Coral Reefs (2026) 45:141–165
https://doi.org/10.1007/s00338-025-02705-x

RESEARCH

Reproductive phenology and sexual propagation of the pink sea fan *Eunicella verrucosa* (Pallas, 1766): implications for coral restoration

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Received: 31 December 2024 / Accepted: 16 June 2025 / Published online: 21 July 2025
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Abstract The widespread decline of coral-dominated ecosystems has highlighted the urgent need for active habitat restoration. Coral restoration using sexually produced individuals instead of clonal fragments is essential to reduce impacts on donor populations and promote genetic diversity, which is vital for adaptability to environmental changes. However, for most coral species critical knowledge of reproduction and larval ecology for ex situ sexual propagation is lacking. To address this gap, this study presents the first report of spawning of the octocoral *Eunicella verrucosa* in the North-East Atlantic and describes larval development and settlement. The annual reproductive timing in South-West Portugal was determined from samples collected as fisheries bycatch from the same habitat and monitored for comparison across distinct durations and conditions. The species exhibited split spawning (three major events approximately every two weeks) over about one month (mid-September–mid-October). Spawning patterns can suggest lunar periodicity but shifted between colonies kept in distinct conditions. Oocytes were positively buoyant and developed into swimming larvae after three days. Settlement trials using substrates such as natural rock, crustose coralline algae (CCA), and gorgonian skeleton, showed larvae started testing the substrates about two weeks after spawning, with settlement activity continuing over up to three months. Fully developed recruits were observed after one month, with sclerite production starting before tentacle development. The observation of new larval settlement up to three months indicates a prolonged competency period. This study provides crucial data for coral restoration efforts using *ex-situ* sexual propagation of a vulnerable species.

Keywords Broadcast spawning · Pelagic larval duration (PLD) · Embryogenesis · Settlement competency · Octocorallia

Introduction

Coral ecosystems are experiencing significant global decline, primarily due to a combination of climate change and other anthropogenic pressures (Carpenter et al. 2008; Hughes et al. 2017b, 2018). Consequences of climate change, such as rising temperatures and ocean acidification adversely affect coral calcification and overall health, making corals more susceptible to diseases and environmental stressors (Feng et al. 2016; Pendleton et al. 2016). Local human activities, such as pollution, overfishing, and coastal development, exacerbate these challenges, often leading to more immediate and severe impacts than climate change alone (Ferrario et al. 2014; Høegh-Guldberg et al. 2018). Tropical coral reefs have lost approximately 50% of their living coral cover since the 1950s, with a corresponding 60% decline in fish populations associated with these habitats (Eddy et al. 2021; Hughes et al. 2017a). These losses threaten biodiversity and undermine the ecosystem services that coral reefs provide, and which

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00338-025-02705-x.

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are vital for the livelihoods of millions of people (Hughes et al. 2017a, b; Mercado-Molina and Suleimán-Ramos 2023). As coral reefs continue to degrade, the potential for recovery diminishes, creating a feedback loop that perpetuates the decline of these critical marine environments (Carpenter et al. 2008; Pandolfi et al. 2003; Pratchett et al. 2012). Since conservation alone appears no longer sufficient for the long-term persistence of many ecosystems (Hughes et al. 2017a; O'Connor et al. 2020; Orth et al. 2020; Smith et al. 2023), the United Nations and European Union have outlined the critical role of biological restoration to recover degraded ecosystems, including the marine realm, through initiatives such as the UN Decade on Ecosystem Restoration 2021–2030, the EU Biodiversity Strategy for 2030 and the EU Nature Restoration Law.

In active coral restoration, several approaches have gained noticeable traction over the last years (Boström-Einarsson et al. 2020; Suggett and Van Oppen 2022). The most common and widely applied method is asexual propagation, achieved by fragmenting of donor colonies or using opportunistic coral sources like fishing bycatch and broken pieces from storms (Boch and Morse 2012; Garrison and Greg 2008; Plucer-Rosario and Randall 1987; Montseny et al. 2019, 2020, 2021b). Corals can be grown in nurseries and subsequently out-planted on the reef or directly transplanted (Forrester et al. 2019). However, asexual propagation carries risks such as loss of genetic diversity and potentially overlooked impacts on the donor colonies, and it may not be self-sustaining (Baums et al. 2019; Henry et al. 2021; Oppen et al. 2015). A relatively new but steadily growing approach is restoration through sexual propagation, where sexually produced recruits can then be reintroduced onto the reef (Henry et al. 2021). Coral spawn can either be collected in situ and then reared in the laboratory or field (Chamberland et al. 2015; Heyward et al. 2002; Suzuki et al. 2020), or the parent colonies can be maintained to spawn in captivity (Dela Cruz and Harrison 2020; Henry et al. 2021; O'Neil et al. 2021; Pollock et al. 2017; Viladrich et al. 2022). Ex situ aquaculture offers the opportunity to provide a consistent supply of corals to support research and assist complementary reef restoration efforts (Lam et al. 2023). Sexual propagation offers the significant advantage of producing many genetically unique individuals thereby boosting genetic diversity. This diversity enhances the ability of populations to adapt to changing environments by providing a rich source of genetic variability for natural selection. Additionally, precise manipulations and targeted selection techniques, such as assisted evolution, can further increase the resilience of the offspring (Baums 2008; Doropoulos et al. 2019; Oppen et al. 2015, 2017), although long-term trade-offs still need to be assessed. In tropical coral reefs, methods have been further developed and simplified, particularly to upscale restoration efforts by conservation organisations implementing these techniques in the field (www.secore.org; Bayraktarov et al. 2019; Boström-Einarsson et al. 2020).

Restoration of colder and deeper marine habitats has received significantly less attention compared to tropical counterparts (Ros et al. 2019; Montseny et al. 2021a), despite growing interest of conservation practitioners and recreational divers in these underexplored ecosystems (Ankamah-Yeboah et al. 2020; Mengerink et al. 2014). This disparity stems from a combination of ecological, logistical, and financial challenges. Shallow tropical environments such as coral reefs, mangroves, and seagrass meadows have attracted most restoration efforts, primarily due to their accessibility and perceived immediate socio-economic benefits (Bayraktarov et al. 2020; Williams et al. 2017). In contrast, deep-sea restoration is hindered by technical difficulties, high operational costs, and limited public and policymaker awareness (Ounanian et al. 2018; Ros et al. 2019; Montseny et al. 2021a).

Nevertheless, the ecological value of temperate and deep-sea habitats is considerable. They provide essential habitat for a diverse array of species, including those of commercial importance, and are as vulnerable to anthropogenic pressures as tropical reefs (Bongiorni et al. 2010; Buhl-Mortensen et al. 2017, 2018; Danovaro et al. 2010; Lange et al. 2023). Many coral species occupy broad depth and geographic ranges (Buhl-Mortensen et al. 2018), complicating efforts to delineate their distributions and thereby challenging both protection and restoration strategies.

The ecological complexity and slow recovery rates characteristic of temperate and deep-sea ecosystems further hinder restoration efforts. Many species exhibit long lifespans, and ecological interactions remain poorly understood. For most deep-water coral species, detailed information on life history, reproductive biology, and ecological requirements is lacking (Montseny et al. 2021a; Randall et al. 2020). As a result, restoration often requires fundamental research before implementation and tends to progress more slowly, discouraging investment and sustained scientific engagement (Prouty et al. 2016; Ros et al. 2019). Restoration practices for these ecosystems remain limited, often confined to small-scale interventions and asexual propagation techniques (Boch et al. 2019; Roik et al. 2015; Ros et al. 2019; Montseny et al. 2020, 2021b), thus exposing a critical gap in marine conservation (Ounanian et al. 2018; Ros et al. 2019; Montseny et al. 2021a).

Deep-water and cold-water coral habitats differ markedly from tropical shallow reefs in environmental conditions and species composition (Bridge et al. 2013; Menza et al. 2007; Price et al. 2019). Coral gardens, dense, forest-like habitats dominated by one or multiple coral species, are a type of marine animal forests (sensu Rossi et al. 2017) that can extend from shallow depths to several hundred meters. Coral gardens dominated by gorgonians (i.e.,

branching octocorals) are three-dimensional habitats that support diverse benthic and pelagic communities (Baillon et al. 2012; Buhl-Mortensen et al. 2017; Watling et al. 2011; Grinyó et al. 2018).

One such Gorgonian species is *Eunicella verrucosa* Pallas, 1766, a habitat-forming gorgonian widely distributed across the Eastern Atlantic and Mediterranean Sea, from western Ireland to Angola, down to 200 m depth (Chimienti 2020; Coz et al. 2012; Pikesley et al. 2016; Carpine 1963; Grasshoff 1992). Like other temperate corals, *E. verrucosa* exhibits slow growth (0.62–3.33 cm/year) and long lifespans, increasing its vulnerability to anthropogenic impacts such as bottom-contact fishing and anchoring (Sartoretto and Francour 2012; Watling and Norse 1998; Dias et al. 2020). These stressors compound the effects of climate change, including storms and marine heatwaves, which are becoming more frequent and severe (Hall-Spencer et al. 2007; Sheehan et al. 2013, 2017; Garrabou et al. 2022).

Classified as "Vulnerable" by the IUCN since 1996, *E. verrucosa* faces a moderate to high extinction risk, particularly in southern Portugal, where it frequently appears as fishing bycatch (Dias et al. 2020). Despite its ecological importance, little is known about its reproductive biology. Munro (2004) showed that populations in the UK are gonochoric, and spawning presumed to occur in late summer via broadcast spawning. This lack of reproductive data limits the development of effective restoration techniques. Critical traits—such as reproductive mode, larval behaviour, and planktonic larval duration (PLD)—influence larval dispersal, recruitment patterns and population connectivity and are essential for conservation and restoration, including methods like sexual propagation (Fogarty and Botsford 2007; Jones et al. 2007; Marti-Puig et al. 2013; Waller et al. 2023).

This study aims to characterize the reproductive and larval biology of *E. verrucosa* and explore methods for sexual propagation in captivity. Specifically, we document, for the first time, the reproductive phenology of populations from southwestern Portugal under short- (a couple of months) and long-term (1 and 2 years) aquarium conditions, describe larval development, and assess settlement preferences, with the overarching goal of producing sexually derived recruits to support habitat restoration efforts.

Methods

Inference of reproductive timing

The timing of reproduction in *E. verrucosa* was inferred by examining the stages of gamete development in samples collected as fishing bycatch around Cape St. Vincent (southern Portugal) in 2020 and 2021 (see Dias et al. 2020 for details on fishing areas) at the Centro de Ciências do Mar (CCMAR). Sampling focused on the summer and early autumn periods, following available information on reproductive patterns of the species in the UK (Munro 2004) and other *Eunicella* spp. in the Mediterranean (Ribest et al. 2007; Gori et al. 2007, 2012; Viladrich et al. 2022). The presence and maturation state of the gametes were assessed through polyp dissection and histological sectioning at CCMAR. All samples were fixed in a 10% neutral buffered formalin solution (Sigma-Aldrich), washed three times with distilled water, and gradually dehydrated in EtOH 70% until further analysis. Dissection of the polyps was performed under a stereomicroscope to distinguish female and male individuals by identifying their oocytes and spermaries where possible. The number of gonads per polyp and branch order (sensu Brazeau and Lasker 1988) was then counted and those individuals with higher number of reproductive polyps were selected for histological sectioning. For the histological study, branchlets of approximately 2 cm were cut from the first and second order branches of four colonies. Samples selected for histology were hydrated and treated with 2.1 M EDTA (pH 8) for two days to decalcify the sclerites embedded in the coral tissue, following the method used for sea bream scales (Vieira et al. 2011). After decalcification, the samples were washed several times with deionized water to remove any residual EDTA and then dehydrated through a graded ethanol series. The samples were saturated in xylene, followed by impregnation and embedding in low melting point paraffin wax (Histosec, Merck) using an automatic embedding processor. Serial sections of 5 µm were cut from the paraffin block using a manual rotary microtome (Leica RM 2135, Germany) and mounted on glass slides coated with 3-aminopropyltriethoxysilane (APES; Sigma-Aldrich, Madrid, Spain). For each wax block containing a piece of coral branch, 2–3 sections were cut from the base of the polyps to sample the gonadal tissue. The sections were dried overnight at 37 °C, then cooled to room temperature for storage or staining. The sections on the slides were dewaxed and rehydrated before being stained with hematoxylin and eosin (H&E) according to the method described by Najafpour et al. (2020), mounted in Tissue-Tek Resin (Sakura Finetek), and covered with a glass coverslip. The stained slides were investigated under light microscope (Zeiss Observer. D1) to identify the reproductive structures of the polyps. The gametogenic maturation classification system defined by Waller (2005) was used to describe the ripening process of the gametes.

Spawning observations and larval rearing

The observations of spawning and settlement were conducted for corals collected as fishing bycatch from approximately the same location as the corals used to determine the spawning timing (Cape St. Vincent, southern Portugal).

However, observations were made on corals collected during three consecutive years (2021, 2022 and 2023) and kept at two separate facilities: the Ramalhete Marine Station of CCMAR in Faro (corals from 2023) and the Oceanário de Lisboa (ODL; corals from 2021 and 2022).

Short-term monitoring during the reproductive season (1–2 months, CCMAR)

In 2023, coral colonies were opportunistically collected from early July to mid-August. A total of 70 colonies, varying in colour, size, and health, were collected in several batches and then transferred to tank systems at Ramalhete Marine Station for spawning observations. Approximately 50 colonies were maintained in a cooled, semi-dark outdoor flow-through system, consisting of two 500 L tanks, while 20 colonies were kept in a ~ 150 L indoor aquarium, which was dark and semi-closed, with a temperature-controlled system set to 14–16 °C (the lowest temperature maintainable in the system). Out of the 70 colonies collected, 35 were randomly selected and sexed through polyp dissection to ensure both tank systems contained male and female colonies. Water flow was provided by wavemaker pumps, and corals were fed daily with frozen rotifers, copepods, and red zooplankton, which were passed through a 150 µm net to avoid oversized food particles. During feeding, the inflow and outflow of water were stopped for 1–3 h to prevent the food from being washed out. The tank bottoms were hoovered daily to maintain good water quality. During the expected spawning period, perforated PVC cylinders with a 150 µm mesh fitting were attached to the outflow of the tanks to collect released offspring. A venturi airlift was also installed at the water surface of the outdoor tanks. The airlift, outflow filters, and colonies were monitored daily for egg and/or larval release. Additionally, polyps were regularly dissected to check for the presence of mature oocytes and sperm sacs.

During spawning, propagules (i.e., oocytes, embryos, and larvae) were collected both directly from the water column using a transfer pipette as well as from the two airlifts (in case of the outdoor tanks) and the outflow filters, by gently washing them into plastic beakers. The propagules were counted, and the overall number of propagules collected per day was categorized as high (> 250 propagules) or low spawning output (10–250 propagules). Release of fewer than 10 propagules was not considered as an event. All propagules were kept in plastic jars (1–10 L), sorted by collection date, and stored in a temperature-controlled room at 16 °C. Gentle aeration was provided via air tubes producing a few bubbles per second, and approximately two thirds of the water was changed every other day using a 5 mm hose with a small, perforated tube with a 150 µm plankton net wrapped at the end to prevent larvae from being sucked out.

Long-term monitoring (1–2 years, ODL)

A total of 15 colonies collected in 2021 and 9 colonies from 2022 were maintained together in two tanks (100 × 50 × 43 cm) within a closed indoor system at the Oceanário de Lisboa (ODL). The setup included an EcoDrift 4.2 pump from Aqua Medic Direct and a Hydor Seltz L 700 pump in each aquarium, a 50 µm filter bag at the inlet of a 1300 L sump containing bioballs, a 20 µm cartridge filter, two UV lights, a Frimar C1000 chiller and a HydroAir pump (model AV50-20N-S). The aquaria received indirect sunlight and moonlight from east-facing windows and ambient light from the room ceiling (between 7:30 h and 16:30 h). The moon cycle was simulated using a 54W actinic light set with a timer and an intensity adjuster, following the moon cycle at Sagres (from the website Timeanddate.Com, n.d.). Temperature modulation was based on seasonal variation patterns. The corals were fed live and frozen zooplankton and phytoplankton three times a day. The food concentrations were adjusted based on the observations of seasonal patterns (Villa et al. 1997).

From 26th of July until 16th of November, egg collectors were placed at the surface skimmer of each aquarium from 16:00 to 8:00. Water flow was reduced, and circulation pumps were turned off to avoid damaging eggs and embryos. In the morning, the collectors were rinsed with saltwater to flush all propagules into a plastic beaker, allowing their observation under a stereomicroscope. The collected propagules were transferred to 4 L circular boxes with 125 µm mesh at the bottom and with slow water flow, connected to the main system, where the breeding colonies were maintained.

Embryogenesis and larval development

Embryonic and larval development stages were observed and imaged using a ZEISS Stemi 508 stereo microscope with a ZEISS Axiocam 208 colour camera system, at Ramalhete Marine Station (CCMAR). Qualitative observations were conducted on > 10 batches of 50–600 propagules each, throughout the development period to ensure consistency. Samples of various stages of development were collected for scanning electron microscopy (SEM). These samples were fixed overnight in 4% glutaraldehyde buffered in 0.1–0.5 M Sørensen's phosphate buffer (pH 7.1), at 4 °C. On the following day, the samples were washed three times in pure Sørensen's phosphate buffer and transferred to 30% EtOH where they were stored until further analysis. All SEM imaging was conducted at the SNSB—Bavarian State Collection for Zoology in Munich, Germany. Samples were then dehydrated using a graded acetone series (30%, 50%, 75%, 95% and 100%). The specimens were soaked for 10 min at each step, and twice in 100% acetone. They were then

critical point dried using a Polaron E3000, mounted on SEM stubs with self-adhesive carbon stickers, and gold-coated for 3 min in an argon atmosphere using a Polaron SC510. Three embryos or larvae of each stage of development were analyzed with a LEO 1430 VP SEM at a voltage of 15 kV (method described in Melzer et al. 2021; Torres et al. 2021). Size measurements of propagules were taken with help of Adobe Photoshop© 22.2.0 from > 5 propagules per stage on LM images and on all SEM images, using the scale bar.

Larval settlement, metamorphosis and early life ecology

Larval survivorship and settlement substrate choice (experiment 1)

A settlement experiment was conducted at CCMAR to document larval settlement and metamorphosis as well as to test settlement preferences using natural substrates. Three types of substrate were offered for settlement: rocky substrate collected as bycatch along with the corals encrusted with a variety of taxa, including natural biofilms and/or crustose coralline algae (CCA) which are presumably implicated in inducing coral settlement and metamorphosis (Zelli et al. 2020); chips of an unidentified species of CCA retrieved with the aforementioned substrate; and pieces of conspecific bare gorgonian skeleton, which larvae of other octocorals have been observed to settle on (Weinberg and Weinberg 1979; authors personal observations). Larval settlement was quantified for two cohorts of larvae spawned on October 11 (Cohort 1) and September 30 (Cohort 2), aged 6 and 16 days at the start of the experiment, respectively. For each cohort, 5 replicates of 50 larvae each were exposed to the three types of substrates. All replicates were maintained in open plastic containers (8 cm diameter, 4 cm height with ~ 250 ml of seawater). Approximately 50% of the water was changed after each counting. The containers were kept in a separate room with the same ambient temperature as the coral indoor tank system, and pH was regularly checked to monitor for variations due to influences from the organic or inorganic substrates. On the 28th of October (day 11 of the experiment of Cohort 1 and day 12 of the experiment of Cohort 2 (one day difference to make the monitoring feasible) the experiments had to be relocated to a different room kept at 18 °C due to a complete failure of the air conditioning in the original room.

Larval settlement (i.e., attachment and metamorphosis) was detected and counted as the attachment of larvae or the presence of recruits on each substrate in each of the 5 replicates. Monitoring of larval settlement was conducted every other day at the beginning of the experiment and alternating for each cohort (experiments started on 16th and 17th of October for Cohorts 2 and 1, respectively). After 11 days, the monitoring intervals were increased to 3–4 days and to 7 days after day 34. On day 62 (Cohort 2) and 63 (Cohort 1), more substrate was added to each replicate to test for a potential settlement bottleneck caused by the occupation of available space by settlers as settling rates seemed to decrease. Larval settlement was evaluated for both, the substrate type and total settlement (i.e., irrespective of substrate type) levels, using the age of the larvae to compare settlement rates between the two cohorts. After settlement, primary polyps were transferred to the indoor tanks containing the parental colonies and provided with the same food.

Settlement success and long-term survivorship of recruits (experiment 2)

Larval settlement and post-settlement mortality were assessed in two additional experiments conducted separately at CCMAR and ODL (Experiment 2). At CCMAR, settlement success and recruit survival were tracked for 6–7 months post-settlement across 4 larval cohorts (Cohorts 1–4, aged 6–16 days) and 3 egg cohorts (Cohorts 5–7). Cohort 1 (n = 250) and Cohort 2 (n = 250) were the pooled larvae from Experiment 1 and 2 and Cohort 3 (n = 250) and Cohort 4 (n = 180) were two additional replicates. The fertilized oocytes of the replicate cohorts Cohort 5 (n = 226), Cohort 6 (n = 200) and Cohort 7 (n = 100), as well as the larvae were provided with the same substrates as described above for Experiment 1 (CCA, gorgonian skeleton and natural rock) during days 6–16. The number of settlers was counted at the settlement peak for each cohort, and the survival of the primary polyps (i.e., recruits) that were moved into the tanks with parental colonies was monitored at 4 months and 6–7 months post-settlement. Both, total survival from fertilized egg to single-polyp recruit and subsequent recruit survival, were calculated. Individual recruits were tracked over the period of one year to document their development and imaged using the previously described stereo microscope.

At ODL, larvae from the major spawning events observed in September and October were transferred 12 days after fertilization from the circular boxes to four 4 L rectangular boxes with 200 µm mesh sides receiving water from the main system. For settlement, larvae were provided with CCA-encrusted rocks wild-collected 2 months earlier, as well as with basaltic rocks conditioned in the gorgonian system for over 7 months. The microalgae *Chaetoceros calcitrans* and *Tisochrysis lutea* were fed to the larvae from day 5 after (presumed) fertilization. The same microalgae and, additionally, living *Acartia tonsa, Brachionus plicatilis* and frozen Copepods (Ocean Aquaculture ®) were fed after the first primary polyps were observed. The polyps were kept in the same boxes until day 197, then they were transferred to one of the aquaria containing the adult colonies. Monitoring of larval settlement and polyp survival was conducted every

two weeks until month 3 and monthly thereafter using a Nikon SMZ745T stereo microscope in Oceanário de Lisboa. Only data from one cohort (Cohort 8, 1621 larvae, collected on the 6th of September) are presented here.

Results

Inference of reproductive timing

The histological analysis of gamete development in samples of *E. verrucosa* collected in 2020 and 2021 suggested that reproduction occurred in late summer or early autumn in both years. In 2020, dissections of polyps from multiple female colonies revealed a significant decrease in the number of oocytes from June to September, indicating potential spawning during this period (see Fig. S1 in Supplement 1). Histological sectioning of samples from 2021 indicated spawning occurring in a similar timeframe as in 2020, with female colonies still showing late stage 4 vitellogenic oocytes on August 5th and 26th as well as in mid-September (Fig. 1a–c). The spermatocytes showed a ripening process progressing from small, growing (stage 2) spermatocytes in early August to stage 3 spermatocytes in mid-September (Fig. 1d–f). This shows that the accelerated ripening indicates the approach of the spawning period. Polyp dissections of male and female colonies collected in August 2023 for spawning observations revealed vitellogenic or late vitellogenic oocytes (stage 3 or 4) and visible spermatocytes in most of the colonies (data not shown). In none of the polyp dissections and histological sections embryos or larvae could be observed inside the polyps which indicates that *E. verrucosa* is a gonochoric broadcast spawner.

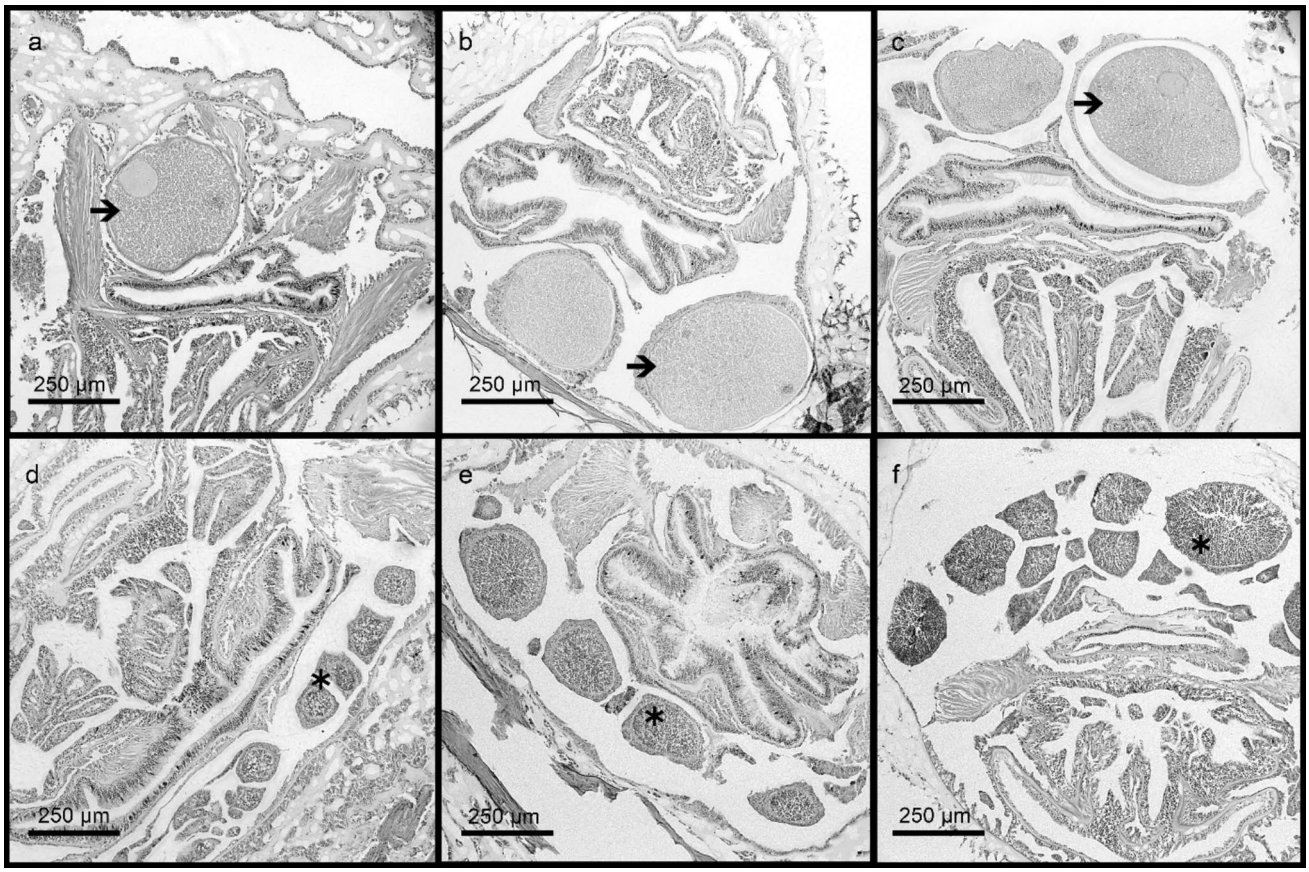


Fig. 1 Histological sections of polyps of *Eunicella verrucosa* preserved at three different dates: **a-c** Female polyps with visible oocytes Stage 4 late vitellogenic oocyte (arrows) in specimens preserved in (**a**) early August (05/08/2021), (**b**) late August (26/08/2021) and (**c**) mid-September (16/09/2021); **d-f** Male polyps with visible spermatocytes (asterisk); **d** small, growing (stage 2) spermatocytes in early August (05/08/2021), **e** Developing (stage 2) spermatocytes late August (26/08/2021) and **f** stage 3 spermatocytes in mid-September (16/09/2021)

Spawning observations

Short-term monitoring during the reproductive season (CCMAR)

For the 2023 reproductive season, of the 35 colonies dissected to determine sex, 16 were identified as males and 18 as females and one was undetermined (i.e., no gametes found), indicating a male-to-female sex ratio of 1 to 1.125. Spawning was first observed on September 2nd, when minor release of large (~300–400 µm in diameter), positively buoyant eggs and developing embryos were floating in both the inside and outside tank systems synchronously, thereby confirming that *E. verrucosa* is a broadcast spawner. Most of the release then occurred as split spawning in three major events: the first one over two consecutive days on 12th and 13th September, the second one on the 26th and 30th of September, and the third one on the 11th of October (Fig. 2). Each large spawning event was preceded and followed by minor egg releases (Fig. 2). Despite spawning peaks of the largest event appearing to correspond with the moon phase, with the largest events consistently occurring between 5 days before and 3 days after the full or new moons, no clear evidence for a correlation with a single lunar phase was evident (Fig. 2).

Long-term monitoring (1–2 years, ODL)

For *E. verrucosa* colonies kept in captivity at ODL for up to two years, egg release started earlier, with minor releases first observed on August 4th and extending through 14th of November, although very low spawning activity was observed after the 23rd of October (only 3 oocytes) (Fig. 2). The major spawning events occurred on the 6th and 7th of September (6 days before the large event documented at CCMAR) and on 5th, 6th and 15th of October (Fig. 2). The first four major events occurred 6–7 days after the full moon, with spawning times for the first three events beginning between 5:15 and 6:10 h after moonrise. During the major spawning event in September, almost all eggs and embryos were positively buoyant. However, only a minor fraction of those spawned in October exhibited positive buoyancy.

Embryogenesis and larval development and behaviour

Embryos collected at CCMAR developed into gastrulae within 24 h of egg collection from the tank system. Fertilization rates of the eggs appeared very high, as all observed zygotes started cleaving. Once cleavage began, the embryos were observed to sink towards the bottom of the rearing containers, indicating negative buoyancy. Partial cleavage (meroblastic) of the embryos was observed until the 8-cell stage (Fig. 3a, d and video in Supplement 2). Similar observations were made for embryos reared at ODL. The greater part of the yolk remained in the initial (egg) cell at the beginning. In some cases, embryos started segmenting into one large and four to five smaller compartments that did not cleave entirely, reverting instead to the initial rounded shape before segmenting again and then proceeding to cleave into 8 and finally 16 evenly sized cells (Fig. 3e, f and video in Supplement 2). The arrangement of the blastomeres appeared spiralic, and beyond the 32-cell stage the

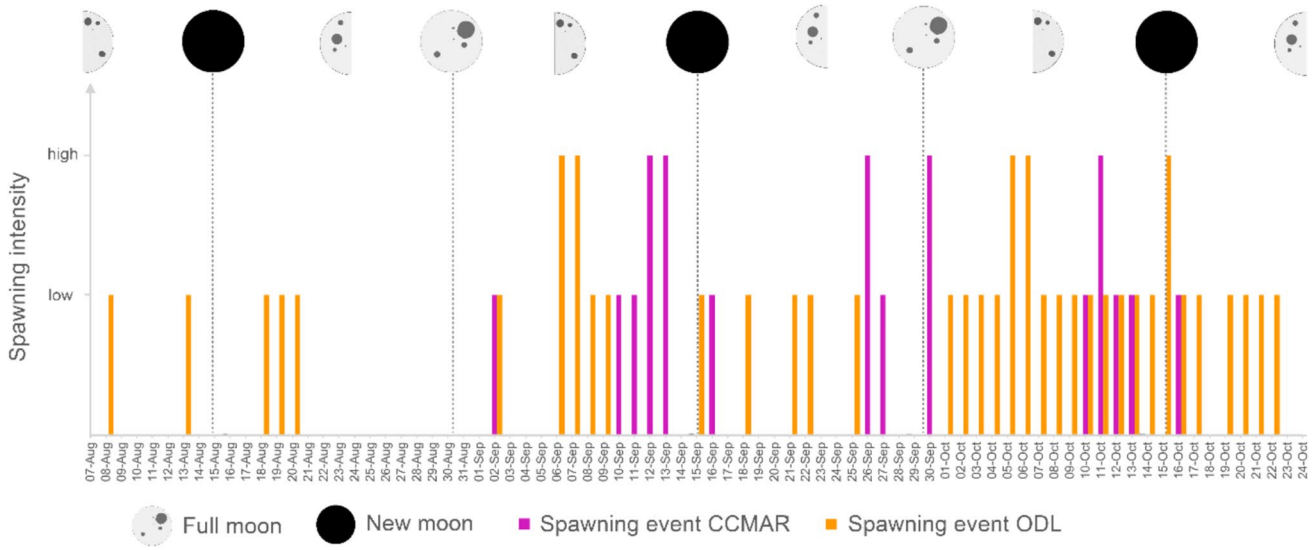
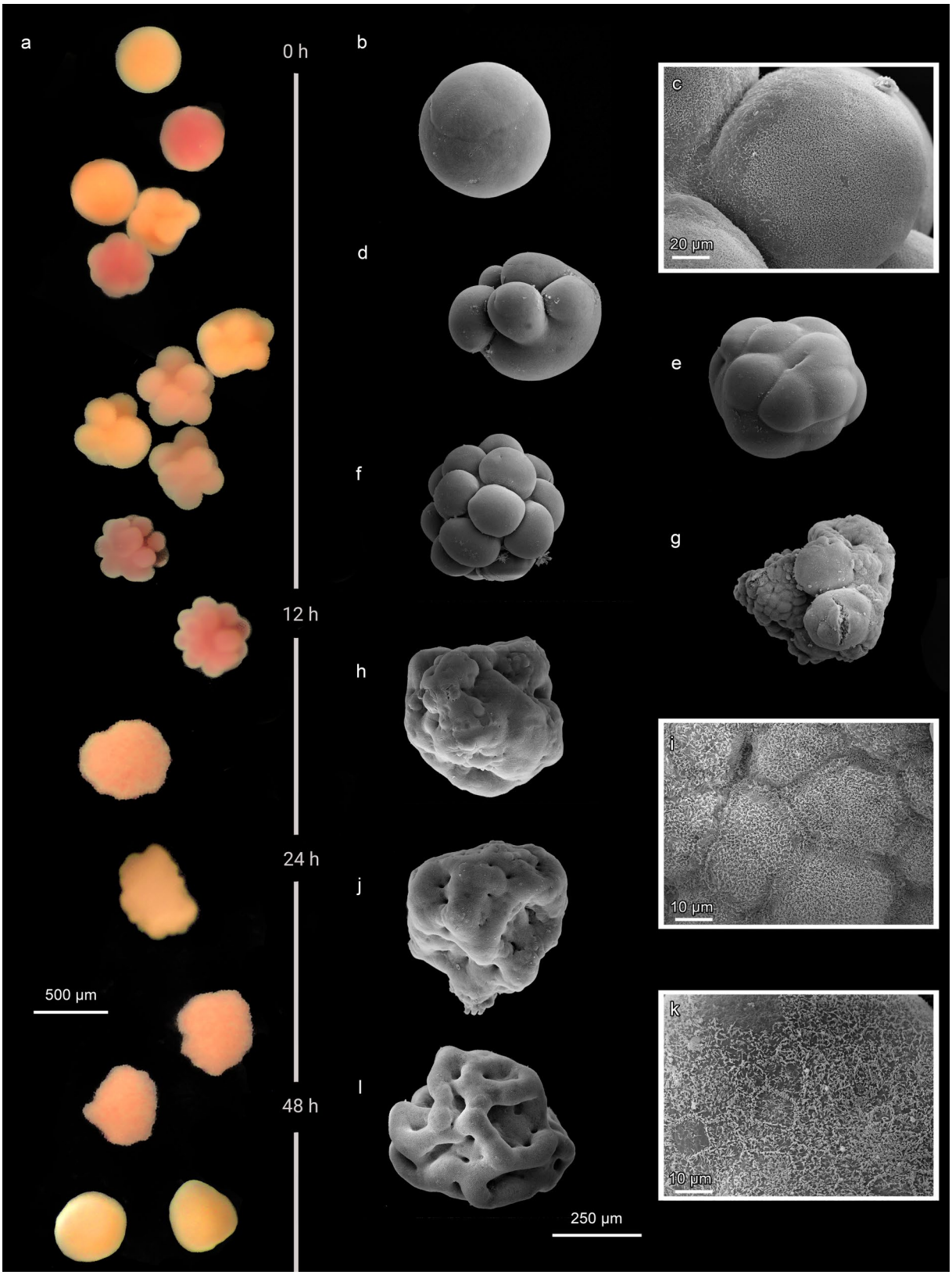


Fig. 2 Spawning intensity of *Eunicella verrucosa* kept in captivity across the 2023 lunar cycle at the Centro de Ciências do Mar (CCMAR) and at Oceanário de Lisboa (ODL). The qualitative spawning index is as follows: high (> 250 propagules); low (10–250 propagules). Egg release below 10 propagules was not considered as an event


a
0 h
b
c
20 µm
d
e
f
g
12 h
h
i
10 µm
24 h
j
500 µm
k
10 µm
48 h
l
250 µm

◂**Fig. 3** Light and Scanning Electron Microscopy images of the embryonic development of the *Eunicella verrucosa*, across 72 h. **a** Light Microscopy images displaying the variations in embryonic development (panel left of the timeline). **b-l** SEM micrographs. **b** Oocyte presumably fertilized (i.e., Zygote). **c** Magnification of cleaving area in a 8-cell embryo. **d** Meroblastic cleavage between 4- and 8-cell stadia; **e** Early 16-cell stadium embryo. **f** 16-cell stadium embryo. **g** 64-cell or above stadium embryo with irregular sized cells and shape. **h** 12 h old embryo above 64-cell stadium. **i** Magnification of 6 angled cells of a 12-24 h old embryo during gastrulation. **j** 24 h old embryo with several invaginations. **k** Magnification of a 48 h old embryo with 6 angled cells and microvilli. **l** 48 h old embryo with pronounced invaginations

pattern evolved into irregular-sized cells forming six squares and an irregular-shaped embryo (Fig. 3 g, i). While the six squared cells became more equal in size with further cleavage, the embryo retained a somewhat irregular shape and developed several infoldings and invaginations during gastrulation (Fig. 3j, k, l).

Seventy-two hours after fertilization, the first oval-shaped larvae (~350 µm long) started moving and actively swimming upwards toward the water surface in the rearing containers (Fig. 4a, b and videos in Supplement 3). Five to six days after egg collection, larvae had elongated (Fig. 4a, d) and were approximately three times as long as wide (~750 µm long, ~250 µm wide). These observations were consistent for larvae collected at both CCMAR and ODL. Between 3 and 9 days, the larval flagellation was sparse, with short flagella covering the larvae body during this period (Fig. 4c) and flagellation increasing until day 17 (Fig. 4e, g). The increase in larval flagellation coincided with an increase in swimming activity. Larvae between 7 and 12 days post-spawning began to partially leave the water surface and to adopt an upright posture in the water column. After 13 days, larvae frequently swam up and down and started probing the substrate (see video 1 in Supplement 4). During that phase, the oral pore became more visible, flagellation became denser, and a clear propulsion direction developed (Fig. 4e–k). With advancing age, the larvae became more transparent and shorter but remained motile up to 100 d post spawning (Fig. 4j, k).

Larval settlement, metamorphosis and early life ecology

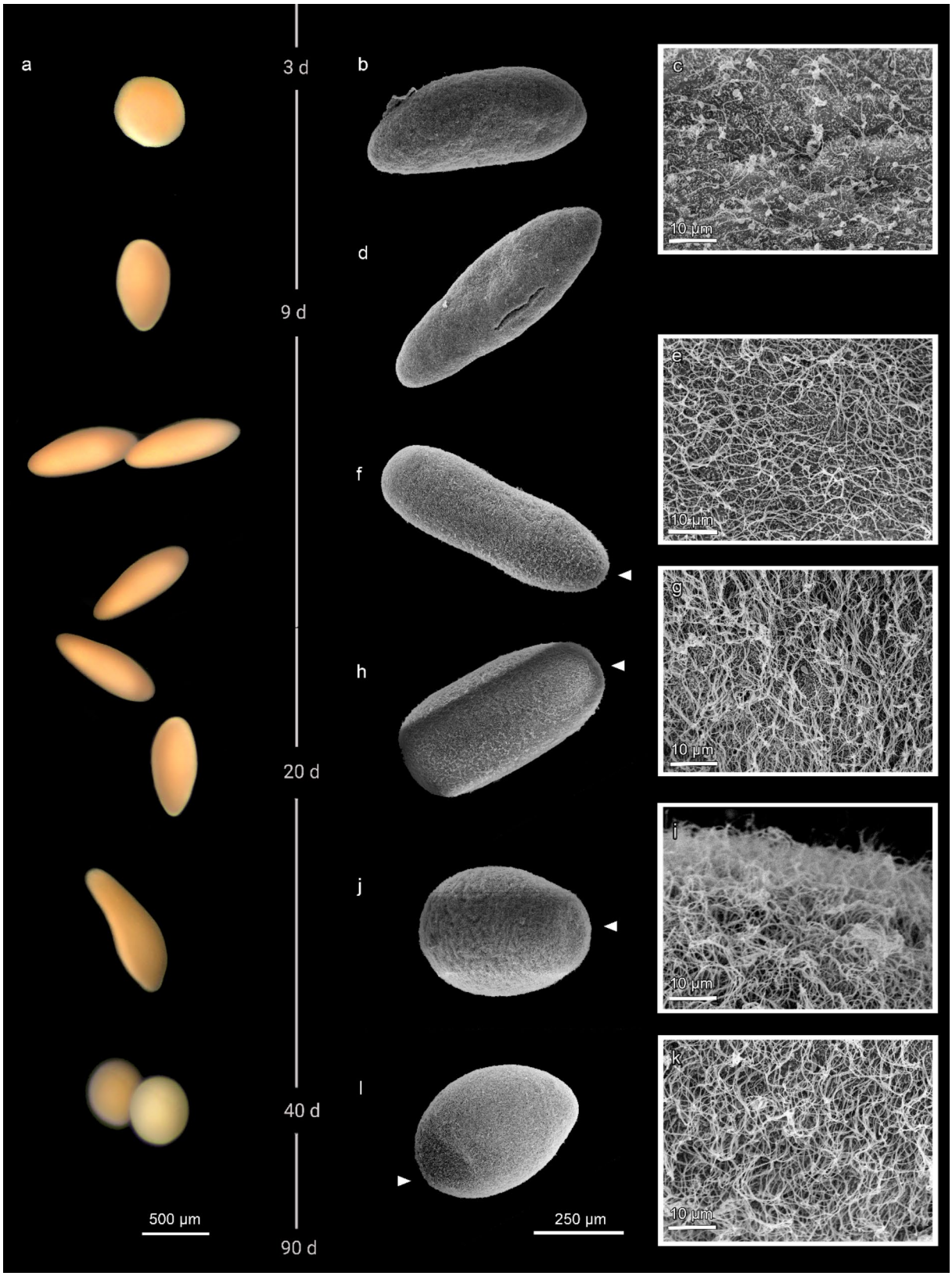
Detailed imaging of coral settlement, metamorphosis, and budding

The first attachment of larvae to the substrate offered in the settlement experiments at CCMAR was observed 15 days after spawning, when the larvae temporarily attached with the oral pole to the provided substrate (Fig. 5a and video 2 in Supplement 4). The onset of settlement started shortly thereafter and continued over the next two months. After successful settlement, metamorphosis occurred over several days (Fig. 5b), during which the settlers sequentially developed mesenteries, a mouth and tentacles. The primary polyps appeared healthy, apparently began feeding, and started developing sclerites within a few weeks (Fig. 5b, c). These sclerites formed in eight vertical rows surrounding the mesenteries (Fig. 5c) and later developed into acuminate leaflets enclosing the mesenteries similar to petals (Fig. 6a). When stimulated or stressed, these leaflets formed a complete, enveloping spherical shell around the contracting polyp (Fig. 6a). Growth in the aquarium was slow. Within the first three months after settlement, the settlers grew from 0.5 mm to a maximum length of 1–2 mm (Fig. 6 a, b). By nine months, they had expanded from 0.5 mm to 1 mm in width and reached up to 5 mm in height (Fig. 6a–f). The first deposition of the proteinaceous skeletal axis was observed at six months post-settlement (Fig. 6b) and was much more distinct at nine months post-settlement (Fig. 6e). Shortly thereafter, branching of the second polyp was noted (Fig. 6c, e). The internal axis in the primary polyp began to develop, bending away from the mouth region (Fig. 6b), while the second polyp branched in the opposite direction from the axis below the primary polyp (Fig. 6c, e). When the third polyp developed, it emerged from the axis between the first and second polyps (not shown), while the fourth polyp developed below them (Fig. 6f). Concurrent with budding of the second polyp, the recruits also started to deposit a holdfast on the substrate to which they were attached (Fig. 6c, e).

At ODL, the first recruits were observed 20 and 21 days after the major spawning event (6th-7th September). Settlement continued over a period of 3–4 months, similar to the observations made at CCMAR. The first tentacles with pinnules were observed 36 days after spawning and the first observation of a secondary polyp occurred 204 days or 6.5 months after spawning, shortly after the transfer to the aquarium housing the adult colonies. Settlers with three or more polyps were observed almost one year after spawning (data not shown).

Larval survivorship and settlement substrate preference (experiment 1)

In the settlement experiment conducted at CCMAR, two small larval settlement peaks were observed: at 15 days after spawning in Cohort 1 (release of 11th October, larvae were 6 days old when experiment started) and at 19 days in Cohort 2 (release of 30th September, larvae were 16 days old when experiment started) (Fig. 7). These settlement peaks did not result in successful settlement, as no settlers were detected on the following monitoring day. This either indicates temporary detachment of the 'settlers' or failure to complete metamorphosis (Fig. 7). After this, the number of settlers increased gradually until the larval ages of 77 days in Cohort 1 and 88 days in Cohort


a
3 d
b
c
10 µm
d
9 d
e
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g
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k
10 µm
l
40 d
500 µm
250 µm
90 d

◂**Fig. 4** Light and Scanning Electron Microscopy images of the larval development of *Eunicella verrucosa*, over 90 days. **a** Light Microscopy images displaying changes in shape over time (panel to the left of the timeline). **b-l** SEM micrographs: **b** Young larva (5 days old) at the onset of swimming activity; **c** Magnification of the preliminary sparse flagellation of an early larva (9 days). **d** Elongated 9-day old larva. **e** Flagella at the aboral part of a 17-day old larva. **f** 17-day old larva. **g** Flagella at the oral part of a 17-day old larva. **h** 20-day old larvae with visible oral pore. **i** Magnification the oral pole of a 39-day old larva. **j** 39-day old larva. **k** Magnification of the dense flagellation of a 39-day old larva. **l** 39-day old larva, picked and preserved while substrate probing. Arrows indicate the oral pole of the larvae

2, followed by a stronger increase in settlement until 96 (Cohort 1) and 95 days (Cohort 2) after spawning, when maximum counts of 19 and 29 settlers were observed, respectively. The increase in settlement occurred after the addition of new substrate when larvae were 68 (Cohort 2) and 79 (Cohort 1) days old. There was no obvious change in settling behaviour after the room change on days 11 (Cohort 1) / 12 (Cohort 2) of running the experiment (17 and 28 days old larvae, respectively) (Fig. 7). Beyond a larval age of ~ 95 days no more additional settling was observed. Figure 8 shows the pooled average numbers of larvae and settlers over time for Cohorts 1 and 2. In both cohorts the number of survivors decreased relatively rapidly until ~ 45 days (likely due to mortality or failure of attachment or metamorphosis), then declined steadily until ~ 95 days. Afterward, the average survivorship stabilized and remained almost constant until the end of the experiment (Fig. 8).

Regarding to substrate preference our data did not permit formal statistical analysis due to the limited number of larvae and replicates used (two cohorts, each with 250 larvae in 5 replicates, n = 50) and the overall low larval settlement (total maximal number of settlers was only 19 in Cohort 1 and 29 in Cohort 2). Nevertheless, some key observations are noteworthy: Substrate preference appeared to vary over time in both Cohorts 1 and 2, as well as between cohorts. Initially, settlers appeared to prefer to attach to bare gorgonian skeleton, but this preference decreased over time. Larvae at later stages of development apparently settled more on the rocky substrates, particularly in Cohort 2 (Fig. 9).

In Cohort 1 (Fig. 9), the highest average number of settlers on rock over the five replicates (n = 50) was 2 (± 0.9), (Fig. 9a) and the highest total number of settlers was 9 (Fig. 9b) on day 99. On CCA (coralline crusts) the highest average number of settlers was 0.4 (± 0.2) and 4 in total, and on gorgonian skeleton it was 0.6 (± 0.6) on average and 6 in total observed on both days 96 and 99.

In Cohort 2, the highest average number of settlers on rock was 3.6 (±2.1), (Fig. 9a) and the highest total number of settlers was 19 (Fig. 9b), observed on both days 72 and 79. On CCA (coralline crusts) the highest number of settlers was as low as 0.2 (± 0.2) on average and 2 in total on day 79, and on gorgonian skeleton it was 1.6 (± 1.4) on average and 6 in total, observed on days 65, 72 and 79.

At ODL settlement was only observed on rocks encrusted with CCA, with no settlers observed on the basaltic rocks. Furthermore, from the October major spawning events where most of the oocytes were negatively buoyant, none of the larvae settled.

Settlement success and long-term survival of recruits (experiment 2)

In the CCMAR experiment tracking settlement and survival of 6–16-day-old larvae, 61 out of the 930 larvae (6.6%) successfully settled across four batches. The highest percentage of larval settlement was observed in Cohort 2 with 11.6% (see Fig. 10a for data on individual cohorts). Four months post-settlement, 35 of these settlers were still alive (57.4%), declining to ~ 28% by 6–7 months after spawning. This corresponds to an overall survival rate of 1.8% of the original 930 larvae.

For the second part of the experiment, where settlement and overall survival were tracked from the presumed time of egg fertilization (i.e., collection from the tanks), a total of 56 propagules out of the 526 eggs (11%) monitored at CCMAR in Cohorts 5, 6 and 7, successfully settled, with the highest percentage of settlement observed for Cohort 5 at ~ 16% (Fig. 10a). After four months, 33 of those 56 settlers were still alive, yielding a survival rate of 59% of the settlers. At more than 6 months post-settlement, 36% of the initial settlers were still alive, resulting in an overall survival rate of 3.8% from egg to 6–7 months post-settlement (see Fig. 10a for data on individual cohorts).

At ODL only 29 out of 1621 eggs (1.8%) developed into larvae and settled within 4–5 months (Fig. 10a). At 6–7 months after fertilization 25 settlers were still alive, corresponding to a post-settlement survival rate of 86% and an overall survival of 1.5% from zygote stage to 6–7-month-old recruit. Nine months after fertilization, some mortality was detected, and the survival rate decreased to 59% of the settlers (1.0% in total). Ten settlers were still alive 12 months after fertilization, corresponding to a survival rate of 34% among the settlers (0.61% in total).

Discussion

Reproductive cycle and spawning

The histological investigations revealed that in 2021 female oocytes present in female colonies of *E.verrucosa* were already close to being fully mature (stage 4: late vitellogenic oocyte) throughout August, at least 1.5 months before spawning. In contrast, the spermaries seemed to ripen more

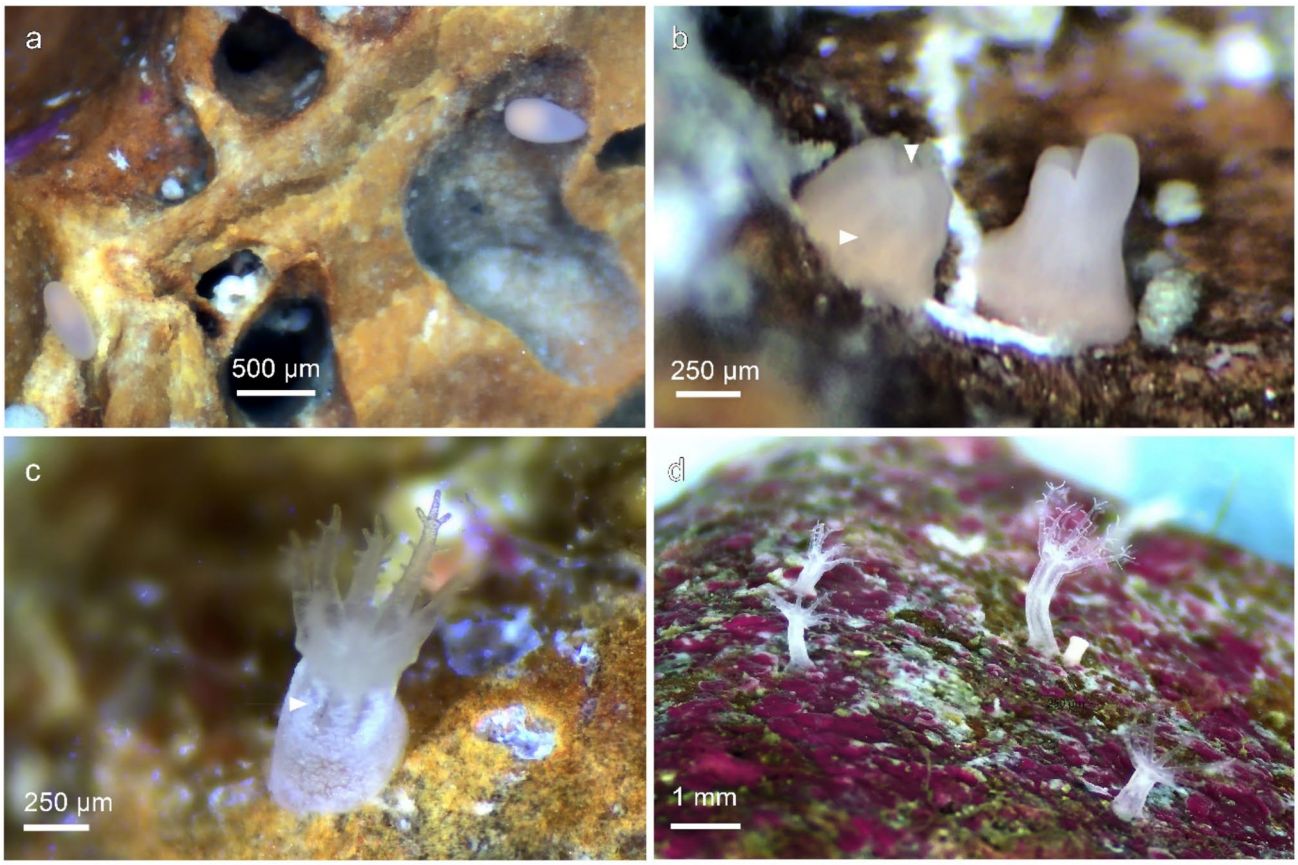

Fig. 5 Attachment, settlement and metamorphosis of *Eunicella verrucosa*, larvae. **a** Loose attachment of larvae to rocky substrate with the aboral pole after 15–17 days. **b** Settlers metamorphosing and developing eight mesenteries (horizontal arrowhead) and a mouth (vertical arrowhead). **c** Development of tentacles, pinnules and sclerites (arrowhead indicates sclerites arranged in rows). **d** Three-month-old recruits are growing in length

quickly from immature (stage 2) to nearly mature (stage 3) while becoming noticeably larger within the same period. These findings suggest a distinct difference in the maturation timelines of oocytes and spermaries in this species. Similar patterns where spermatogenesis is shorter than oogenesis with a relatively quick maturation of spermaries in the month(s) leading to gamete release have been observed in many corals (reviewed in Harrison and Wallace 1990; Kahng et al. 2011), including gorgonian species occurring in the adjacent Mediterranean Sea such as *Paramuricea clavata* and the congeneric *Eunicella singularis* (Coma et al. 1995b; Ribes et al. 2007; Weinberg and Weinberg 1979) and in *E. verrucosa* populations in the UK (Munro 2004).

Polyp dissections and histological sectioning data (2021 and 2022) indicated that *E. verrucosa* spawned in late summer to early autumn, a finding later confirmed by ex situ observations in aquaria during 2023. This contrasts with several shallow-water Mediterranean gorgonians, including the congeneric *E. singularis* and *E. cavolini*, which typically release propagules in spring or early summer (Gori et al. 2007, 2012; Ribes et al. 2007; Koch 1887; Weinberg and Weinberg 1979). However, a mesophotic population of the Mediterranean species *Paramuricea macrospina* has also been documented to release larvae during the autumn months (September–October) (Grinyó et al. 2018), similar to our observations for *E. verrucosa* in southwestern Portugal. In the UK, *E. verrucosa* colonies have been inferred to spawn in August or September, although no direct observations have been reported (Munro 2004).

Inter-regional differences in reproductive timing are likely influenced by environmental factors such as temperature regimes, stratification, currents, and tides, which vary between the Atlantic Ocean and the Mediterranean Sea. Regional variation in reproductive timing across coral species and populations is not uncommon (Harrison and Wallace 1990), including within the Mediterranean (e.g., Gori et al. 2007), and is often linked to local temperature dynamics (Foster and Gilmour 2020; Kersting et al. 2013; Osman et al. 2024; Sakai et al. 2024). Depth also appears to play a significant role, as multiple environmental factors vary dramatically with depth. In this study (NE Atlantic), the *E. verrucosa* colonies originated from a mesophotic

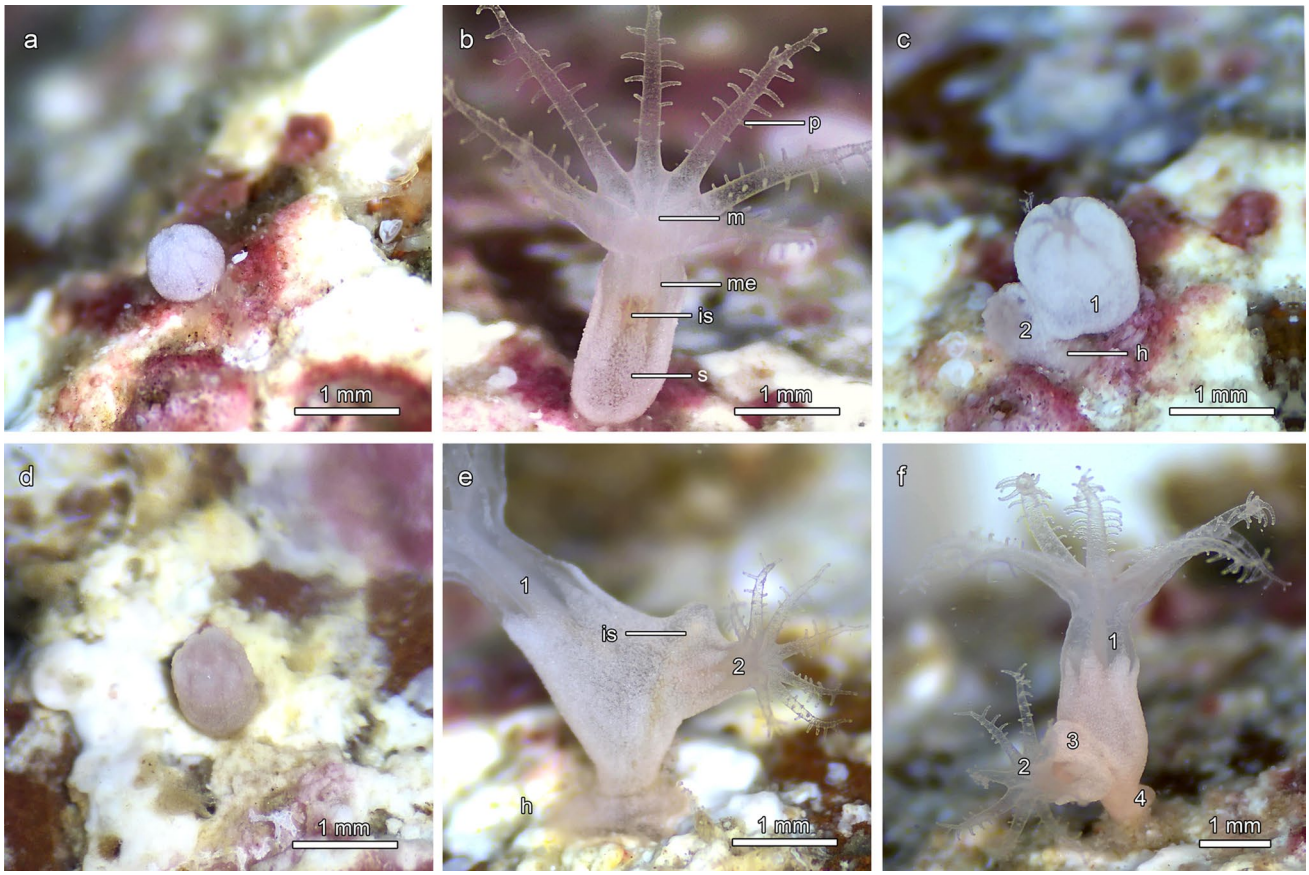

Fig. 6 Development of two recruits of the pink sea fan *Eunicella verrucosa* over the period of one year. Recruit 1 (**a-c**)**: a** Primary polyp retracted three months following settlement. **b** At 6 months with the proteinaceous skeletal axis visible (brown darkened area in the center marked with 'is'. **c** At ten months following settlement, after budding off a second polyp and showing a secrete holdfast. Recruit 2 (**d-f**): **d** At 6 months following settlement. **e** At nine months with internal skeleton, a second polyp and a clearly deposited holdfast. **f** At 10 months showing the budding of a third and fourth polyp and increase in height. Abbreviations are as follows: **h**, holdfast; **is**, proteinaceous skeletal axis. **p**, pinnules; **m**, mouth; **me**, mesenteries; **s**, sclerites; **1**, primary polyp; **2**, secondary polyp; **3**, third polyp; **4**, fourth polyp

habitat (below 60–70 m depth), similar to those studied for *P. macrospina* in the Mediterranean (Grinyó et al. 2018). Both species reproduce during the same period, in contrast to other shallow-water Mediterranean corals, suggesting that environmental factors associated with depth rather than geographic region may play a more dominant role in shaping reproductive ecology in deeper habitats. However, this remains largely untested, particularly across populations of the same species.

Several environmental cues and variables are known to influence the onset of spawning in tropical corals, including solar insolation, moonlight intensity, day length, and temperature (Hatta et al. 1999; Kaniewska et al. 2015; Paxton et al. 2016; Woesik et al. 2006). However, for temperate and intermediate-water species, where some of these cues may be absent or differ significantly, our understanding is limited, partially due to the challenges of studying these species at depth (but see Grinyó et al. 2018). In our study, coral colonies were maintained in both indoor and outdoor tank systems. The indoor system was kept at a stable temperature of 14–16 °C, while the outdoor system, although cooled, experienced temperature fluctuations exceeding 18 °C during the summer. Despite these differences, spawning occurred simultaneously in both systems during at least one of the major spawning events (September 12th-13th), suggesting that temperature is not the primary driver of spawning synchrony, although it may still influence gamete maturation. Interestingly, colonies collected in previous years and maintained for 1–2 reproductive cycles under different conditions at the ODL spawned during the same general period, though not on the exact same days. The natural seasonal temperature fluctuations and moon cycle (i.e., light intensity) were simulated within ODL's closed tank system to mirror in situ conditions as closely as possible based on available information, which supports the hypothesis that temperature plays an

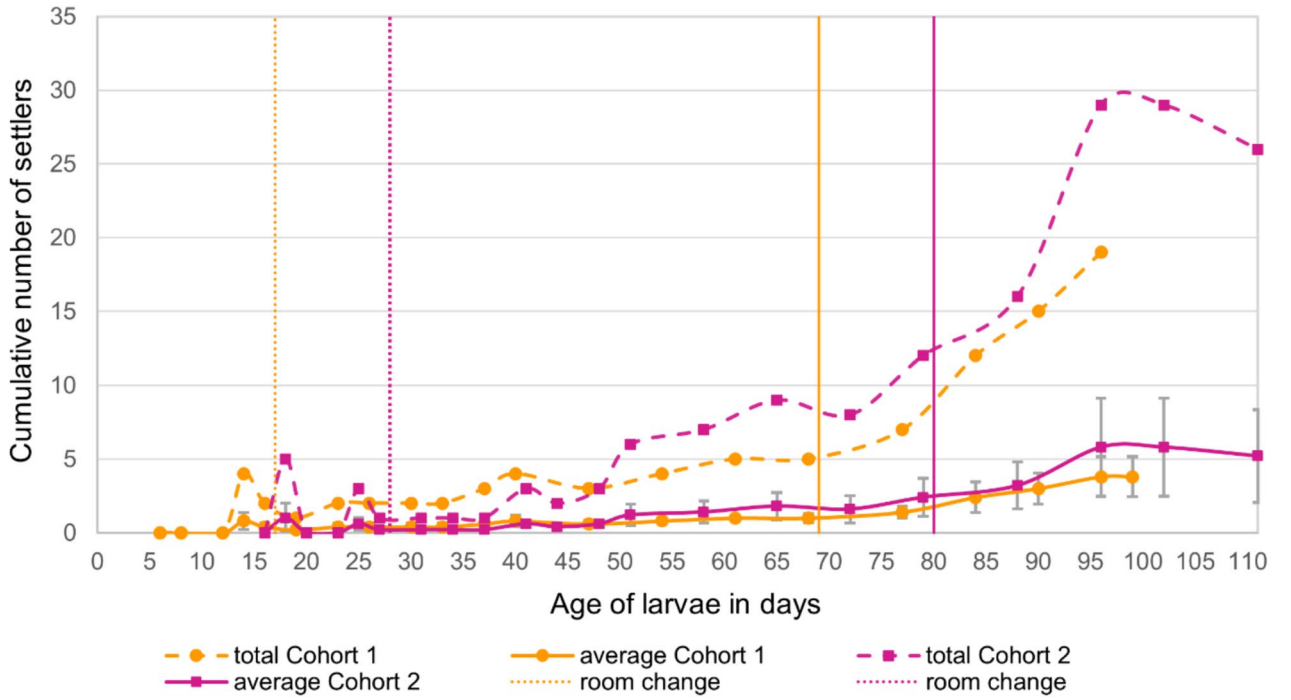

Fig. 7 Total and average n umber of settlers (±SE) of *Eunicella verrucosa* followed over time in Experiment 1 in two cohorts of larvae (n = 5 replicates of 50 larvae for each cohort): Cohort 1—spawning of October 11th, challenged with substrate at 6 days after spawning; Cohort 2 – spawning of 30th of September, provided with substrate at day 16. The data presented represent the cumulative number of settlers irrespective of the type of substrate on which larvae settled (see Methods). The vertical lines indicate the points in time when rooms were changed and substrates were replaced, respectively

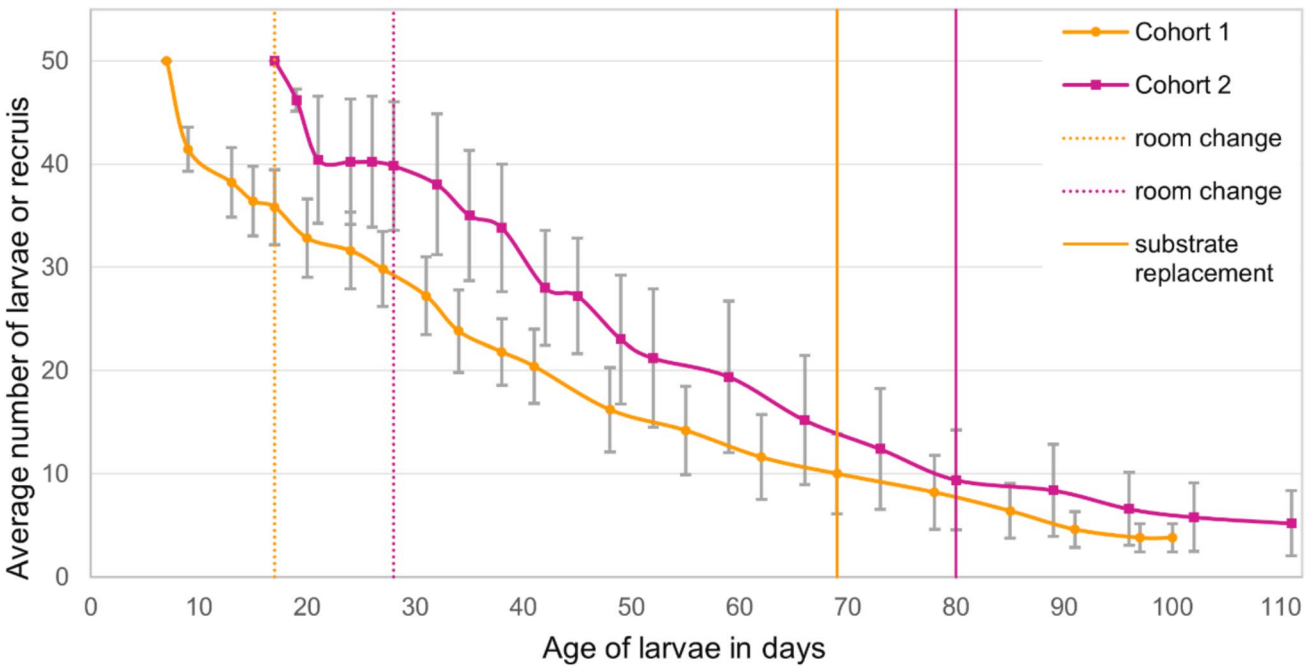

Fig. 8 Average (±SE) survival of larvae and recruitsof *Eunicella verrucosa* for the two cohorts followed in Experiment 1 (n = 5 replicates of 50 larvae for each cohort): Cohort 1—spawning of October 11th, challenged with substrate at 6 days; Cohort 2 – spawning of 30th of September, challenged with substrate at 16 days. The data presented represents the cumulative number of larvae and settlers irrespective of the type of substrate on which larvae settled (see Methods). The vertical lines indicate the points in time when rooms were changed and substrates were replaced, respectively

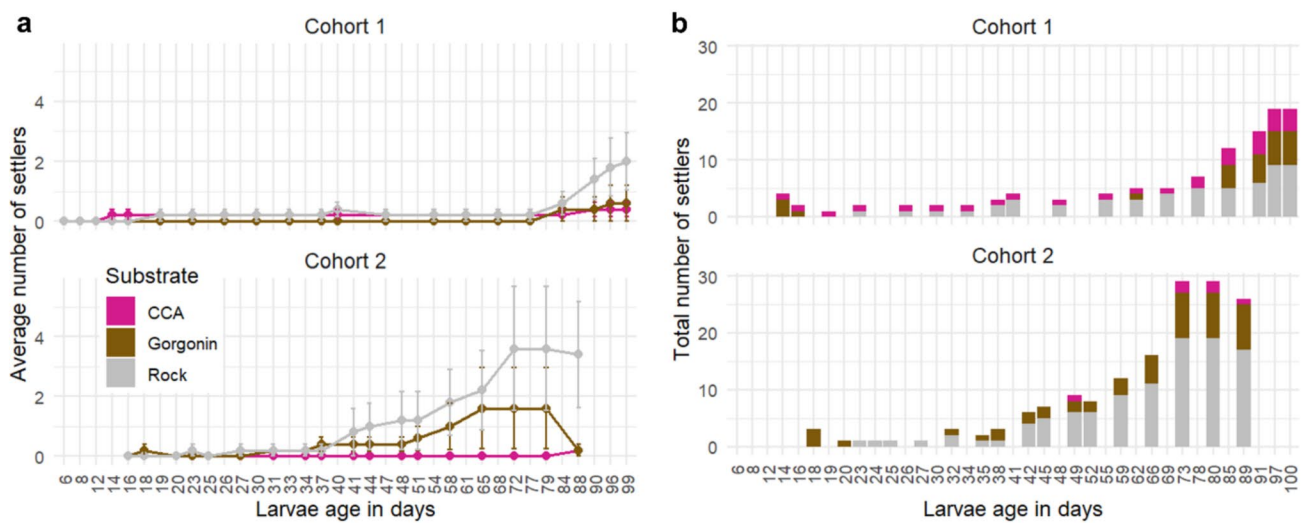

Fig. 9 Settlement preferences of *Eunicella verrucosa* larvae when provided with rock, crustose calcareous algae (CCA) and bare gorgonian skeleton of two cohorts of larvae: Cohort 1, challenged with substrate 6 days after spawning and Cohort 2, challenged with substrate 16 days after spawning. Panel **a** shows the average number of settlers (± SE) and panel **b** the total number of settlers on each substrate for the two cohorts followed in Experiment 1 (five replicates per cohort, n = 50 larvae)

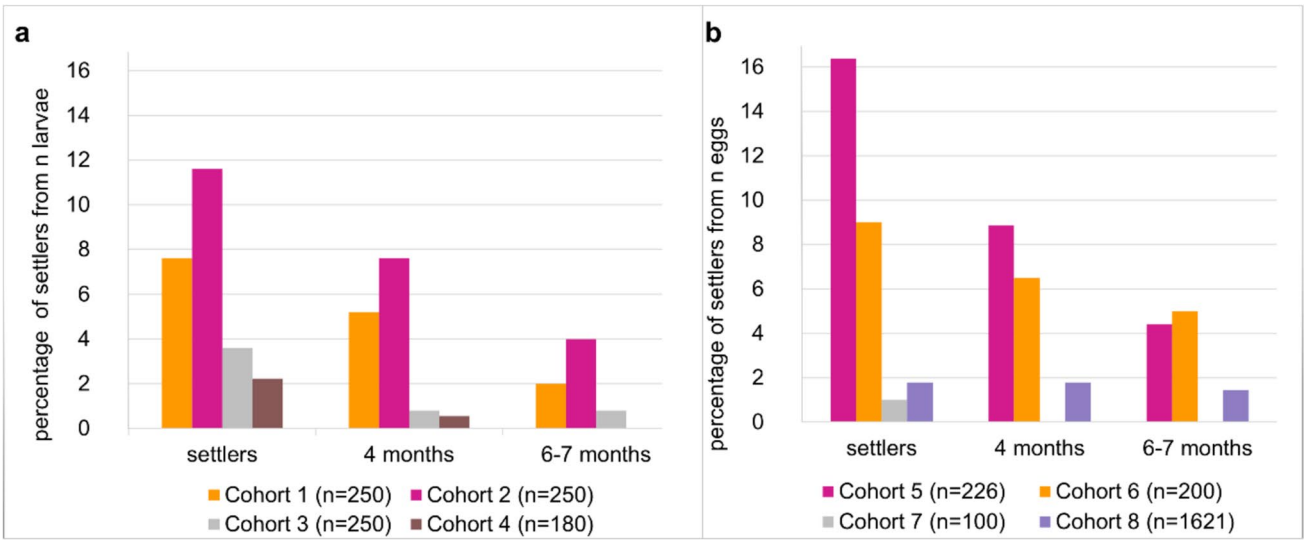

Fig. 10 Experiment 2: Total settlement success and recruit survivorship for multiple cohorts of *Eunicella verrucosa* fertilized oocytes (**a**) and larvae (**b**) over the period of 7 months post settlement. Panel **a** includes data of 4 cohorts of larvae followed at Centro de Ciências do Mar do Algarve (CCMAR), including Cohort 1 and 2 of Experiment 1 (see Material and Methods and Results). Panel **b** includes data of 3 cohorts of eggs followed at CCMAR (Cohort 5, 6 and 7), as well as one cohort of eggs (Cohort 8) from Oceanário de Lisboa (ODL) of *Eunicella verrucosa* over the period of 7 months post settlement

important role in regulating the annual gametogenic cycle of corals (Gori et al. 2007; Sakai et al. 2024). The incomplete synchronization of spawning time between colonies kept at CCMAR (two tank systems) and ODL likely results from fine-tuned responses of corals to other environmental conditions specific to each captivity system, as well as to inter-colony variability (Gilmour et al. 2016; Monfared et al. 2023).

The spawning period of *E. verrucosa* lasted several weeks, with minor egg releases occurring between large spawning events. At CCMAR, peak spawning occurred around the full and new moons, whereas at ODL, three spawning peaks were recorded, two of which occurred 6–7 days after the full moon. Similar extended spawning periods have been reported for other temperate and cold-water corals (Coma et al. 1995a; Waller et al. 2023;

Weinberg and Weinberg 1979). While the lunar cycle and likely moonlight are recognized as important environmental cues synchronizing spawning in many tropical broadcast spawners (Kaniewska et al. 2015; Randall et al. 2020; Sorek and Levy 2014), the reproductive patterns are more variable in many coral species. This variability suggests that the role of moon phases may not be as consistent and widespread, especially in temperate and cold-water corals (Villadrich 2022). Many cold-water corals live beyond the reach of moonlight, but *E. verrucosa* spans approximately 10–200 m in depth (Grasshoff 1992), including depths where moonlight remains detectable (Kaartvedt et al. 2019). At CCMAR, only outdoor tanks were exposed to natural moonlight, yet spawning occurred in both outdoor and indoor systems during full and new moons. At ODL, the timing of spawning events may have been influenced by artificial moonlight and, by extension, lunar cues, despite the absence of a consistent pattern in our data and the overall lack of detailed, long-term observations for most temperate gorgonians. More likely, spawning is governed by an endogenous biological clock shaped by a broader set of environmental factors. Differences in spawning timing between CCMAR and ODL may reflect colony condition, with freshly collected colonies used in experiments at CCMAR possibly more attuned to environmental cues than colonies held in captivity at ODL for 1–2 years.

Our observations confirm that *E. verrucosa* is a broadcast spawner, as previously suggested by Munro (2004). This contrasts with other species of the genus, such as *E. singularis* and *E. cavolini*, which are internal brooders (Ribes et al. 2007; Theodor 1967; Koch 1887; Weinberg and Weinberg 1979), further highlighting that reproductive mode is relatively plastic in corals (Kahng et al. 2011; Kerr et al. 2011). While broadcast spawning is the dominant reproductive strategy in shallow-water scleractinian corals, approximately half of the studied octocoral species are internal or surface brooders (Kahng et al. 2011). Fewer deep-water species, however, have been studied, making it difficult to identify broader patterns (Eckelbarger et al. 1998; Rakka et al. 2021, 2017; Sun et al. 2010, 2009, 2011; Waller 2005; Waller et al. 2023).

Embryonic development

Embryonic development in *E. verrucosa* showed several notable differences compared to other members of the genus. First, while zygote segmentation in closely related species, such as *E. singularis* is described as holoblastic (Weinberg and Weinberg 1979) where the zygotes cleave into two equal-sized blastomeres that then further divide into 4, 16, and so on until the gastrulation stage, we observed partial (meroblastic) cleavage in the majority of the *E. verrucosa* embryos. Most of the yolk remained in the original first cell and the cleavage process was incomplete, with blastomeres not fully separated by membranes (Brun-Usan and Salazar-Ciudad 2020). Most studies on coral embryonic development report holoblastic cleavage patterns (Brun-Usan and Salazar-Ciudad 2020; Linares et al. 2008; Okubo et al. 2013; Rakka et al. 2021), similar to what has been observed in *E. singularis*. However, it is not unusual for cleavage patterns to vary across closely related species, particularly among non-bilaterian invertebrates like cnidarians (Brun-Usan and Salazar-Ciudad 2020). Meroblastic cleavage is common in yolk-rich eggs and occurs because the dense yolk interferes with the cytoskeleton formation during cell division (Adamska et al. 2011; Martin 1997). Whether *E. verrucosa* exhibits this pattern due to high lipid content remains to be assessed but it may help explain the species' positive buoyancy and prolonged planktonic larval duration (PLD) observed in this study (Viladrich et al. 2021).

In other cnidarians, chaotic cleavage patterns and temporal syncytial stages—where random blastomeres fuse—have been observed, resulting in variability even among individuals of the same species (Brun-Usan and Salazar-Ciudad 2020). Such cleavage patterns may help explain our observations for *E. verrucosa* embryos, where partially cleaved embryos containing one large blastomere and four to five smaller ones, sometimes fused back into a single large cell before progressing to the final cleavage stage, producing 8 blastomeres. Between the 8- and 32-cell stages, cleavage became more organized. However, beyond the 32-cell stage, the embryos became asymmetric, with some blastomeres remaining very large while others were much smaller. These variations were consistent across multiple individuals. As cell sizes became more uniform and the embryos developed regular six-sided shapes, the embryos exhibited relatively deep and pronounced infoldings more closely resembling a tangle rather than the "raisin-like" formation that has been described in other tropical gorgonians (Lasker, personal communication, Lasker and Kim 1996; Tonra et al. 2021).

Larval development, behaviour and settlement

The eggs (300–400 µm in diameter) and larvae (500–750 µm in length, 250–350 µm in width) of *E. verrucosa* were larger than those of other temperate Mediterranean gorgonians, such as the surface-brooder *P. clavata* (eggs: 250–350 µm; larvae: 500–800 µm long but much thinner; Linares et al. (2008), yet smaller than the larvae of the internal brooder *E. singularis* (approximately 2500 µm long, 500 µm wide; Weinberg and Weinberg 1979). Although we did not quanitify propagule (oocyte and embryo) buoyancy or larval behaviour, preliminary qualitative observations are noteworthy. First, like many other broadcast spawning corals, *E. verrucosa* eggs were positively buoyant, remaining at the seawater surface for several hours. However, buoyancy

appeared to decrease as cleavage began, with embryos becoming negatively buoyant for up to three days until the onset of active larval swimming. This shift of buoyancy during embryogenesis has been documented in other species (e.g., Coelho and Lasker 2016a) and is likely due to lipid depletion during development (Figueiredo et al. 2012; Harii et al. 2007). Second, larvae of *E. verrucosa* consistently exhibited upward swimming during the first two weeks despite SEM images showing incomplete ciliation at this stage. As development progressed, larvae displayed more complex vertical swimming patterns and increased substrate probing. These behavioural changes, along with further development of flagellation, appeared important for acquiring competence to settle (though this remains untested).

Despite offering settlement substrate to larvae at two different points in time (Cohort 1, 7-day-old larvae *vs.* Cohort 2, 17-day-old larvae), both cohorts began substrate probing and settlement around a similar time frame at days 15 and 19, respectively (Fig. 7). While data on settlement dynamics in temperate and cold-water coral species remain sparse, particularly for broadcast spawners, such a prolonged delay in the onset of settlement competence has been previously documented in deep-sea and temperate octocorals (Rakka et al. 2021; Zelli et al. 2020). Estimating the onset of settlement competence under suboptimal ex situ conditions is challenging, and we cannot exclude that our estimate potentially overrates the pre-competency period duration in nature. However, our data appears remarkably consistent across two larval cohorts of the settlement experiments at CCMAR and an additional cohort of the separate system at ODL, suggesting that *E. verrucosa* has a delayed onset of settlement. Whether this is a common pattern in temperate and cold-water broadcast spawners, presumably due to a longer larval development period caused by low seawater temperature remains unknown.

One factor that determines behaviour and settlement of the larvae is the potential larval survival in the water under laboratory conditions, which can be quite long for some species. For example, *Corallium rubrum* larvae can survive for up to 42 days (Martínez-Quintana et al. 2015), *P. clavata* up to 64 days and *E. singularis* > 78 days (Guizien et al. 2020). Koch (1887) observed *E. cavolini* larvae remaining in the water column under water flow for months. In contrast to such previous studies on temperate and cold-water octocorals, our studies of *E. verrucosa* showed that, despite low overall settlement rates, larvae remained competent to settle for a relatively long period. Under laboratory conditions the PLD reached up to 110 days and settlement was observed up to 96 days. For example, larvae of the Mediterranean internal brooder *E. singularis* can settle within 13 days but survive up to 79 days (Theodor 1967; Weinberg and Weinberg 1979; Zelli et al. 2020), and *P. clavata* have been observed to metamorphose into polyps without attaching to the substrate between 8 and 25 days (Linares et al. 2008). For *E. verrucosa*, we only recorded the total number of settlers at each monitoring time point, without tracking individual recruits. As a result, settlement may have been underestimated if some settlers died and went undetected. Additionally, while aquarium conditions may tend to overestimate PLD (Sciascia et al. 2022) and should not be directly extrapolated to nature, our observations support the conclusion that *E. verrucosa* larvae remain in the water column for an extended period under optimized laboratory conditions (e.g., removal of predation and reduced exposure to environmental stressors). This finding aligns with the broadcast spawning reproductive strategy which generally results in longer PLDs compared to brooding species (Harrison and Wallace 1990). Moreover, the observed patterns of embryonic cleavage—indicating highly yolk-rich propagules—further supports our observations of a prolonged PLD with larvae competent to settle for up to 96 days.

Coral larval settlement is known to be influenced by various complex environmental and biological cues. These cues are not fully understood, yet, and knowledge is predominantly limited to tropical shallow-water coral species. These cues can be chemical or physical signals, with chemical compounds produced by crustose coralline algae (CCA) and/or associated microbial communities and biofilms. Such kinds of substrate have previously shown to induce settlement in multiple species of corals (Gómez-Lemos et al. 2018; Sneed et al. 2014; Tebben et al. 2015). We therefore selected substrates known to encourage settlement in temperate octocorals: gorgonian bare skeleton for *E. singularis* (Weinberg and Weinberg 1979), CCA covered rocks for *E. singularis and P. clavata* (Zelli et al. 2020) and rocks from the same area as the breeding stock used in our experiments. At CCMAR, however, no clear preference for any substrate was observed. Settlement was observed to shift with larval age, likely due to limited replication in the experimental setup and to overall low settlement rates (Fig. 9). At ODL settlement was even lower and only occurred on CCA encrusted rocks. Hierarchical settlement induction through certain cues has been assessed by several recent studies (Jorissen et al. 2021; Petersen et al. 2023; Wahab et al. 2023). Some CCA species may even provide positive microbial cues that initiate the settlement process, but later also deter attachment and metamorphosis, leading larvae to choose alternative substrates (Jorissen et al. 2021). Overall, *E. verrucosa* appeared not restricted to a particular type of substrate, settling on all types of substrates tested, except conditioned basaltic rocks at ODL. Since we did not test the substrates individually, we cannot exclude the potential influence of positive settlement cues across substrate types (e.g., like CCA bacteria settling on the other substrates), and future experiments are necessary to investigate this further.

Implications on larval dispersal and population connectivity

Incorporating population dynamics and connectivity patterns into marine conservation and restoration strategies, especially for sessile invertebrates like corals, is critical for effective biodiversity preservation (Jones et al. 2007; Marti-Puig et al. 2013; Possingham et al. 2015). The primary goal of coral restoration efforts is to rehabilitate degraded habitats into healthy, self-sustaining breeding populations, based on robust, scientifically grounded restoration frameworks. However, such frameworks are largely absent from most coral restoration projects (Boström-Einarsson et al. 2020; McDonald et al. 2016). For instance, dispersal potential and patterns of population connectivity are crucial considerations for conservation. Yet, key biological traits that influence larval dispersal, such as PLD, larval behaviour (e.g., buoyancy and swimming), and reproductive strategies (brooding vs. broadcast spawning), are often unknown or remain overlooked in restoration planning and implementation (Coelho and Lasker 2016b; Cowen et al. 2007; Cowen and Sponaugle 2009; Randall et al. 2020; Suggett and Oppen 2022). Our findings reveal that the PLD of *E. verrucosa* is exceptionally long as is the competency period, which started late (earliest at day 15). This suggests that coral larvae can disperse over large distances, which has important implications for population connectivity. For example, genetic studies focusing on *E.verrucosa* have detected significant genetic structure at the regional scale, suggesting that dispersal over 500–2000 km is infrequent, with regional clustering and a pattern of isolation by distance across the northeastern Atlantic and the Mediterranean Sea in this species (Holland et al. 2017; Macleod et al. 2024). Macleod et al. (2024) further modelled larval dispersal under two hypothetical PLDs (14 and 21 days), due to the absence of data for the species and to represent the central ranges of PLDs observed in other octocorals. These assumptions differ substantially from our laboratory observations. While the effective PLD of *E. verrucosa* in the field may be shorter than under laboratory conditions due to factors such as predation, exposure to environmental stressors and/or advection to unsuitable habitats (Sciascia et al. 2022), our findings suggest that settlement competency likely does not begin before 15 days post-fertilization and may extend up to three months. Consequently, the mean and maximum dispersal distances estimated by Macleod et al. (2024) likely underestimate both the true dispersal potential of *E. verrucosa* and the frequency of rare, long-distance dispersal events. These discrepancies underscore the limitations of generalizing species-specific biological traits in dispersal and connectivity models, which are increasingly used to guide marine conservation and management strategies.

First steps into restoration through sexual propagation

While data on reproductive and early-life ecology are crucial for better understanding biology and population dynamics of *E. verrucosa* and corals in general, this information is also the basis for our broader goal: developing methods and workflows for habitat restoration through sexual propagation. Below we provide a brief discussion of several key aspects.

Coral collection and rearing of parent colonies

Numerous approaches have been developed to obtain coral offspring from tropical scleractinian corals (see Randall et al. 2020 for an overview), but methods for octocorals, especially temperate or deep-water coral species remain limited (Fava et al. 2010; Montseny et al. 2021a). On-site collection is feasible only for species with predictable spawning times and those located at dive-accessible depths. Obtaining offspring from aquarium-kept corals collected as fisheries bycatch offers the advantage of accessing large biomass that would otherwise perish. This can result in a substantial spawning output and diverse genotypes, providing a good representation of the population (Montseny et al. 2021b). However, relying on destructive fishing techniques is unsustainable and should generally not be encouraged as the impact of such practices should be mitigated or eliminated.

The collection of parent corals from bycatch is opportunistic, dependent on the availability, timing, location, and depth of fishing activities, factors that are largely uncontrollable. Additionally, the condition of the colonies can vary, as they are often entangled and damaged in nets, experiencing high stress levels that may negatively affect reproductive output and gamete nutritional reserves. Nevertheless, we view coral bycatch as a valuable opportunity to establish a large-scale coral nursery that could be maintained for many years, ensuring a consistent annual supply of offspring. Although the corals at CCMAR were kept under less controlled lighting and temperature conditions, and other factors such as feeding with frozen food, several colonies produced eggs the following year, indicating the persistence of their gametogenic cycle despite the suboptimal conditions. In contrast, at the ODL, the breeding colonies were maintained over 1–2 years in a closed system with precise water quality management, high-quality food, and regulation of key environmental parameters such as moonlight and temperature. This resulted not only in the completion of the reproductive cycle but also in spawning, settlement, and the development of healthy recruits. This demonstrates the potential for *ex-situ* sexual reproduction of *E. verrucosa*, reducing the need to collect adult corals annually, an essential step in case of limited bycatch availability or depletion of wild populations due to anthropogenic or natural pressures.

Although propagule release and/or capture efficiency was higher at ODL (~5500 eggs from 15 colonies) than at CCMAR (~3000 eggs from 70 colonies), settlement success was considerably higher in the experiments conducted at CCMAR. This discrepancy may be attributed to less suitable substrates or less competent larvae obtained at ODL, possibly due to suboptimal maintenance conditions and insufficient energy reserves in the cultured colonies, as opposed to the fresh, wild-collected colonies used for the experiments conducted at CCMAR. This suggests that long-term captive maintenance may not be the most efficient restoration strategy, yet. Future studies should therefore focus on improving reproductive output, enhancing settlement success, and increasing recruit survival. This could be achieved by boosting nutrient input for parent colonies, providing adequate space for individuals, optimizing temperature control, and adjusting lighting. Such year-round measures to better replicate the natural environment can potentially improve both adult survival and offspring production. Meeting the nutritional needs of deep and cold-water corals remains a major challenge, given their dependence on external food sources. Although this has been the focus of several studies (Cocito et al. 2013; Gori et al. 2012; Rakka et al. 2021; Ribes et al. 1999), optimal feeding regimes have yet to be developed.

Reproduction, settlement and survival of recruits in captivity

The broadcast spawning of *E. verrucosa* and the extended release period offers significant advantages for restoration efforts. Broadcast spawning facilitates egg collection and rearing, whereas brooding species are more challenging in this regard (Randall et al. 2020). We collected spawn using air-driven suction traps positioned in the tanks, filters in the outflow, as well as manually by picking eggs with a pipette. Although all methods were similarly effective, pipetting was highly time-consuming, whereas part of the eggs or embryos collected in the filters were squeezed or damaged. Additionally, we were unable to quantify the number of eggs lost by wall adhesion or air bubbles. The choice of methods highly depends on the availability of human resources though filters and traps proved effective during spawning events where human presence was unavailable, e.g. during night-time. For many coral species, the limitation to one or a few annual spawning events is a major bottleneck (Randall et al. 2020). However, *E. verrucosa*'s prolonged spawning over more than a month offers greater flexibility. Investigating the drivers behind *E. verrucosa*'s spawning synchronicity could further enhance the predictability and management of spawn collection. However, this may require several more years of observation and experimenting.

During embryo and larval rearing, maintaining the larvae in large plastic containers (5–10 L) with gentle aeration appeared to result in good survival rates. We observed larval settlement of up to 16% (Fig. 10), which, although less than the much higher settlement rates reported for tropical corals (e.g., Jorissen et al. 2021; Tebben et al. 2015), represents a very promising outcome for these first settlement trials with this species. Settlement rates in temperate and deep-water corals are generally much lower in species studied up to date (but see Viladrich et al. 2022), and comparative analyses are challenging due to the overall lack of data on settlement dynamics (Linares et al. 2008; Rakka et al. 2021; Weinberg and Weinberg 1979). Studies like Zelli et al. (2020) highlight the great potential of exploring settlement cues in temperate and cold-water corals further. Larval settlement was a bottleneck in this study, but post-settlement survival of the recruits kept in captivity remained high over 6–7 months. This contrasts, for instance, with the near-zero survival of *P. clavata* recruits deployed in protective cages in the field (Linares et al. 2008), which highlights that comparative study of recruit survival in captivity and in the field is a critical missing research gap.

Eunicella verrucosa recruit growth, was slow, with ~2–3 mm length achieved in about 3 months and secondary polyps forming after 6.5–12 months. In contrast, *E. singularis* showed faster growth in laboratory studies, with budding observed after just two weeks (Weinberg and Weinberg 1979). Following the settlement experiments conducted at CCMAR, the recruits were not fed beyond what was provided to adult colonies (e.g., frozen rotifers, copepods). The feeding regime for recruits kept at ODL, which included living microalgae and zooplankton, seemed to enhance growth, with the first budding observed already 6.5 months after spawning (compared to 11–12 months after spawning or 9 months post-settlement at CCMAR). This underscores the importance of further research on optimal nourishment for recruits, as improved feeding has been shown to significantly boost early growth in tropical corals (Petersen et al. 2008; Toh et al. 2014). Substrate type also appeared to play a crucial role in recruit survival. Natural rock substrates generally proved to be suitable for settlement, particularly those with numerous crevices and holes. On the other hand, surface structures tended to accumulate debris, likely reducing recruit survival. Nearly all surviving recruits were found to grow on smooth, exposed surfaces free of debris obtaining adequate water flow for self-cleaning, emphasizing the importance of current-exposed, sediment-free surfaces for successful coral settlement and growth.

Conclusions

This study provides the first description of the spawning and early life ecology of the widely distributed, forest-forming, and vulnerable pink sea fan *E. verrucosa*. This

information is vital for managing, protecting, and restoring habitats dominated by this important structuring species, and it also provides key data for dispersal and connectivity models. Our findings reveal a relatively late onset of larval competency to settle, along with an extended period during which larvae remain competent to settle (up to three months). Our results on settlement and recruit survival also represent early progress toward obtaining sexually derived recruits for restoration. We demonstrate that larvae can successfully settle onto natural substrates, recruits survive and grow under laboratory conditions, and adult colonies can be maintained in captivity through multiple reproductive cycles, completing gamete development and spawning thereby enabling the production of sexually derived recruits ex situ.

This study also marks the first steps toward breeding of this vulnerable species, laying the groundwork for establishing coral nurseries for restoration. Working with such sensitive organisms poses significant challenges in planning, but our findings pave the way for broader research and restoration efforts. A key aspect of the study was the collaboration between a scientific research center (CCMAR) and a major public aquarium dedicated to promoting ocean literacy (ODL), highlighting the potential of such institutional collaborations as platforms for large-scale restoration initiatives.

Acknowledgements We thank Capucine Récasens and Laura Balsalobre for their help examining gamete development, particularly polyp dissections, and histological sectioning, as well as Elsa Couto and Deborah Power for technical and laboratory support with the histological examinations. We also thank João Reis and André Lopes for their technical support at the Ramalhete Marine Station. We are especially grateful to master Casimiro and his fishing crew for the collaboration and help collecting samples for this study along the Sagres region in SW Iberia.

Author contribution C.E. conducted the main research, wrote the main manuscript text, and prepared the figures. C.M. conducted the settlement experiments and supported the research B.M. supported the research activities A.E. supported the research and reviewed the manuscript R.M. supervised the SEM work and reviewed the manuscript E.S. carried out the studies at Oceanário do Lisboa M.F. carried out the studies at Oceanário do Lisboa N.B. carried out the studies at Oceanário do Lisboa E.S. supervised and secured funding for the study and reviewed the manuscript M.C. supervised the main research and reviewed the manuscript substantially.

Funding Open access funding provided by FCT|FCCN (b-on). Fundação para a Ciência e a Tecnologia (Doctoral Scholarship SFRH/BD/151455/2021, DivRestore/0013/2020, projects UIDB/04326/2020 and LA/P/0101/2020), BiodivRestore ERA-NET COFUND (GA N°101003777), Fundação Belmiro de Azevedo (CORALFORESTS 2022),

Data availability No datasets were generated or analysed during the current study.

Declarations

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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