA**.

Transcriptome is the sum of all the messenger ribonucleic acid (**mRNA**) transcribed from an organism's active genes (≅**ORFs**; Lexico 2019).

Nourishing **Vitellarium** secreted from vitelline cells enriches yolk which assists embryonic development (Caira 2010).

Vitellus, yolk.

Zooxanthellate is an organism with symbiotic dinoflagellate "algal"-partners.

Zygotes are formed when the nuclei of a spermatozoan and egg fuse after which additional fertilisation cannot occur.

Appendix II

Tables 3. to 6. feature the sexual mode and reproductive strategy of 277 tropical species of Scleractinia. Adapted from Baird et al. 2009.

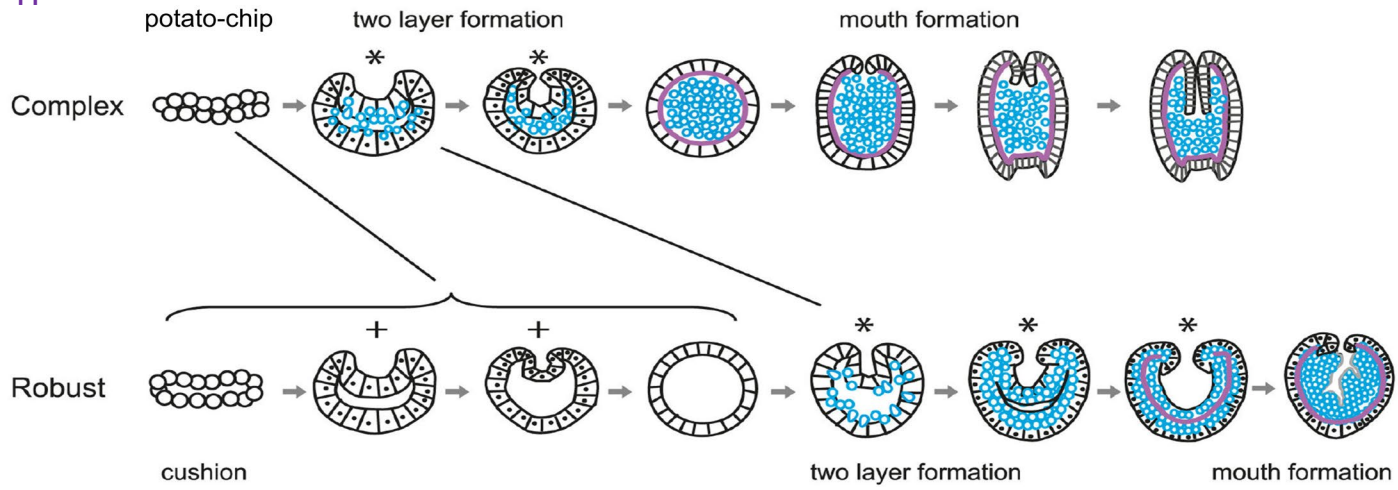
Table 3.		
Species/Genus	Sexual Mode	Reproductive Strategy
67 *Acropora*	Hermaphrodite	Broadcaster
Acanthastrea echinata	Hermaphrodite	Broadcaster
Acanthastrea hillae	Hermaphrodite	Broadcaster
Acanthastrea lordhowensis	Hermaphrodite	Broadcaster
Agaricia agaricites	Gonochoric	Brooding
Agaricia fragilis	Gonochoric	Brooding
Agaricia humilis	Gonochoric	Brooding
Alveopora gigas	Hermaphrodite	Broadcaster
Alveopora japonica	Hermaphrodite	Brooding
Alveopora tizardi	Hermaphrodite	Broadcaster
Alveopora verrilliana	Hermaphrodite	Broadcaster
Anacropora puertogalerae	Hermaphrodite	Broadcaster
Anacropora spinosa	Hermaphrodite	Broadcaster
Astrangia poculata	Gonochoric	Broadcaster
Astreopora gracilis	Hermaphrodite	Broadcaster
Astreopora listeri	Hermaphrodite	Broadcaster
Astreopora myriophthalma	Hermaphrodite	Broadcaster
Astroides calycularis	Hermaphrodite	Brooding
Balanophyllia elegans	Gonochoric	Brooding
Balanophyllia europaea	Hermaphrodite	Brooding
Blastomussa wellsi	Hermaphrodite	Broadcast
Caryophyllia smithii	Gonochoric	Broadcast
Catalaphyllia jardinei	Gonochoric	Broadcaster
Caulastrea furcata	Hermaphrodite	Broadcaster
Cladopsammia rolandi	Gonochoric	Brooding
Colpophyllia natans	Hermaphrodite	Broadcaster
Ctenactis echinata	Gonochoric	Broadcaster
Cynarina lacrymalis	Hermaphrodite	Broadcaster
Cyphastrea chalcidicum	Hermaphrodite	Broadcaster
Cyphastrea microphthalma	Hermaphrodite	Broadcast
Cyphastrea ocellina	Hermaphrodite	Brooding
Cyphastrea serailia	Hermaphrodite	Broadcaster
Diploastrea heliopora	Gonochoric	Broadcaster
Diploria labyrinthiformis	Hermaphrodite	Broadcaster
Diploria strigosa	Hermaphrodite	Broadcaster
Echinophyllia aspera	Hermaphrodite	Broadcaster
Echinophyllia orpheensis	Hermaphrodite	Broadcaster
Echinopora ashmorensis	Hermaphrodite	Broadcaster
Echinopora gemmacea	Hermaphrodite	Broadcaster
Echinopora horrida	Hermaphrodite	Broadcaster
Echinopora lamellosa	Hermaphrodite	Broadcaster
Echinopora pacificus	Hermaphrodite	Broadcaster
Enallopsammia rostrata	Gonochoric	Broadcaster
Euphyllia ancora	Gonochoric	Broadcaster
Euphyllia divisa	Gonochoric	Broadcaster
Eusmilia fastigiata	Gonochoric	Broadcaster
Favia favus	Hermaphrodite	Broadcaster
Favia fragum	Hermaphrodite	Brooding
Favia gravida	Hermaphrodite	Brooding
Favia helianthoides	Hermaphrodite	Broadcaster
Favia laxa	Hermaphrodite	Broadcaster
Favia lizardensis	Hermaphrodite	Broadcaster
Favia matthaii	Hermaphrodite	Broadcaster
Favia pallida	Hermaphrodite	Broadcaster
Favia rotumana	Hermaphrodite	Broadcaster
Favia speciosa	Hermaphrodite	Broadcaster
Favia stelligera	Hermaphrodite	Broadcaster
Favia veroni	Hermaphrodite	Broadcaster
Favites abdita	Hermaphrodite	Broadcaster
Favites chinensis	Hermaphrodite	Broadcaster
Favites complanata	Hermaphrodite	Broadcaster
Favites flexuosa	Hermaphrodite	Broadcaster
Favites halicora	Hermaphrodite	Broadcaster
Favites pentagona	Hermaphrodite	Broadcaster
Favites russelli	Hermaphrodite	Broadcaster
Flabellum alabastrum	Gonochoric	Broadcaster
Flabellum angulare	Gonochoric	Brooding
Flabellum curvatum	Gonochoric	Brooding
Flabellum impensum	Gonochoric	Brooding
Flabellum thouarsii	Gonochoric	Brooding
Fungia fungites	Gonochoric	Broadcaster

Table 4.		
Species/Genus	Sexual Mode	Reprodutive Strategy
Fungiacyathus marenzelleri	Gonochoric	Broadcaster
Galaxea astreata	Gonochoric	Broadcaster
Galaxea fascicularis	Gonochoric	Broadcaster
Galaxea horrescens	Gonochoric	Brooding
Goniastrea australensis	Hermaphrodite	Broadcaster
Goniastrea edwardsi	Hermaphrodite	Broadcaster
Goniastrea favulus	Hermaphrodite	Broadcaster
Goniastrea palauensis	Hermaphrodite	Broadcaster
Goniastrea pectinata	Hermaphrodite	Broadcaster
Goniastrea retiformis	Hermaphrodite	Broadcaster
Goniopora columna	Gonochoric	Broadcaster
Goniopora djiboutiensis	Gonochoric	Broadcaster
Goniopora lobata	Gonochoric	Broadcaster
Goniopora minor	Gonochoric	Broadcaster
Goniopora norfolkensis	Gonochoric	Broadcaster
Goniopora savignyi	Gonochoric	Broadcaster
Goniopora stutchburyi	Gonochoric	Broadcaster
Goniopora tenuidens	Gonochoric	Broadcaster
Heteropsammia cochlea	Gonochoric	Broadcaster
Hydnophora exesa	Hermaphrodite	Broadcaster
Hydnophora pilosa	Hermaphrodite	Broadcaster
Hydnophora rigida	Hermaphrodite	Broadcaster
Isopora brueggemanni	Hermaphrodite	Brooding
Isopora cuneata	Hermaphrodite	Brooding
Isopora palifera	Hermaphrodite	Brooding
Leptastrea purpurea	Gonochoric	Broadcaster
Leptastrea transversa	Gonochoric	Broadcaster
Leptopsammia pruvoti	Gonochoric	Brooding
Leptoria phrygia	Hermaphrodite	Broadcaster
Leptoseris explanata	Gonochoric	Broadcaster
Lobophyllia corymbosa	Hermaphrodite	Broadcaster
Lobophyllia hemprichii	Hermaphrodite	Broadcaster
Lobophyllia pachysepta	Hermaphrodite	Broadcaster
Lophelia pertusa	Gonochoric	Broadcaster
Madracis decactis	Hermaphrodite	Brooding
Madracis formosa	Hermaphrodite	Brooding
Madracis pharensis	Hermaphrodite	Brooding
Madracis senaria	Hermaphrodite	Brooding
Madrepora oculata	Gonochoric	Broadcaster
Manicina areolata	Hermaphrodite	Brooding
Merulina ampliata	Hermaphrodite	Broadcaster
Monomyces rubrum	Gonochoric	Brooding
Montastrea annularis	Hermaphrodite	Broadcaster
Montastrea cavernosa	Gonochoric	Broadcaster
Montastrea curta	Hermaphrodite	Broadcaster
Montastrea magnistellata	Hermaphrodite	Broadcaster
Montastrea valenciennesi	Hermaphrodite	Broadcaster
Montipora aequituberculata	Hermaphrodite	Broadcaster
Montipora altasepta	Hermaphrodite	Broadcaster
Montipora cactus	Hermaphrodite	Broadcaster
Montipora capricornis	Hermaphrodite	Broadcaster
Montipora crassituberculata	Hermaphrodite	Broadcaster
Montipora danae	Hermaphrodite	Broadcaster
Montipora digitata	Hermaphrodite	Broadcaster
Montipora efflorescens	Hermaphrodite	Broadcaster
Montipora foliosa	Hermaphrodite	Broadcaster
Montipora foveolata	Hermaphrodite	Broadcaster
Montipora gaimardi	Hermaphrodite	Broadcaster
Montipora grisea	Hermaphrodite	Broadcaster
Montipora hirsuta	Hermaphrodite	Broadcaster
Montipora hispida	Hermaphrodite	Broadcaster
Montipora hoffmeisteri	Hermaphrodite	Broadcaster
Montipora informis	Hermaphrodite	Broadcaster
Montipora malampaya	Hermaphrodite	Broadcaster
Montipora mollis	Hermaphrodite	Broadcaster
Montipora monasteriata	Hermaphrodite	Broadcaster
Montipora peltiformis	Hermaphrodite	Broadcaster
Montipora samarensis	Hermaphrodite	Broadcaster
Montipora spumosa	Hermaphrodite	Broadcaster
Montipora stellata	Hermaphrodite	Broadcaster
Montipora tuberculosa	Hermaphrodite	Broadcaster

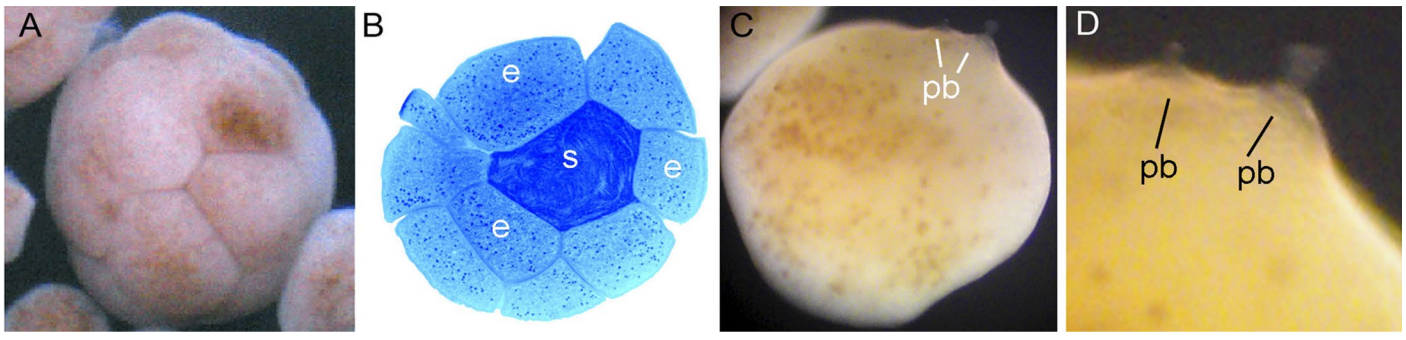
Species/Genus	Table 5. Sexual Mode	Reprodutive Strategy
Montipora turgescens	Hermaphrodite	Broadcaster
Montipora turtlensis	Hermaphrodite	Broadcaster
Montipora venosa	Hermaphrodite	Broadcaster
Montipora verrucosa	Hermaphrodite	Broadcaster
Mussismilia braziliensis	Hermaphrodite	Broadcaster
Mussismilia harttii	Hermaphrodite	Broadcaster
Mussismilia hispida	Hermaphrodite	Broadcaster
Mycedium elephantotus	Hermaphrodite	Broadcaster
Mycedium robokaki	Hermaphrodite	Broadcaster
Mycetophyllia ferox	Hermaphrodite	Brooding
Oculina varicosa	Gonochoric	Broadcaster
Oulastrea crispata	Hermaphrodite	Broadcaster
Oulophyllia bennettae	Hermaphrodite	Broadcaster
Oulophyllia crispa	Hermaphrodite	Broadcaster
Oxypora glabra	Hermaphrodite	Broadcaster
Oxypora lacera	Hermaphrodite	Broadcaster
Pachyseris foliosa	Gonochoric	Broadcaster
Pachyseris rugosa	Gonochoric	Broadcaster
Pachyseris speciosa	Gonochoric	Broadcaster
Paracyathus stearnsii	Gonochoric	Broadcaster
Pavona cactus	Gonochoric	Broadcaster
Pavona clavus	Gonochoric	Broadcaster
Pavona gigantea	Gonochoric	Broadcaster
Pavona varians	Gonochoric	Broadcaster
Pectinia alcicornis	Hermaphrodite	Broadcaster
Pectinia lactuca	Hermaphrodite	Broadcaster
Pectinia paeonia	Hermaphrodite	Broadcaster
Physogyra lichtensteini	Gonochoric	Broadcaster
Platygyra contorta	Hermaphrodite	Broadcaster
Platygyra daedalea	Hermaphrodite	Broadcaster
Platygyra lamellina	Hermaphrodite	Broadcaster
Platygyra pini	Hermaphrodite	Broadcaster
Platygyra ryukyuensis	Hermaphrodite	Broadcaster
Platygyra sinensis	Hermaphrodite	Broadcaster

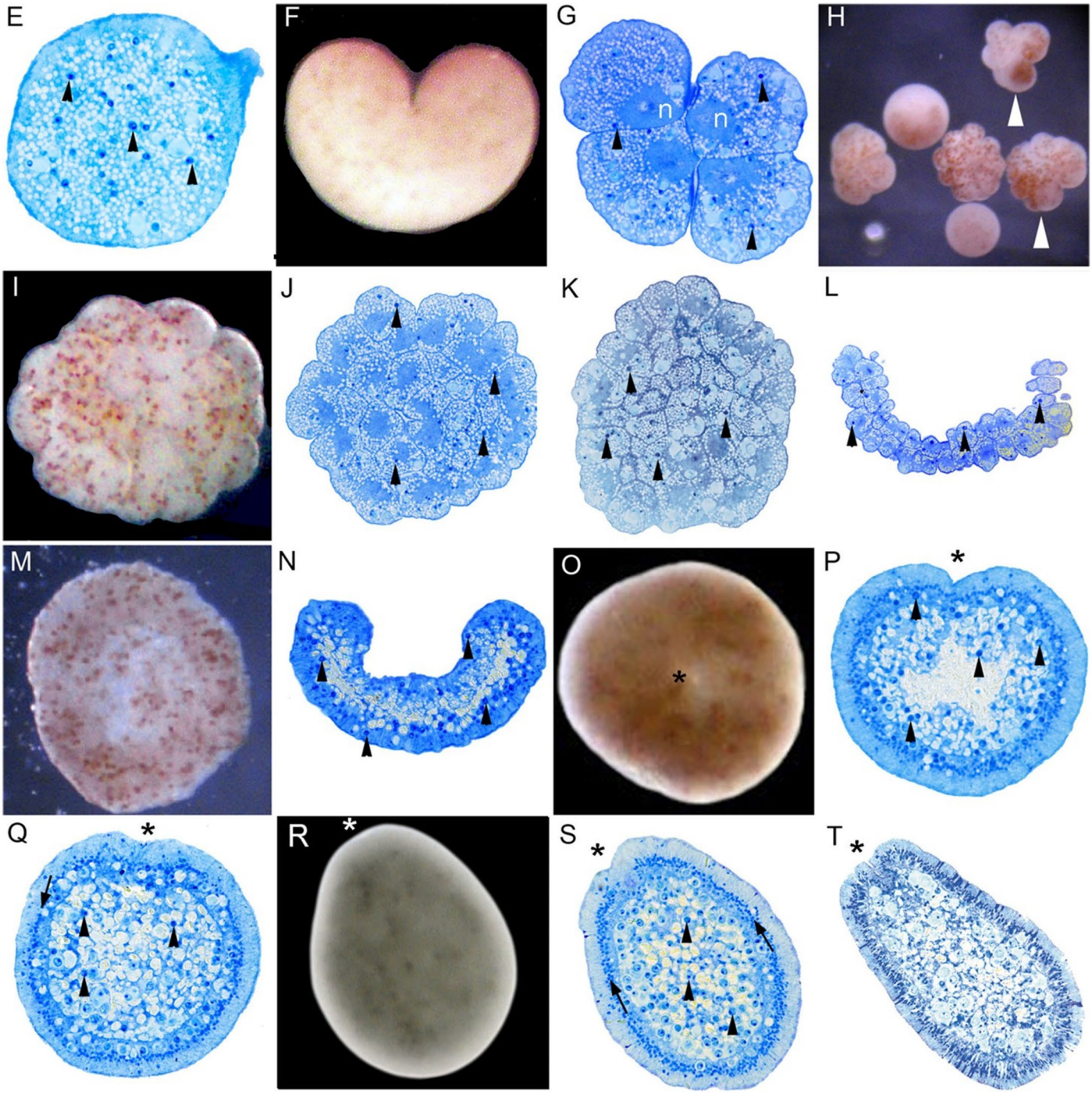
Species/Genus	Table 6. Sexual Mode	Reprodutive Strategy
Plerogyra sinuosa	Gonochoric	Broadcaster
Pocillopora elegans	Hermaphrodite	Broadcaster
Porites astreoides	Gonochoric	Brooding
Porites australiensis	Gonochoric	Broadcaster
Porites compressa	Gonochoric	Broadcaster
Porites cylindrica	Gonochoric	Broadcaster
Porites evermanni	Gonochoric	Broadcaster
Porites furcata	Gonochoric	Brooding
Porites heronensis	Gonochoric	Brooding
Porites horizontalata	Gonochoric	Broadcaster
Porites lobata	Gonochoric	Broadcaster
Porites lutea	Gonochoric	Broadcaster
Porites panamensis	Gonochoric	Brooding
Porites porites	Gonochoric	Brooding
Porites rus	Gonochoric	Broadcaster
Porites solida	Gonochoric	Broadcaster
Psammocora stellata	Gonochoric	Broadcaster
Pseudosiderastrea tayamai	Hermaphrodite	Broadcaster
Sandalolitha robusta	Gonochoric	Broadcaster
Scapophyllia cylindrica	Hermaphrodite	Broadcaster
Scolymia vitiensis	Hermaphrodite	Broadcaster
Seriatopora caliendrum	Hermaphrodite	Brooding
Seriatopora hystrix	Hermaphrodite	Brooding
Siderastrea radians	Gonochoric	Brooding
Siderastrea siderea	Gonochoric	Broadcaster
Stylaraea ounctata	Hermaphrodite	Brooding
Stylophora pistillata	Gonochoric	Brooding
Symphyllia radians	Hermaphrodite	Broadcaster
Symphyllia recta	Hermaphrodite	Broadcaster
Symphyllia wilsoni	Hermaphrodite	Broadcaster
Trachyphyllia geoffroyi	Hermaphrodite	Broadcaster
Turbinaria frondens	Gonochoric	Broadcaster
Turbinaria mesenterina	Gonochoric	Broadcaster
Turbinaria reniformis	Gonochoric	Broadcaster

Appendix III



From prawn-chip/cushion blastulae to teardrop/elongate gastrulae in “complex” and “robust” scleractinian clades. The former’s blastulae are stereo and solid lacking a blastocoel void. Cell bilayers shrink, thicken, and roll inward forming a bowl-like stage whereafter the cells in the concavity are overgrown by ectodermis. The undifferentiated cells and yolk granules of the core are remodelled into endodermis enveloped in a mesogleal sphere [purple]. The blastopore remains closed through spheroidal gastrulation whereafter the mouth is formed through an invagination of the animal pole (Okubo & Motokawa 2008). “Robust” blastulae are hollow with a pronounced blastocoel void into which no material is excreted while “pseudo-blastopores” [+] close during spheroidal gastrulation whereafter a conventional blastopore materialises, remains open, and eventually forms the mouth during which the blastocoel is filled by cellular ingress. Compare with figure 16. Drawings courtesy of Okubo et al. 2013 and the Creative Commons Attribution Licence.





The sperm and egg bundles and early embryonic development of "complex" hermaphroditic *Montipora hispida* that vertically infect their ova with zooxanthellae from eight to 32 hours before broadcasting: [A] exterior of sperm and egg packet where zooxanthellate eggs surround a spermatozoan core [B]; [C and D] ovum polar bodies (pb); [E] histological section through an egg where coccoid Symbiodiniaceae are indicated by arrowheads; [F] initial cleavage akin to figure 16 a; [G] the result of second cleavage where nuclei occupy most of the cytoplasm and are positioned on the innermost edge; [H] four to 16 cell morulae unevenly speckled with symbionts; [I] zooxanthellate 32 to 64 cell blastulae and histological cross-section [J]; [K] blastula section after subsequent cleavage; [L] prawn-chip cross-section; [M] overhead bowl-like phase; [N] a thickened "M" comparable cross-section; [O] spheroidal stage with the blastopore marked by an asterisk; [P] "O"-analogous cross-section where "algal"-partners are migrating into the blastocoel while mesoglea is forming on the periphery; [Q] spheroidal gastrula with defined mesoglea (arrow) and endodermal cell maturation with discrete nuclei (arrowheads); [R] teardrop stage planula and cross-section with defined endoderm and mesoglea [S]; [T] elongate planula with a pharynx and differentiated ecto- and endo-derms. Courtesy of Okubo et al. 2013 and the Creative Commons Attribution Licence.

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Chris Aslett

As the principal director of Reef Ranch Publishing Ltd (https://reefranch.co.uk/) and author of The Complete Reef Aquarist – A Conservation Manual (https://reefranch.co.uk/reef-aquarium-guide/), Chris has over 55 years of experience keeping aquatic animals with 47 of them nurturing marine species. His innate passion for system dynamics drove him from the laboratory to university where he gained a greater appreciation of biochemistry, biotechnology, epidemiology, genetics, histology, inorganic and organic chemistry, mariculture, molecular and microbiology, saltwater zoology, and the diagnosis and treatment of aquatic diseases. His dedicated marine livestock supplier, The Reef Ranch™, demanded he devise, streamline, and establish protocols for combined acclimation and prophylactic pest/parasite clearance, and innovate system design, optimisation, maintenance, and husbandry in the face of incessant influxes of hundreds of delicate marine animals. With exceptional, uncompromising, and likely the UK's most disease-free reef and fish-only facilities, losses were less than one resident every six months. 20 years hence, he has refined his expertise for digesting, authoring, editing, and publishing reef conservation-driven scientific literature (https://reefranch.co.uk/reef-research-and-aquarium-advice/), to an end of diminishing the impact the tropical marine ornamental industry exerts in the wild.

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