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Coral restoration through the optimization of early life-stage dynamics: The case of the Mediterranean red coral (*Corallium rubrum*)

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ABSTRACT

The recovery of ecosystem-engineering taxa, such as corals, is a critical conservation priority for maintaining habitat complexity, biodiversity, and ecosystem functioning, and requires integrated strategies that combine conservation and active restoration. In coral restoration, sexual propagation techniques may support the recovery of depleted populations by overcoming early-life demographic bottlenecks. Here, we present the first successful method for rearing the temperate octocoral, *Corallium rubrum*, from larval release to the juvenile stage, combining *in-situ* and *ex-situ* experiments to examine larval settlement, post-settlement growth, survival, and spatial distribution, and identify optimal conditions. Settlement success was higher *ex-situ* (28 ± 11%) than in natural conditions (1.5–5.5%), suggesting the possible advantages of controlled environments during the corals' earliest developmental stages. However, recruits reared *in-situ* exhibited higher growth and survival (43% *in-situ versus* 16% *ex-situ* after two years). By integrating *ex-situ* settlement with subsequent *in-situ* maintenance, cumulative two-year recruitment success increased to 12 ± 4.7%, representing a substantial improvement over either method alone. These findings confirm that early demographic bottlenecks strongly influence coral recruitment dynamics and underscore the importance of controlling the recruitment environment to optimize early-life stages. Our findings represent a promising pathway for restoring Mediterranean coral populations by incorporating sexual propagation techniques into current transplantation protocols. We suggest the implementation of hybrid coral restoration strategies that integrate both sexual and asexual propagation. This approach could harness the high survivorship of transplanted adults together with the high recruitment potential generated through sexual propagation, hence accelerating population recovery and enhancing the resilience of restored coral assemblages.

1. Introduction

Protecting and restoring ecosystem-engineering organisms, such as corals, is crucial for maintaining habitat complexity, biodiversity, and ecosystem functioning (Cebrian et al., 2021). Urgent actions to protect corals and other ecosystem engineers are needed due to the cumulative impacts of historical and contemporary disturbances, which often exceed the natural resilience of many marine species. As a result, widespread ecosystem degradation and biodiversity loss have been documented across numerous marine systems, affecting their ecological integrity and threatening the human communities that rely on the benefits they provide (O'Leary et al., 2017; Aronson et al., 2020; Worm and Lotze, 2021). Ecosystem engineers' long-term persistence, therefore, requires integrated approaches, combining conservation, active restoration, and adaptive management, to halt further decline and promote the recovery and long-term resilience of marine ecosystems (Knowlton et al., 2021).

To address the decline of coral populations, restoration programs

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have traditionally relied on asexual propagation techniques, primarily transplantation. These involve collecting donor colonies that can be entirely transplanted or fragmented before transplantation (Rinkevich, 1995). On the other hand, sexual propagation techniques (also known as coral seeding, rearing, or breeding) offer an alternative approach to transplantation (Omori, 2019; Randall et al., 2020). These methods harness corals' natural capacity to produce vast numbers of larvae (Chamberland et al., 2017; Henry et al., 2021), enabling the production of large numbers of juveniles without harming donor populations and ensuring genetic recombination (Rinkevich, 1995; Banaszak et al., 2023).

However, using sexual reproduction for active restoration poses several challenges. Like many sessile marine organisms, corals face severe demographic bottlenecks during early life stages. Few larvae survive long enough to settle, constrained by dispersal, high predation pressure, and the limited availability of suitable substrates (Thorson, 1950; Wilson and Harrison, 2005; Penin et al., 2011; Edmunds et al., 2024). Even after settlement, recruits remain highly vulnerable to algal overgrowth, inter- or intra-specific competition for space, and grazing (Vermeij and Sandin, 2008; Ritson-Williams et al., 2009). Only individuals that grow beyond a critical size-escape threshold have a higher chance of survival (Doropoulos et al., 2012). Sexual restoration should therefore be accompanied by measures to mitigate early life stage bottlenecks by 1) promoting larval settlement, which involves reaching a suitable habitat, and 2) enhancing post-settlement survival. When combined effectively, these interventions can act as an ecological shortcut, accelerating coral recruitment by increasing the number of juveniles that reach the size-escape threshold and contribute to population recovery (Cruz and Harrison, 2017).

From an evolutionary perspective, when carried out within a population, sexual restoration maintains the adaptive potential of restored populations by assisting genetic recombination, whereas clonal transplantation does not (Baums, 2008; Baums et al., 2019; Miller et al., 2024). In any case, care must be taken with both methods in the population-genetics context in which they are carried out. Sexual restoration techniques have been widely applied in tropical environments, especially on broadcast spawner species. In these systems, coral gametes, embryos, or larvae can be sourced from natural spawn slicks (Doropoulos et al., 2019; Langley et al., 2024), collected *in-situ* with nets or spawning cradles (Suzuki et al., 2020; Miller et al., 2022), or produced *ex-situ* through controlled spawning events in aquaculture facilities (Severati et al., 2024; Ramsby et al., 2026a, 2026b). Coral seeding techniques differ greatly in cost and technical complexity, and they can range from simple, low-cost larval rearing in floating basins or pools (Miller et al., 2022; Harrison, 2024), to advanced aquaculture systems where inoculation with thermally tolerant symbionts (Nitschke et al., 2024), climate conditioning, and selective breeding (Van Oppen et al., 2015; Miller et al., 2024) can be performed. The choice of restoration strategy depends on multiple factors, including facility costs, accessibility of donor and recipient sites, regulatory constraints, species-specific ecology, and overall restoration objective (Randall et al., 2025). These factors determine whether to use *in-situ* or *ex-situ* breeding protocols. In practice, restoration programs often integrate both approaches, applying them either concurrently or sequentially. Optimizing their implementation and selecting the most context-appropriate option are integral components of the restoration decision framework, which may also incorporate complementary interventions such as adult transplantation.

Despite several advantages, sexual propagation techniques require more technology and facilities than asexual propagation ones. However, recent advances demonstrate that the core knowledge and protocols required for reliable larval rearing are now well established (Pollock et al., 2017; Banaszak et al., 2023, and references therein, Ramsby et al., 2026a, 2026b). The major remaining challenge lies in scaling up these approaches to address the vast extent of reef degradation, given current technical and financial constraints, making large-scale implementation a key priority for the future of coral restoration (Bayraktarov et al., 2016; Vardi et al., 2021; Nixon et al., 2025). In addition, although large-scale propagation techniques for broadcast-spawning corals have advanced considerably, progress with brooding gonochoric species remains limited. Because these corals release individual larvae rather than gamete bundles, conventional collection methods are ineffective, underscoring the need for novel methods (Banaszak et al., 2023).

In the Mediterranean Sea, research on coral restoration remains limited compared to the efforts made in the tropics (Boström-Einarsson et al., 2020; Fraschetti et al., 2021). Early transplantation experiments on Mediterranean corals date back almost five decades (Weinberg, 1979). However, the first publication explicitly addressing restoration appeared in the early 2000s (Linares et al., 2008a). Since then, related research interest has expanded in response to the urgent need for interventions to protect and restore degraded ecosystems and the increased attention of institutions toward restoration initiatives (*e.g.*, EU Restoration Law; UN Sustainable Development Goal 14 "Life below water", where restoration actions are explicitly mentioned in Target 14.2, Recuero Virto, 2018). Studies have primarily focused on transplantation techniques (*e.g.*, Linares et al., 2008a; Villechanoux et al., 2022), which have often been conducted through small-scale pilot projects designed to test restoration feasibility and outcomes (Musco et al., 2017; Roveta et al., 2023; Necci et al., 2025). Other approaches have included low-budget methods based on the use of fishery coral bycatch (Montseny et al., 2020; Casoli et al., 2022), artificial structures (Bramanti et al., 2007; Montseny et al., 2019), pruning techniques (Sanchez-Tocino et al., 2017), and larval enhancement (Villechanoux et al., 2022). However, large-scale restoration initiatives remain scarce (Montseny et al., 2020; Casoli et al., 2022; Manea et al., 2023), and only a few studies have explored coral sexual restoration (Terrón-Sigler, 2016; Villechanoux et al., 2022).

Among Mediterranean corals, several species have already suffered severe impacts from climate change, including mass mortality events associated with marine heatwaves (Garrabou et al., 2022; Bramanti et al., 2023). Many of these species have become candidates for restoration programs. However, one species stands out for its ecological and socio-economic value: the Mediterranean red coral, *Corallium rubrum* (Linnaeus, 1758). This octocoral is characterized by a calcified red skeleton, which has been highly prized in the jewelry market, making it one of the most valuable marine species worldwide (Tsounis et al., 2010). As a result, *C. rubrum* has faced centuries of intense exploitation, leading to the depletion of many shallow red coral populations (Tsounis et al., 2013). In addition to overexploitation, other anthropogenic pressures, such as climate change (*e.g.*, Bramanti et al., 2013; Prioux et al., 2023), have raised significant concerns about the risk of local extinctions. Furthermore, the slow growth rate of the species (radial growth: 0.2–0.3 mm yr^{-1}; Marschal et al., 2004; Gallmetzer et al., 2010; Bramanti et al., 2014) and its high levels of self-recruitment (Costantini et al., 2007b; Ledoux et al., 2010) pose substantial challenges for population recovery and the recolonization of depleted areas.

Conservation efforts, such as regulating fishing activities and establishing marine protected areas, are crucial for protecting this species (Linares et al., 2010; Cannas et al., 2019; Toma et al., 2022). Beyond these management measures, active restoration programs focused on increasing the local stock of *C. rubrum* may be an effective tool for addressing the risk of local extinction (Zentner et al., 2025). One of the first experimental transplantation projects for this species reported survival rates exceeding 90% four years after transplantation, confirming that, in favorable conditions, transplanted colonies can persist (Montero-Serra et al., 2018). Here, we emphasize the need to combine adult transplantation and sexual restoration techniques to overcome *C. rubrum*'s low recruitment success (Montero-Serra et al., 2015) and enhance the potential effectiveness of its restoration. However, the output of sexual restoration actions will primarily depend on the

capacity to optimize the survival, health, and growth of coral offspring throughout their early life stages (Hancock et al., 2021; Henry et al., 2021; Banaszak et al., 2023).

This research represents the first attempt to rear *C. rubrum* from larval release through settlement and subsequent juvenile survival, providing a foundation for developing a standardized rearing protocol to support the restoration of this species. Here, we present a detailed analysis of early settlement and post-settlement dynamics of *C. rubrum* under controlled (*ex-situ*) and natural (*in-situ*) conditions. Our objective is to identify the rearing conditions that optimize larval settlement, growth, and survival of newly settled individuals. In addition, we investigate post-settlement mortality by analyzing temporal changes in spatial distribution patterns to assess whether mortality events occur stochastically or are attributable to conspecific interactions.

2. Materials and methods

2.1. Experimental system for the in-situ study

To study the dynamics of *C. rubrum* settlement and recruitment under natural conditions, two systems of artificial caves were set up in the North-Western Mediterranean Sea, one deployed off the coast of Banyuls-sur-Mer, France, at a depth of 30 m, and the second located off the coast of Monaco at a depth of 40 m (Figs. 1, 2). Each system consists of a set of six artificial caves arranged on the vertices of a hexagon, formed by concrete cubes (1 m^3) with only one face open to the outside (Fig. 1E, F, Supplementary Materials 1). Each cave features a ceiling-mounted sliding system that allows easy insertion and removal of nine 20 cm × 20 cm tiles (Fig. 1B, C). *C. rubrum* colonies (*i.e.*, individual coral organisms) can be secured to the tiles using a Teflon screw fixed on an epoxy resin base attached to the base of the colony (Fig. 1A, B). This attachment system allows for easy movement of corals and rearrangement of demographic parameters within the caves, such as density and sex ratio. The availability of two parallel cave systems, one in Banyuls-sur-Mer and the other in Monaco, provided a unique opportunity to test multiple hypotheses simultaneously. Specifically, the cave system in Monaco was employed to evaluate *in-situ* settlement success, while in Banyuls-sur-Mer, larvae were first allowed to settle under controlled aquaria conditions (*ex-situ*) before being reimplanted in the caves or maintained in aquarium tanks. The Banyuls-sur-mer cave system was then used to compare growth and survival between *in-situ* (within the cave system) and *ex-situ* (in an aquarium) environments. Additional details on the experimental designs are provided below (Sections 2.2 and 2.3; Fig. 2 for a summary).

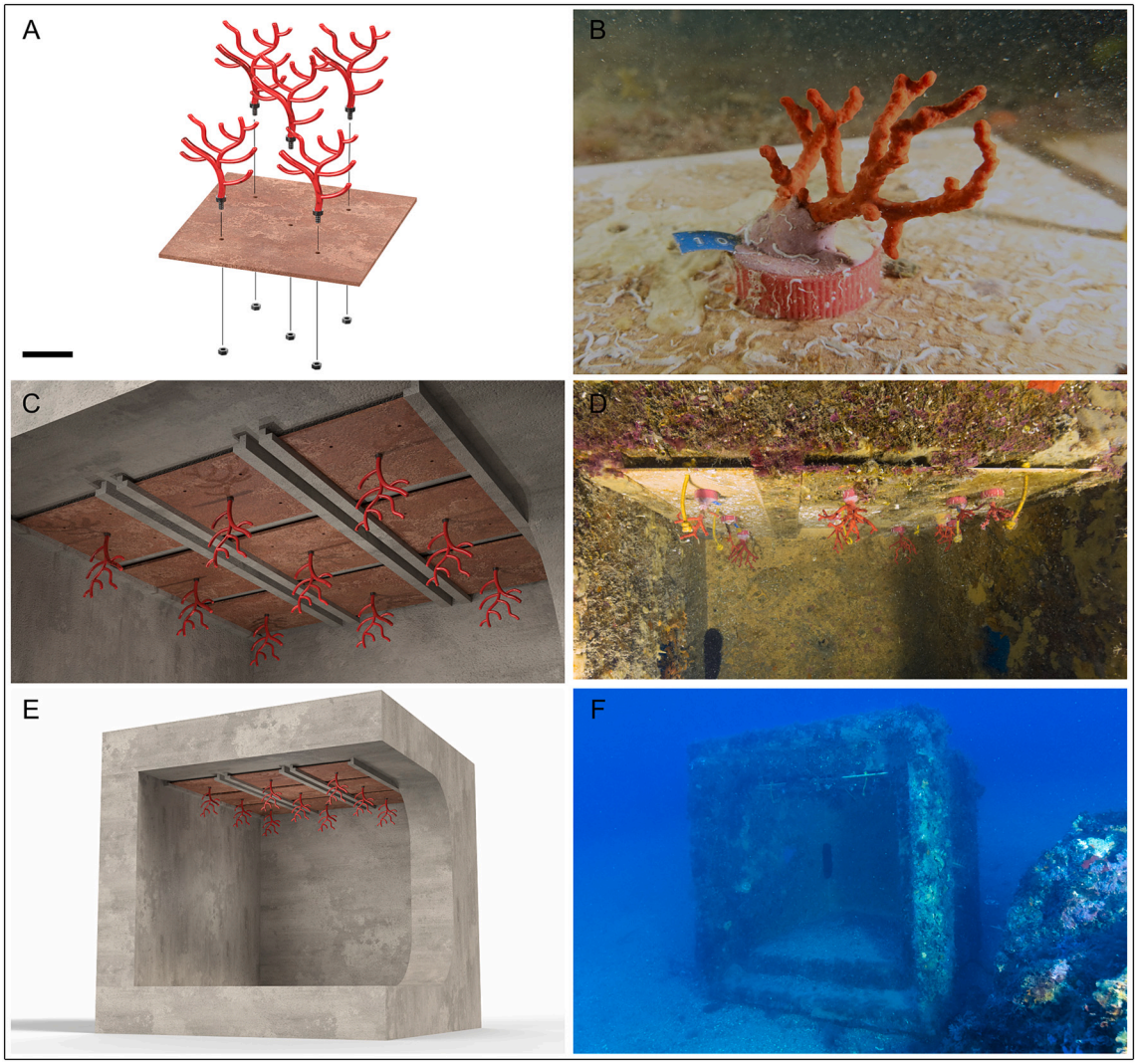

Fig. 1. Artificial submerged cave system. A–B: Method for attaching coral colonies to terracotta tiles thanks to the teflon skrew and i bulloni (scale bars: A = 5 cm, B = 1.25 cm). **C–D:** Sliding rail system used to secure and insert coral colonies, attached to the tiles, onto the cave ceiling (scale bars: C = 10 cm, D = 6 cm). **E–F:** Entire artificial cave module, which is part of a larger system of six caves (scale bars: E = 20 cm, F = 17 cm).

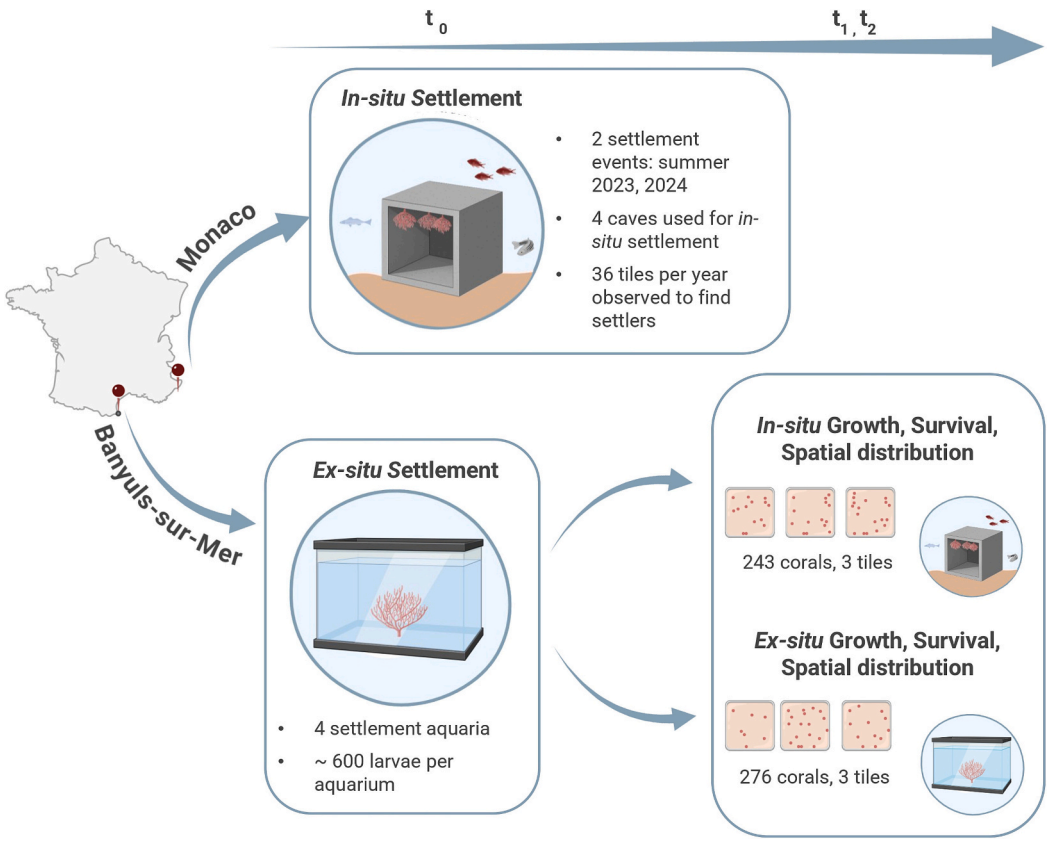

Fig. 2. Experimental design. The Monaco cave system was used to assess *in-situ* settlement success (t_0), while in Banyuls-sur-Mer, larvae were first allowed to settle *ex-situ* (t_0). The Banyuls-sur-Mer cave system was subsequently employed to compare coral growth, survival, and spatial distribution between *in-situ* (artificial caves) and *ex-situ* (aquarium) environments after 1 year (t_1) and 2 years (t_2) from settlement.

2.2. Settlement

Corallium rubrum is a brooding, gonochoric species that releases lecithotrophic larvae approximately between mid-July and the end of August (Santangelo et al., 2003). Even though red coral larvae have a high dispersal potential in open water (Martínez-Quintana et al., 2015), *C. rubrum* populations are characterized by a fine-scale spatial genetic structure, suggesting high larval retention around parental colonies (Costantini et al., 2007b; Ledoux et al., 2010). Here, we studied the settlement rate in both natural (*in-situ*) and controlled (*ex-situ*) conditions.

2.2.1. In-situ settlement

In-situ settlement was monitored during two reproductive seasons (summers 2023–2024) within the Monaco cave system. For the purposes of this study, four of the six caves composing the system were selected, resulting in a total of 36 settlement tiles used in the experiment. Sexually mature adults were attached to these tiles (20 cm × 20 cm) and positioned in the caves at densities ranging between 0.14 and 0.32 individuals dm^{-2}, depending on the cave. Tiles were retrieved the winter following the reproduction (January 2024–2025), and transported to the aquarium facilities in custom-designed containers, specifically engineered to minimize stress on young corals. Tiles were examined in the laboratory, where settlement success was calculated as the ratio of newly settled individuals to the estimated number of larvae released. Settlement was quantified based on the number of settlers recorded on the tiles. These values should be interpreted as conservative estimates of total settlement for two main reasons: (1) although larvae of this species exhibit upward swimming behavior (Martínez-Quintana et al., 2015; Costantini et al., 2018), some recruitment may have occurred on adjacent vertical surfaces; and (2) because observations were conducted in January (approximately four months after settlement), early post-settlement mortality occurring in this timeframe is overlooked. Larval production was estimated from colony fecundity and polyp abundance. Polyp abundance was obtained *via* three-dimensional reconstructions of the colonies used in the artificial cave system, following the protocol developed by Di Fabio et al. (2025). Fecundity values were derived from literature (Santangelo et al., 2003; Priori et al., 2013). Furthermore, settlement density, a parameter previously used to study recruitment rates in natural conditions (Bramanti et al., 2005; Santangelo et al., 2012; Benedetti et al., 2023), was calculated as the total number of recruits per tile divided by the tile's surface area.

2.2.2. Ex-situ settlement

Ex-situ settlement was assessed in the Banyuls-sur-mer aquarium facilities. *C. rubrum* settlers were obtained in controlled conditions in the summer of 2022 from larvae released by a large *C. rubrum* female colony (see Tignat-Perrier et al., 2025 for details). From the end of July to the beginning of August, larvae were collected daily and placed in four semi-closed-circuit aquaria equipped with an air bubbling system, maintained at a constant temperature of 16–18 °C. Approximately 600 larvae were put in each aquarium (600 in aquaria 1 and 2, and 550 in aquaria 3 and 4). Two terracotta tiles (20 cm × 20 cm), previously conditioned for 1 month in open-circuit aquaria to allow the development of a biofilm, were placed in each aquarium and used as settlement substrates. Tiles were mounted on supports, thereby exposing both upper and lower sides as potential settlement surfaces for larvae.

Although adult *C. rubrum* feeds on zooplankton and suspended organic matter (Tsounis et al., 2006), the diet of newly settled individuals remains poorly understood. Personal observations indicated that the food typically offered to adult colonies (*e.g.*, *Artemia salina* nauplii) is not ingested by new settlers, likely because of the small size of

Fig. 3. Different life stages of *C. rubrum* colonies. A: 1-month settler (scale bar 0.6 mm). **B:** 1-year-old recruit (scale bar 0.6 mm). **C:** 2-year-old juvenile (scale bar 1.7 mm). **D**: adult colony (scale bar 1.5 cm).

their polyps. For this reason, settlers were maintained in flow-through tanks supplied with 200 μm–filtered seawater from Banyuls-sur-mer Bay, to provide organic matter and suspended particles of a size compatible with the incompletely developed tentacles of newly metamorphosed polyps.

To minimize handling stress, settlers' counts were performed one month after settlement (October 2022). Each settler was uniquely identified and mapped (see section 2.3.3 for details), and settlement success was calculated as the ratio between the number of settled individuals observed in October 2022 (including those settled outside the tiles, such as on aquarium walls) and the total number of larvae placed in the tanks. As stated in the previous section, this represents a conservative estimate of settlement success, as it does not account for very early mortality occurring during the first month after settlement. Settlement density was calculated as previously described.

2.3. Growth, survival, and spatial distribution

To test the effect of rearing conditions (*in-situ vs. ex-situ)* on the survival, growth and spatial distribution of young *C. rubrum* colonies (*i.e.*, recruits and juveniles), the same pool of *ex-situ* settlers was divided in two groups: half of them (three tiles) were reared *in-situ* (*i.e.*, artificial caves system in Banyuls-sur-mer) and the other half (three tiles) were reared *ex-situ* (*i.e.*, in Banyuls-sur-mer aquarium). Recruits reared *in-situ* were transported from the aquaria to the caves immediately after being counted and measured in October 2022. Recruits reared *ex-situ* were kept in open circuit aquarium maintained at 16–18 °C. These aquaria were supplied with seawater pumped from a depth of 14 m in Banyuls-sur-mer Bay and filtered through a 200 μm filter. Light conditions simulated the seasonal variations in daily irradiance at 25 m (daily irradiance of 3 μmol photons m^{-2} s^{-1} under a cycle of 10-h light-14-h dark; Manea et al., 2025). When fully developed tentacles appeared (approximately 1 months after settlement), the individuals in aquaria were fed daily with rotifers (≃ 3800 rotifers l^{-1}) and twice a week with *Artemia salina* nauplii (≃ 1700 l^{-1}). The rearing experiment lasted two years, during which survival and growth were recorded at t_0 (one month), t_1 (one year), and t_2 (two years) after larval settlement (Fig. 2B). To assess these parameters (*i.e.* growth survival and spatial distribution), tiles were temporarily removed from *in-situ* in late September (t_1: September 2023, t_2: september 2024), transported to the laboratory for measurement, and then reinstalled *in-situ* within two weeks (t_1: early October 2023, t_2: early October 2024. A summary of the timing of all measurements is provided in the Supplementary Materials 2, Table S1). Following Benedetti et al. (2023), corals were classified as settlers (< year old settlers, t_0, Fig. 3A), recruits (one-year-old colonies, t_1, Fig. 3B), and juveniles (two-year-old, non-reproductive colonies, t_2, Fig. 3C). Colonies reaching sexual maturity (> six years old) were classified as adults (Gallmetzer et al., 2010; Fig. 3D).

2.3.1. Survival

The 1-year and 2-year survival rates were assessed by calculating the proportion of surviving individuals at t_1 and t_2, respectively, relative to the number of corals present at t_0 for each treatment (*in-situ vs. ex-situ*). Coral recruits were considered dead if they were absent from the map at t_1 or t_2. Survival was analyzed using a generalized linear mixed model (GLMM) with binomial distribution (lme4 package, Bates et al., 2015, R version 4.5.1). The model included *treatment*, *time*, and their interaction as fixed effects, while individuals (id) were considered as random effects to account for repeated measures. Model assumptions were assessed using simulated residuals (DHARMa package, Hartig, 2026, R version 4.5.1). Residual diagnostics indicated no evidence of overdispersion, zero-inflation, or deviations from uniformity, suggesting an adequate model fit. Visual inspection of residual patterns did not reveal systematic deviations from model assumptions. *Post hoc* pairwise comparisons were conducted using estimated marginal means with Tukey adjustment for multiple comparisons (emmeans package, Lenth, 2016, R version 4.5.1).

2.3.2. Growth

Basal diameter was used as the primary descriptor of *C. rubrum* growth during the first two years of life (Bramanti et al., 2005; Costantini et al., 2018). Diameter was measured from planar images captured with a MikroCam II (20 MP) mounted on an Olympus SZ61 stereomicroscope (2× magnification). The mean diameter was determined by averaging the minimum and maximum measurements, and annual growth was calculated as the difference in mean diameter between two years. Because *C. rubrum* recruits grow two-dimensionally for about two years before developing a calcareous axial skeleton (Giordano et al., 2023; Kahramanoğulları et al., 2022), height was measured only in two-year-old individuals using photogrammetry (Di Fabio et al., 2025). To evaluate the influence of rearing conditions on recruits' growth (*treatment: in-situ VS ex-situ*), diameter measurements taken at multiple time points were analyzed using a linear mixed-effects model (LMM) fitted on transformed data (sqrt transformation; lme4 and lmerTest packages; Bates et al., 2015; Kuznetsova et al., 2017; R version 4.5.1). *Time* and *treatment* (with an interaction term) were included as fixed effects in the model. Individuals (id) were considered as random effects, to account for repeated measurements over time. Model assumptions were assessed by visual inspection of residual plots and by a Levene test, which indicated no major deviations from homoscedasticity or normality. Statistical significance of fixed effects (*time* and *treatment*) was assessed using ANOVA on the fitted LMM, and pairwise comparisons for significant interactions were conducted using estimated marginal means (*emmeans* package, *pairs* function; Lenth, 2016). Chimeras—colonies formed by the fusion of genetically distinct larvae (Giordano and Bramanti, 2021)—were excluded from growth analyses to prevent bias in growth rate estimates (for further information on the incidence of chimerism look at Supplementary materials 2).

2.3.3. Spatial distribution

The position of settlers was mapped on each tile to obtain their spatial coordinates and describe their spatial distribution patterns. Planar images of each tile were processed in ImageJ, cropped, rotated to align axes at 90°, and calibrated using the 20 cm tile width. The origin (x = 0, y = 0) was set at the bottom-left corner. This preprocessing procedure enabled assigning spatial coordinates (x, y) to each settled individual. For spatial distribution analyses, chimeric corals were considered single individuals. Spatial distribution was initially analyzed by evaluating changes in Nearest Neighbor Distance (*i.e.*, the shortest distance between a coral and its closest neighboring) over the two-year period. To further assess patterns of clustering or regularity across multiple scales, we employed Ripley's K-function (Ripley, 1976) using the *spatstat* package in R (Baddeley et al., 2015). Edge effects were corrected using the isotropic correction ("best" option in *Kest*), and significance was tested *via* 99 Monte Carlo simulations under complete spatial randomness (CSR). Analyses were performed at settlement (t_0) and at 1- and 2- years (t_1, t_2).

3. Results

3.1. Settlement

3.1.1. In-situ settlement

In the *in-situ* experiment, the total number of settlers was 179 in 2023 and 621 in 2024. The total number of larvae produced within the caves ranged between 11,350 and 11,897 (estimated on the basis of fecundity values reported Priori et al., 2013 and Santangelo et al., 2003, respectively), resulting in a settlement success comprised between 1.5% and 1.6% in 2023, and 5.2% and 5.5% in 2024. Settlers' density on tiles ranged from 0 to 10.5 settlers dm^{-2} in 2023 (mean ± SE: 1.3 ± 0.6 settlers dm^{-2}), and from 0 to 22.5 settlers dm^{-2} in 2024 (mean ± SE: 4.4 ± 1.5 settlers dm^{-2}, Table 1 for a summary).

Table 1
Summary table of *in-situ* settlement success.

Year	N° larvae	Settlement success	Settlers' density (col dm^{-2})	Adults' density (col dm^{-2})
2023	11,350-11,897	1.5% - 1.6%	0–10.3 1.24 ± 0.63 (mean ± SE)	0.14–0.32 0.20 ± 0.04 (mean ± SE)
2024	11,350-11,897	5.2% - 5.5%	0–22 4.33 ± 1.44 (mean ± SE)	0.14–0.32 0.20 ± 0.04 (mean ± SE)

3.1.2. Ex-situ settlement

In the *ex-situ* experiment, settlement success was higher than in the *in-situ* experiment, with 637 of the 2300 larvae placed in the aquaria that settled and metamorphosed into primary polyps (28%). Most larvae settled on the tiles (556; 87%), while the remaining settled on the aquarium tank walls (13%). However, settlement success was highly variable across the four replicated aquaria, ranging from 53% to 1%. On average, settlement success was 28 ± 11% (Mean ± SE; Table 2). For larvae settled on tiles, a clear preference for the lower side was observed (508 settlers, 91%). Settlers' density on tiles was highly variable, ranging from 0 to 53.3 settlers dm^{-2} with an average settler density of 9.13 ± 4.06 settlers dm^{-2} (Mean ± SE; Table 2).

3.2. Survival

Overall survival of *C. rubrum* colonies after 2 years was 16% and 43% for *ex-situ* and *in-situ* conditions, respectively. In particular, the survival rates of corals grown *in-situ* and *ex-situ* were, respectively, 63% and 43% between t_0 and t_1, and 68% and 38% between t_1 and t_2 (Table 3).

Overall survival was significantly affected by treatment, time, and their interaction (Supplementary Materials 2, Table S2). In general, it differed between treatments, decreased over time, and showed a treatment-dependent temporal pattern. *Post hoc* comparisons confirmed that survival at t_1 was significantly higher than at t_2 within both treatments ($p < 0.0001$). At t_1, *in-situ* survival was significantly higher than aquarium survival ($p = 0.012$), and at t_2 the difference between treatments was even stronger, with survival remaining significantly lower in aquarium conditions compared to *in-situ* ($p = 0.0018$). Overall, these results indicate a general decline in survival over time, with consistently higher survival under *in situ* conditions and a treatment-dependent temporal dynamic.

Table 2
Summary table of settlement success for each aquarium. The number of settlers per aquarium is divided by tiles and orientation (upper side, US, or lower side, LS). Accidental recruitment that occurred elsewhere in the tank is indicated as other settlers.

Tank	N° larvae	Tile ID	Settlers LS	Settlement density (col dm^{-2})		Other settlers	Settlement success
				US	LS		
1	600	3	78	0.5	19.5	22	53%
		1	213	0.8	53.3		
2	600	2	173	0	43.3	15	38%
		5	22	4.2	5.5		
3	550	6	5	1.8	1.3	39	20%
		4	16	11.3	4		
4	550	7	1	0	0.3	5	1%
		8	0	0.5	0		

Table 3
Survival rates (%) of corals grown in *in-situ* and *ex-situ* conditions, first year (t_0-t_1), second year (t_1-t_2).

Survival	*In-situ*	*Ex-situ*
1st year	63 %	43 %
2nd year	68 %	38 %

3.3. Growth

When reared *ex-situ*, the mean diameter (mean ± SD) was 0.79 ± 0.19 mm, 1.38 ± 0.66 mm, and 2.19 ± 0.75 mm for settlers (t_0), recruits (t_1), and juveniles (t_2), respectively (Supplementary Materials 2, Table S2). In contrast, when reared *in-situ*, the mean diameter was statistically higher at t_1 and t_2, reaching 0.83 ± 0.18 mm, 2.06 ± 0.83 mm, and 2.91 ± 1.34 mm for settlers (t_0), recruits (t_1), and juveniles (t_2), respectively (Supplementary Materials 2, Table S2). Despite that *C. rubrum* growth rate was highly variable during the first two years after settlement, settlers kept in aquaria showed consistently lower growth rates of 0.51 ± 0.54 mm yr^{-1} (mean ± SD) for the first year, and 0.34 ± 0.46 mm y^{-1} (mean ± SD) for the second year, than settlers kept in natural conditions with average growth rate of 1.21 ± 0.75 mm yr^{-1} (mean ± SD) for the first year and 0.5 ± 1 mm yr^{-1} (mean ± SD) for the second year.

According to the linear mixed-effects model, Time ($F = 350.9$, $p < 0.001$), Treatment ($F = 9$, $p = 0.003$), and their interaction ($F = 14.9$, $p < 0.001$) had a significant effect on the mean diameter of *C. rubrum* recruits (Supplementary Materials 2, Table S3). Post-hoc pairwise comparisons (*time: treatment*) revealed that at t_0, as expected, there was no significant difference between the diameter of corals reared *in-situ* and *ex-situ*, while an increase with time across all sampling intervals was measured ($t_2 > t_1 > t_0$), both *in-situ* and *ex-situ*. Furthermore, the mean diameter was higher *in-situ* than *ex-situ*, both at t_1 and t_2 (Fig. 4). Of the 184 settlers that survived to the second year (t_2), 22 developed a three-dimensional structure (>2 mm height) suitable for 3D morphometric analysis, 17 of which (77%) grew *in-situ*. Colony heights ranged from 2.00 to 5.15 mm, with a mean of 2.98 ± 0.93 mm (SD).

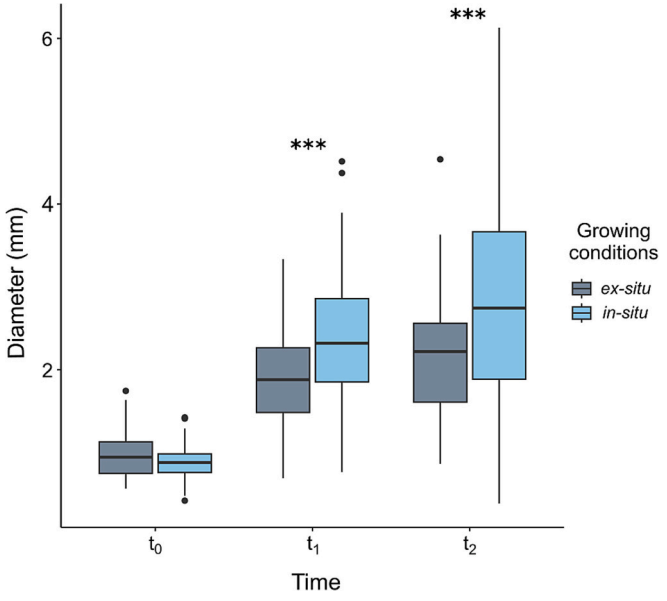

Fig. 4. Boxplot representing *C. rubrum* diameter across time (settlement: t_0; one year, t_1: two years, t_2) for the different treatments (*in-situ* and *ex-situ*). Significant differences between recruits' size due to the effect of treatment over time are reported based on a linear mixed-effects model.

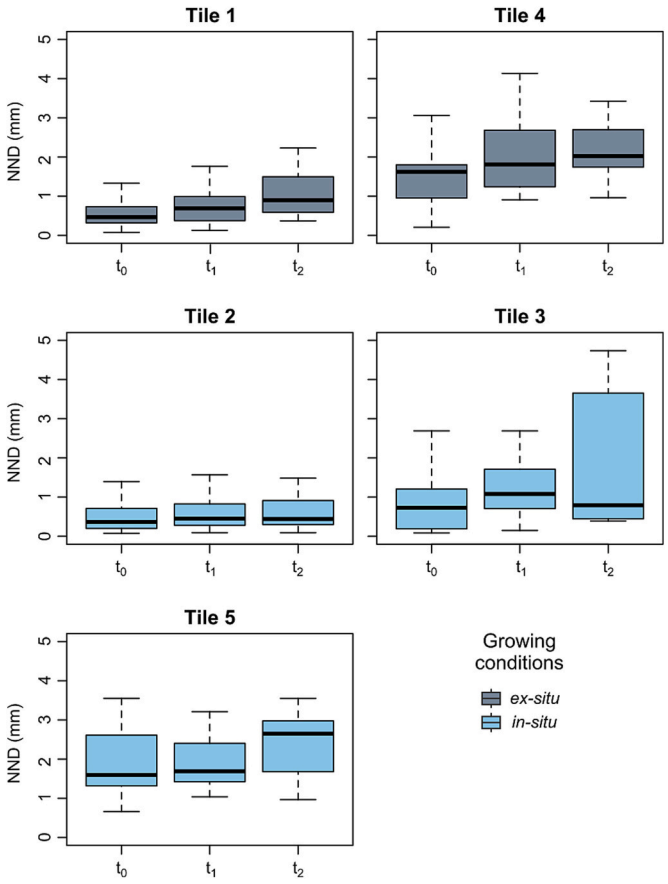

Fig. 5. Temporal changes in nearest neighbor distances (NND) of coral recruits over the 2 years of study in the 5 tiles studied.

3.4. Spatial distribution

During the two-year experiment, nearest-neighbor distances (NND) increased in all tiles, regardless of rearing condition (Fig. 5; Supplementary Materials 2, Table S5). Spatial distribution also varied over time; however, patterns were not consistent across tiles and were not correlated with treatment (Supplementary Materials 2, Fig. S1). At t_0 and t_1, corals on tiles 1 (*ex-situ*), 2 (*in-situ*), and 3 (*in-situ*) exhibited an aggregated spatial distribution, whereas those on tiles 4 (*ex-situ*) and 5 (*in-situ*) displayed a random distribution. At t_2, some distributional changes occurred. Juveniles on tile 1 exhibited a random distribution at small spatial scales but an aggregated distribution at larger scales. The aggregated pattern on tile 2 persisted. Juveniles on tiles 3, 4, and 5 appeared randomly distributed (see Supplementary Materials 2, Table S5, Fig. S1).

4. Discussion

This study presents the first successful rearing of the brooding temperate coral *C. rubrum* from larval release to the juvenile stage under both natural and controlled conditions.

In natural benthic populations, larvae face a severe survivorship bottleneck following settlement, with mortality often reaching 90–99% (*e.g.*, Gosselin and Qian, 1997; Lasker et al., 1998). To date, the early-life stages of *C. rubrum* have been studied almost exclusively under natural conditions, typically through one-year experiments using settlement plates deployed during the reproductive season (Bramanti et al., 2005; Costantini et al., 2018). This approach provides only indirect information, since direct quantification of larval production in the wild is nearly impossible. Although conservative due to the lack of information about

very early post-settlement mortality, this study provides a direct estimate of settlement success by combining aquarium experiments under controlled conditions, in which larval supply and settlement can be precisely quantified, with *in-situ* observations, in which knowledge of colony number and morphology within artificial caves enabled the assessment of larval production.

Previous research have shown that *C. rubrum in-situ* recruitment rate can be highly variable across space and time, ranging from complete absence of recruits (*e.g.*, Benedetti et al., 2023) to 12.3 ± 6.1 recruits dm^{-2} (Bramanti et al., 2005). Our results showed higher settlement success under aquarium conditions, among the highest values reported to date (see Benedetti et al., 2023 for a synthesis). These findings confirm that the removal of factors known to alter settlement success, such as dispersal by flow to unsuitable habitat (Scheltema, 1986), space limitation (Benedetti et al., 2023), predation (Vermeij and Sandin, 2008; Banaszak et al., 2023), and adverse environmental conditions (Rossi et al., 2012; Ricardo et al., 2017), can improve the settlement success of *C. rubrum*. Consistent with previous observations (Costantini et al., 2018), larvae preferentially settled on the underside of tiles. This settlement pattern is consistent with the up-ward swimming behavior of *C. rubrum* larvae (Martínez-Quintana et al., 2015) and explains the presence of *C. rubrum* colonies on the top of caves and crevices (Cau et al., 2016).

Even if *in-situ* settlement was lower than *ex-situ*, it was still comparable to, or in some cases higher than, the settlement observed in natural populations (ranging from 0.56 ± 0.21 to 6.06 ± 1.75 settlers dm^{-2}, Benedetti et al., 2023, and reference therein). This result validates the design of the artificial caves that was conceived to enhance larval retention by reducing flow speed and trapping recirculation within the cavity (Nowell and Jumars, 1984).

Although settlement success was higher under aquarium conditions, this result should be interpreted with caution. A direct comparison between *in-situ* and *ex-situ* treatments is complicated by methodological differences between the two systems, including the timing of settlement assessments and the fact that larval production could be directly quantified *ex-situ* but only estimated *in-situ*. While the observed patterns suggest higher settlement success under controlled aquarium conditions, the magnitude of this difference should not be overstated. Nevertheless, the *in-situ* approach yielded a substantially higher number of recruits and demonstrated its effectiveness as a strategy for generating propagules for restoration purposes.

Furthermore, although settlement success was higher under aquarium conditions, our results showed that corals grown *in-situ* exhibited higher survival and growth rates over the two years of monitoring. Our results are consistent with those of previous studies, which reported *in-situ* growth rates between 0.59 and 0.88 mm y^{-1}, and variable mortality (29–80%) during the first two years of life (Bramanti et al., 2005; Santangelo et al., 2012). Higher *in-situ* post-settlement survival indicates that established juveniles benefit from both biotic and abiotic environmental factors that are difficult to replicate in artificial systems. Although *ex-situ* settlement can be enhanced, it remains a suboptimal solution for supporting long-term survival and growth. Nutritional limitations are particularly critical for early settlers, which cannot exploit the prey accessible to adult colonies (Tsounis et al., 2006). This emphasizes the need for age-specific feeding strategies to ensure effective maintenance, prevent overfeeding, and maintain water quality in cultivation systems (Conlan et al., 2017; Geertsma et al., 2022). Optimized feeding (including live prey such as brine shrimp, rotifers, and microalgae) has been shown to enhance tissue and skeletal growth in tropical scleractinian corals (Ferrier-Pagès et al., 2003; Dixon et al., 2025), improving their survival both before and after transplantation (Toh et al., 2014). Today, beneficial microorganisms (Knowlton and Rohwer, 2003; Blackall et al., 2015) are known for their role in supporting coral health and resilience by supplying nutrients, reducing stress, and controlling pathogens. Furthermore, they may play a role in coral's early life stages, facilitating its development (Peixoto et al., 2021). Importantly, the higher survival observed in natural conditions suggests that sexually produced colonies can be successfully reared in semi-controlled systems that optimize settlement while preserving ecological realism (*i.e.*, natural growing conditions). This represents a critical step toward the incorporation of sexual restoration into active management.

Spatial analyses showed that larvae initially settled following a clustered pattern characterized by high local densities and short nearest-neighbor distances. The high settlement success in aquaria likely reflects the positive effect of larval density on coral recruitment (Suzuki et al., 2012), which similarly explains the aggregated distribution patterns observed on most tiles (Vermeij and Sandin, 2008; Doropoulos et al., 2017). This distribution shifted through time toward a random distribution, with an increase of the mean nearest-neighbor distances, suggesting the presence of density-dependent mortality mechanisms (*i.e.*, self-thinning; Yoda, 1963) which are known for corals (Edmunds et al., 2019; Nelson and Bramanti, 2020) and were previously hypothesized and observed for *C. rubrum* and other Mediterranean benthic suspension feeders (Linares et al., 2008b; Bramanti et al., 2009; Rossi et al., 2012; Cau et al., 2016). These findings confirm that post-settlement processes represent an important demographic bottleneck in *C. rubrum* and that restoration programs must specifically target this vulnerable phase. Although the natural tendency of larvae to settle in aggregated clusters is difficult to control, its negative consequences in active restoration, such as intense intraspecific competition and density-dependent mortality due to self-thinning, may be mitigated by deploying a larger number of smaller, spatially separated settlement substrates. This modular approach should enhance post-settlement survival when units are later transferred into natural habitats.

In summary, we showed that sexual propagation can be optimized by integrating *ex-situ* settlement in aquaria with *in-situ* growth in artificial cave systems, combining the high settlement efficiency of controlled environments with the higher survival and growth conditions provided by natural habitats.

Indeed, cumulative recruitment success after two years, calculated as settlement success multiplied by first-year and second-year survival, ranged from 0.6% to 2.4% *in-situ* and reached 4.6 ± 1.8% *ex-situ*. When combining these two approaches, using *ex-situ* settlement followed by *in-situ* maintenance, cumulative recruitment success after two years increased to 12 ± 4.7%. This rate is one order of magnitude higher than that achieved with *in-situ* artificial caves alone and approximately three times higher than that obtained with *ex-situ* methods alone. Overall, our findings provide novel insights into early-life-history traits and growth dynamics of *C. rubrum*, laying the essential groundwork for species-specific restoration strategies in Mediterranean corals.

4.1. Implications for Mediterranean coral restoration

This study underscores the potential of controlled cave systems as a valuable tool for integrating sexual coral restoration into ongoing restoration efforts. By providing a semi-controlled environment that allows manipulation of coral density, sex ratio, and inter-individual distances while maintaining natural environmental conditions (*e.g.*, temperature, salinity, current, food), such systems can promote the success of early life stages and accelerate the demographic recovery of depleted populations following the out-planting of sexually produced corals. We argue that relying exclusively on transplantation-based approaches may be insufficient. Although previous work has documented the high survival of transplanted colonies (Montero-Serra et al., 2018), demographic models show that natural recruitment alone cannot restore populations within management-relevant timeframes, with projections exceeding 30–40 years (Zentner et al., 2025). Sexual propagation can help address this limitation by increasing larval supply and juvenile survival.

These insights support the future development of integrated strategies that associate adult transplantation with sexual propagation,

combining the resilience of surviving adult colonies and the potential recruitment boost afforded by sexual propagation. Establishing a standardized rearing protocol for *C. rubrum* represents a major step forward for Mediterranean coral restoration, offering a framework to overcome early bottlenecks while preserving genetic diversity generated by recombination during reproduction. This study provides the first empirical foundation for such protocols, demonstrating that temperate octocorals can be successfully reared from larval release through the juvenile stage. Future research should refine these methods by investigating how adult density and sex ratio in the controlled cave systems influence reproductive output (*e.g.*, *via* Allee effect on fertilization success), how substrate characteristics drive settlement preferences, and how feeding regimes can be optimized both in aquarium conditions (*e.g.* by modulating food concentration and delivery frequency) and in the cave system (*e.g.* through the development of light-based plankton attraction devices). Long-term monitoring of reared colonies will also be essential to assess their survival, growth, and reproductive performance once reintroduced into natural habitats. Moreover, similar experiments on other Mediterranean species will be necessary to apply these hybrid methods across a wide range of habitat-forming octocorals and to effectively support the restoration and recovery of these species at a regional scale.

5. Conclusions

Our study demonstrates that sexual propagation of a Mediterranean is feasible and can overcome the demographic constraints of transplantation-based methods. By investigating early settlement, survival, growth, and spatial dynamics under controlled and natural conditions, we pave the path for species-specific restoration protocols tailored to Mediterranean octocorals. The integration of such knowledge into restoration practice will be essential to meet the ambitious targets of the EU Nature Restoration Law and to ensure that conservation investments result in ecologically and demographically successful outcomes.

CRediT authorship contribution statement

B. Giordano: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Data curation, Conceptualization. **K. Guizien:** Writing – review & editing, Conceptualization. **C. Ferrier-Pages:** Writing – review & editing. **S. Reynaud:** Writing – review & editing, Investigation. **E. Manea:** Writing – review & editing, Investigation. **E. Beraud:** Writing – review & editing, Investigation. **A. Catania:** Writing – review & editing, Methodology. **M.I. Marcus Do Noscimento:** Writing – review & editing, Investigation. **Al. Cau:** Writing – review & editing, Supervision. **G. Loentgen:** Writing – review & editing, Investigation. **R. Cannas:** Writing – review & editing, Supervision. **C. Rottier:** Writing – review & editing, Investigation. **P. Ganot:** Writing – review & editing. **R. Tignat-Perrier:** Writing – review & editing. **S. Tambuttè:** Writing – review & editing. **D. Allemand:** Writing – review & editing, Funding acquisition. **L. Bramanti:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that there are no conflicts of interest. This manuscript is based on original research, has not been published previously, and is not under consideration elsewhere. All authors have approved the manuscript and agree to its submission. All sources of funding have been fully disclosed.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2026.111985.

Data availability

Data will be made available on request.

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